Inderjit
(Editor)

Invasive Plants:
Ecological
and Agricultural
Aspects

Invasive Plants: Ecological and Agricultural Aspects

Edited by Inderjit

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Invasive Species (S. D. County)

When I was young, these hills were grey and sere;
So few attractive bushes flourished here
But now wild mustard, blooming in the spring,
Provides a blaze of golden carpeting.

While in this valley, where was once a gleam
Of water, flowing in a wooden stream,
A vast, extending area is filled
With houses that we, new arrivals, build.

Where chapparal and streamlet once had been,
Invasive species dominate the scene.

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Preface

The study of plant invasions is the science that attempts to understand causes and consequences of plant introductions outside their native areas. Invasive plants have an impact on global biodiversity and ecosystem function, and their management is a complex and formidable task. The applied aspects of this study include the health and economic impacts of invasions. Although research on plant invasions has progressed remarkably during recent decades, scientists are still looking for answers to basic questions.

This book is organized around the premise that general principles of ecology should be employed to understand invasions. Specifically, this volume attempts to answer the following questions: 1) What are invaders? 2) Can we predict invaders? 3) What are the mechanisms of exclusion of native species by invaders? 4) How can general principles in ecology be used to predict and understand plant invasions? 5) What makes a habitat susceptible to invasions? 6) What agricultural practices influence invasions? 7) What impact will invaders have on ecosystem processes and community structure? 8) What are the causes, mechanisms and consequences of plant invasions? 9) What are the environmental and economic costs of invasion? 10) What management strategies are needed to check invasion?

To answer these questions, contributing authors have provided up-to-date reviews and discussions of invasion-related research involving natural and agroecosystems. Chapter 1 discusses efforts by invasion ecologists to settle on a terminology that will enhance, not obstruct, efforts to understand and manage invasive species. Chapter 2 discusses the past achievement, present research and future directions of plant invasions with special reference to ecological and managemental aspects. Chapters 3–7 contribute towards the better understanding of ecological concepts in terms of predicting invaders, significance of residence time and replication in invasion, and the relationship between plant diversity and invasion. Chapter 8 discusses the invasion ecology with a specific example of *Centaurea diffusa*, an invader to the United States. Chapter 9 discusses the regional approach for the management of invasive plants and their management. Allelopathy as a mechanism for resisting plant invasion is discussed in Chapter 10. Chapters 11–14 discuss the agroecology and management of weed invasion. The economic, social and management aspects are discussed in chapters 15–17.

I am grateful to all authors for providing their valuable work to this volume. I appreciate the help and cooperation of Dr. Hans Detlef Klüber and Gabriele Poppen, Editorial Department Biosciences, Birkhäuser Verlag AG. It is my hope that book will serve the scientific community, particularly ecologists, well, and equally hope that the book will stimulate young students to pursue research on plant invasions.

Inderjit   December 2004

Foreword

James A. Drake

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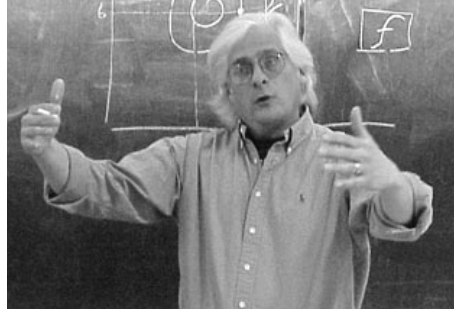
Plant Invasions: Ecological and Agricultural Aspects
Editor: Inderjit

Nature is comprised of both simple and complex systems. Simple systems are those that are reducible to their component parts, parts whose aggregate behavior fully describes the system. However, simple systems can be complicated, containing a dizzying array of parts. Complex systems, on the other hand, may have few or many parts but possess the salient property of irreducibility. The parts of such systems reveal limited information about the operation of the whole. Such is the case with ecological systems. Ecosystems are the result of a convoluted history driven by the physical environment, species interactions, the dynamics and rules directing those interactions, along with a healthy dose of chance. The nature of nature haunts the observer, making experimentation, prediction and policy difficult to implement, but all the more essential in the face of the ever-growing threat posed by biological invasions.

Yet biological invasions are a fundamental aspect of nature and have occurred ever since life first appeared on the Earth. While invasions typically engender thoughts of noxious creatures colonizing in real time, evolution also produces invaders – genes and phenotypes invade, as do the ecological properties, processes, rules and dynamics that accompany them. Invasion is as integral to the face of nature as any other mechanism or process. Ok then, so what is the problem? The problem is the unprecedented and accelerating rate of species invasions caused by the dissolution of natural impediments to dispersal, barriers subverted by human movement and enterprise. Many invasions are apparently innocuous, but others have devastated ecosystems and caused enormous economic damage. Vast landscapes across the Earth now host non-native species rivaling in number their native counterpart. Invasive plants comprise nearly half the flora of New Zealand and Hawaii and entire ecosystems in Northern California have been simply replaced by their alien counterpart. The threat to biodiversity is real.

Plant Invasions: Ecological and Agricultural Aspects is a welcome addition to the rapidly growing and essential invasions literature. Dan Simberloff (2004)[1] has amusingly noted that the number of recent invasion-oriented book volumes has actually eclipsed the number of some invading taxa; a sobering reflection of the ecological, economic and sociological problems posed by biological invasions. The present volume consists of 17 papers written by international cast of invasions biologists. The editor, Inderjit, a plant ecologist at the University of Delhi, has conceived a volume reflecting both ecological and agricultural aspects of plant invasions. This combination of fundamental ecology, theory and application, creates a powerful intellectual feedback loop that can be exploited to further understand the manner in which invasions are changing the Earth's biological operation.

Within the breadth of contributions presented here, several distinct but cogent themes emerge from the author's collective gestalt. A preeminent thread in this volume is the construction of an intellectual framework that integrates academic ecology and theory, with management approaches and societal realities. All too often interactions between academics, managers, and policy makers are adversarial – a function of perspective. To my mind, chapters in this volume suggest that this perceptual discord is readily mended.

Approaches to predicting invasion success across scales of observation, as a function of species characteristics, ecosystem properties, variation in species residence time before establishment, and anthropogenic effects, form a second theme. The authors clearly call for a mechanistic understanding of species invasions that will form the backbone of any operational and conceptual framework. At some scales of observation each invasion is so unique that generality is unlikely. As pointed out by several authors, including scale in invasions biology appears to be a partial solution to this dilemma. However, the case studies of invasions and control efforts presented here provide such profoundly rich detail that one cannot help but ponder devices to keep the details without losing generality and *vice versa*.

A particularly intriguing focus of several papers is that of modifying or engineering habitat vulnerability to invasion. While this cannot be accomplished on very large scales, it is feasible within the confines of agroecosystems, nature reserves, and particularly vulnerable, but local habitats. At the same time we must also observe the physicians credo – do no damage. Nevertheless, exploring community and ecosystem invasibility may provide that mechanistic, and at the same time phenomenological, substance needed to understand invasions.

Together the chapters presented here highlight the complexity of nature and tell us that we are in for a difficult struggle with respect to biological invasions. A struggle complicated by a growing human population, implicate societal needs and economic skews – all in the face of global change.

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[1] Simberloff D (2004) A review of some recent books on biological invasions. *BioScience* 54: 247–253

From the editor

Each chapter included in this book is peer-reviewed by two or more experts in the field. I am indebted to referees for their constructive comments and suggestions, and extend my sincere appreciation for time and effort the following scientists have spent on evaluating each manuscript.

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About the symposium

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Biological invasion is a multidisciplinary field that includes concepts, ecology, conservation biology, sociology and economics to explore the determinants and consequences of the establishment, reproduction and spread of non-native invasive species. Biological invasions constitute a global environmental challenge that attracts the attention of scientists and policy makers across the world. Almost all countries have been actively engaged in evolving strategies that eradicate, prevent, control or contain the alien invasive species. India is invad-

From left to right: Prasanta C. Bhowmik, Hans Lambers, Leslie Weston, Inderjit, John Romeo, Neil Harker and Fakri A. Bazzaz

ed by several alien plant species, and some of them include: *Ageratum cony-zoides, Chromolaena odorata, Eichhornia crassipes, Eupatorium adenopho-rum, Ipomoea carnea, Lantana camara, Mikania micrantha, Mimosa invisa, Parthenium hysterophorus* and *Prosopis juliflora.* The alien invasive species form a major threat to terrestrial (forest and agricultural) and aquatic ecosystems across the Indian subcontinent, and functioning of these ecosystems is distrupted to such an extent that local vegetation types have vanished. For example, water hyacinth wiped out aquatic vegetation in native waterbodies. The invasion of grassland communities by *Parthenium hysterophorus* has virtually eliminated native grass species of fodder value. Invasion of *Prosopis juliflora* has eliminated native *P. cinererea* from Aravallis. The economic losses includes not only in the productivity of these distrubed ecosystems but also in the eradication of these alien invasives and restoration of the ecosystems. In India, for example, annual expenditure in physical removal of water hyacinth alone amounts to several million US dollars.

The Centre for Environmental Management of Degraded Ecosystems (CEMDE) – an interdisciplinary research centre of the University of Delhi that was established in 1991 – is a constituent of the School of Environmental Studies, Faculty of Science, University of Delhi. The CEMDE has been working in areas interfocusing with the environment and ecology with respect to ecosystem functioning and restoration of degraded ecosystems. The centre has also been carrying out research and development programs relating to biological invasions and restoration of biotic communities. An International Symposium on *Ecology of Biological Invasions*, was held at the CEMDE, University of Delhi, in December 2003. The aim of the symposium was to discuss the ecological issues pertaining to biological invasions. Oversea participants included: Fakri A. Bazzaz, Prasanta C. Bhowmik, Neil Harker, Hans Lambers, R. Muniappan, John Romeo and Leslie Weston. Questions raised in the symposium included: 1) Is it possible to predict invasiveness? 2) What are the factors that make the community prone to invasion? 3) What are the functional traits of an invasive species? 4) What factors govern the dominance of invaders in their naturalized range? 5) What long-term changes are expected in the ecosystem as a result of biological invasion? This book includes some papers presented at the symposium and provides an insight on the science of biological invasions. In addition, scientists who could not attend the symposium were invited to contribute their work also to the book, resulting in a complete review of current status of ecological research on biological invasions. The Symposium could not have been possible without the generous financial support from the University of Delhi, Department of Science and Technology, and Council of Scientific and Industrial Research.

December 2004

In search of an operational lexicon for biological invasions

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> 'We cannot improve the language of any science without at the same time improving the science itself; nor can we, on the other hand, improve a science without improving the language or nomenclature'
> Antoine Lavoisier

Introduction

The French scientist and founder of modern chemistry, Antoine Lavoisier, sits among a number of prominent scientists and philosophers, extending from Plato to Kuhn, who recognized the importance of terminology to scientific investigation. Lavoisier is perhaps best known for his work refuting the existence of phlogiston, a colorless, odorless, tasteless, and weightless substance believed to be released during combustion. Not only did Lavoisier recognize the importance of quantifiable entities, he recognized the intimate relationship between language and science and introduced a system of chemical nomenclature used as a basis for the language of modern chemistry.

Today, the importance of clear definitions is recognized by philosophers of science, but seems to be poorly appreciated by many scientific investigators. The English ecology literature seems particularly prone to phlogiston-like concepts, perhaps owing to the preference of ecologists for common English terms to describe ecological entities and processes [1, 2]. Ambiguous or contrasting definitions for terms like 'ecosystem', 'niche', 'community', 'diversity', and 'stability', often reflect an underlying disagreement or misunderstanding surrounding the concepts for which such terms were introduced to describe (see [1–3]). This is particularly true for the terminology of biological invasions, as poignantly demonstrated by recent debate over criteria for the term 'invasive' and its derivatives [4–9].

In this chapter, I focus on the importance of a concise, operational terminology for the study of biological invasions. I begin with a review of the current state of invasion terminology, with particular focus on two contrasting views of 'invasive' species. I then describe a model for invasion terminology that is intended to bridge these views towards a standardized lexicon for inva-

sion ecology. The model attempts to define species based on observable ecological processes; therefore I compare this alternative model to current thinking in invasion ecology and end with a discussion on how it might help to improve invasion theory and current management practices, and particularly how it can aid to integrate the two.

Invasion terminology: Current confusion

The importance of clarity and consensus of scientific definitions for key terms like 'invasive', 'invasion success', 'naturalized', and 'nonindigenous' is more than semantic, though many fail to appreciate this fact. Clear definitions with universally accepted, operational criteria are crucial for the development of scientific theories, the formation of hypotheses and the design of experiments capable of rejecting them. For example, the frequently used 'invasion success' may be defined as the successful establishment of self-reproducing populations, the successful spread of an invader from a relatively isolated area to a large geographic range, the increase in abundance or dominance of habitats by an invader in its novel range, or a combination of these. The common term 'invasion success' has been applied to all three cases, yet the processes underlying them may be quite different. In the case of establishment, propagule pressure (i.e., the number of individuals introduced), combined with biotic and abiotic conditions affecting survival and population growth rate are important (see Chapter 2). Local spread may be more due to transport vectors and passive dispersal, whereas the abundance or dominance of an invader likely depends more upon biotic and abiotic factors [10, 11] (see also Chapter 2). The term 'invasion success' should therefore be a general term that applies to success at all three stages – establishment, spread and proliferation – and authors should be more explicit in the particular type of success that a given process is likely to confer (note that use of the term 'proliferation' in this essay refers to an increase in abundance and may or may not include spread).

Concise definitions are crucial to the development of invasion ecology as a scientific discipline, yet disagreement still exists over some of the most fundamental terms in the discipline. Problems with the most widely employed terms like 'invasive', 'naturalized' and 'nonindigenous' have been expressed often. Almost a decade ago, Pyšek [12] found that studies of biological invasions frequently used the term 'invasive' (and its derivatives, including 'invasion' and 'invader') without explicitly defining the criteria used to define the term, noting at least 13 different uses. Pyšek suggested that the term 'invasive' should apply to '…an alien whose distribution and/or abundance in the area is increasing'. Five years later, Richardson et al. [6] noted that the problem had persisted, and identified a similar problem with the term 'naturalized' and its derivatives, which was defined as: 1) 23% of cases – self-perpetuating nonindigenous populations, 2) 8% of cases – persisting only in habitats largely undisturbed by humans, 3) 25% of cases – as nonindigenous species (NIS),

and iv) 29% of cases – as invasive species. More recently, Pyšek et al. [13] argued that the use of terminology in the development of species lists may be crucial to developing theories relevant to invasion ecology, and Colautti and MacIsaac [14] noted at least 32 overlapping terms used to describe various aspects of species invasions.

Contrasting definitions for key terms have been perpetuated in the primary research literature for years, prompting Davis and Thompson [4] to introduce a novel framework for the definition of biological invaders. The Davis and Thompson (DT) model is based on the concept of Rabinowitz's [15] classification of species rarity and thereby categorizes colonizing species based on three criteria: dispersal distance, novelty to the region, and impact. Of the resultant eight categories, the DT model allows two classifications of 'invasive species' that differ only in their dispersal distances (short, or long-distance dispersers); the two key criteria for invasive species are novelty to the region and large impact. Therefore, the DT model identifies 'invaders' as both 1) native species that colonize naturally and 2) species introduced by human activity to areas where they have no evolutionary history. A contrasting model, by Richardson et al. [6], classifies invaders by their ability to overcome several ecological barriers such as reproduction, local dispersal, and environmental barriers in human-disturbed or more natural vegetation. Subsequently, the DT model was heavily criticized for its dependence on impact, which is often a highly subjective measurement [7, 9]. Moreover, there is a large intellectual rift over the inclusion of impact in the definition of an 'invasive' species between ecologists on one side, and resource managers and politicians on the other. This creates confusion for newcomers to the discipline, and impedes the rapid and unambiguous dissemination of knowledge from ecological experiments to the formation of strategies designed to protect natural habitats from problematic invaders.

Outline for a universal terminology

Despite the intensity of disagreement over the term 'invasive', careful examination of the dichotomy between the Richardson and DT models suggests a number of criteria that I believe may be crucial for achieving a consensus on invasion terminology [14]. First, definitions of invaders should reflect underlying ecological processes already identified in the literature on biological invasions, whereby species are introduced by humans, to areas outside of their historic range, where they may establish self-sustaining populations, spread to other nearby locales, and/or increase in abundance (e.g., [6, 16]). The issue of impact raised by the DT model is important, but much more complicated and controversial, as impact definitions often involve subjective criteria that are ultimately a matter of perception [6, 7, 9, 14]. For example, several fish species have been introduced globally for game, aesthetics, and biological control, often to the detriment of native species [17]. Concern over the ecological effects of introduced fishes today likely reflects a shift in societal concern for

resource conservation more than a shift in ecological impacts. Moreover, 'impact', if defined as the effect of an invader on its recipient community, is proportional to the spread and abundance of invaders [18].

Second, terminology should allow for clear, operational definitions that are universally accepted and consistently applied [1, 2]. The specific criteria will likely vary between systems of analysis (e.g., invasions by pine trees compared to aquatic invertebrates), and will therefore require specific knowledge of the ecosystem, habitat or taxonomy of analysis. Whatever the criteria, they should be consistent across similar taxa or communities and should be reasonably analogous across systems (e.g., as a series of stages). Third, it may be difficult or impossible to redefine terms, like 'invasive', that are both widely and disparately defined. Instead, the introduction of categories with no *a priori* definitions should allow for a *tabula rasa* upon which concise, universally accepted criteria might be defined and refined [14].

Finally, there should be some way of comparing biological invaders moved over long distances with native species that colonize locally (i.e., 'native colonizers' *sensu* [4]). A recent shift in the focus on invasive species to invasive populations of species reflects a growing understanding that human-mediated invasions are inherently different from native colonizers in at least two important ways [6, 14] (see Chapter 2). First, NIS are generally moved over large isolating barriers thereby bringing together species with separate evolutionary histories. In contrast, native colonizers are likely to have interacted with species in the recipient community at some time in the recent past, at least on an evolutionary timescale. Acknowledging these differences may lead to important insights into the interplay between evolution and ecology, for example when looking for evolutionary changes in species of the invaded community. Second, the introduction of NIS reflects an intimate interaction between NIS and humans, with important ecological and evolutionary consequences. For example, movement of individuals from geographically isolated populations can increase genetic diversity in the introduced range [19]. Alternatively, bottlenecks during the invasion process may reduce the number of enemies introduced with their host [10]. Chapter 1 also describes a number of hypotheses that recognize an inherent difference between NIS and native colonizers.

Despite these differences, there are numerous criteria by which nonindigenous species are no different from native species, and greater effort should be taken to integrate invasion ecology with other sub-disciplines [20]. This is because, as the DT model posits, processes affecting the establishment, spread, and abundance of invaders may not always be inherently different from those affecting native colonizers [5]. Thus I argue that it is important to keep invaders conceptually separate from native colonizers, but to allow for comparison or even equal treatment at some levels of analysis, such as when investigating factors that affect the susceptibility of communities to invasion or factors that cause species outbreaks.

Colautti and MacIsaac [14] proposed a neutral, stage-based terminology, based on previous models of the invasion process (e.g., [6, 16]). This stage-

based framework begins with individuals in a source region (stage 0), a sub-sample of which are taken into a transport vector (stage I), for example as contaminants in ballast tanks or seedstock (Fig. 1). Of these, many may not survive the transit and only some will be introduced to a novel region where they
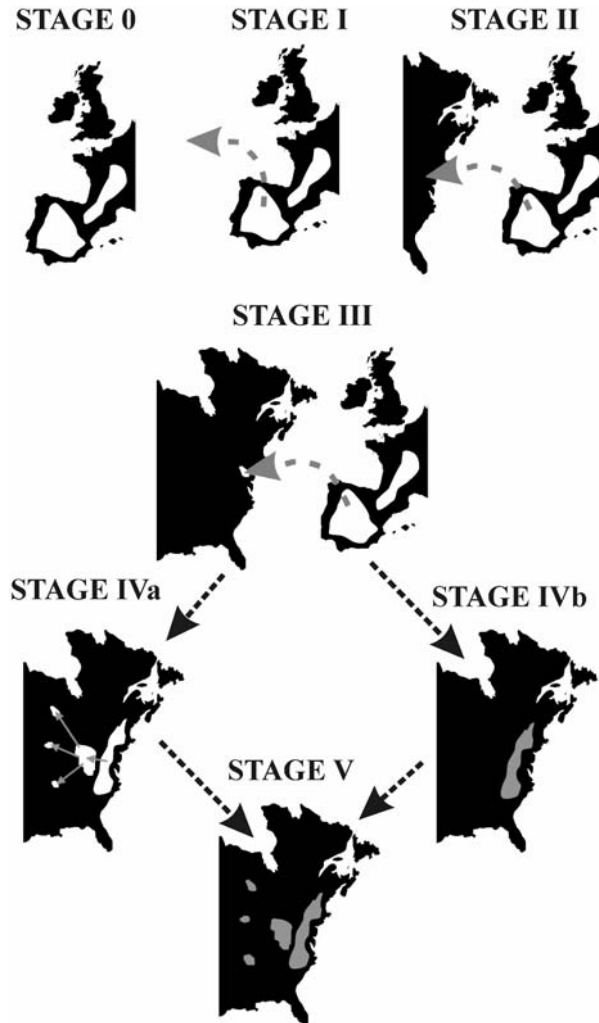
Figure 1. Schematic of definitions derived from a stage-based terminology. White patches indicate populations of low density, gray represents high density. Stage 0 – species or population(s) resident in a source region; stage I – species/populations found in a transport vector; stage II – species/populations identified as introduced to a novel region, but not establishing self-reproducing populations; stage III – formation of a self-sustaining population; stage IVa – several independently established populations, owing to either multiple introductions (i.e., long-distance introduction) or subsequent, local spread, but remaining low in density; stage IVb – a small number of populations, but with a high density of individuals; stage V – multiple populations that are generally high in density.

may survive only transiently or persist with human aid (stage II), or they may establish self-sustaining populations (stage III). After establishment, many species will persist at low abundance in a relatively restricted area, but some will drastically increase their range (stage IVa), become dominant in the communities they invade (stage IVb), or both (stage V). Rather than attempting to redefine contentious terms like 'invasive' and 'naturalized', the Colautti and MacIsaac (CM) model acts as a supplementary lexicon, whereby the definitions particular to ecologists or resource managers can be supplemented through identification of the stage of interest.

The CM model defines invaders by a set of categories with no *a priori* definitions, like the DT model, but is conceptually more similar to the widely cited models of invasion as a process of transitory stages (e.g., [6, 16]). The CM model also allows comparison of native and nonindigenous colonizers, as they noted "…this shift of focus to invasion stages renders moot the issue of whether the taxa involved are native regionally or originate from other biogeographical areas. Using this framework, even resident native species and established (stage III) NIS might be modeled by the same or similar factors affecting later stages within a given system" [14]. Finally, the CM model alludes to the potential for the development of operational definitions under this framework. Below I explore in more detail some problems with the CM model, as well as some potential solutions, using some specific examples. I then demonstrate how the CM model might help to unify concepts in the management and ecology of biological invasions, with a focus on the utility of the model as a framework for the development of both ecological theories and management strategies.

Problems with the CM model

Careful consideration of the criteria used to define invasion stages quickly reveals a few key difficulties with the CM model (Fig. 1). First, the difference between stage III (establishment), and stage IVa (spread) is not self-evident. Clearly any criteria for these stages will be scale-dependent, such as inter- *versus* intra-continental transfers. One possible solution is to choose the scale of analysis based on the primary transport vector(s) involved. The term 'vector' *sensu* [21] describes the physical mechanism by which a species is moved to a new region. Using as an example aquatic plant invasions in the Great Lakes via ship ballast, it is largely irrelevant whether source populations are from the Black Sea in Europe, or the Atlantic coast of North America (stages 0–III). Conversely, recreational boaters and passive dispersal act as vectors of subsequent spread of many nonindigenous plants to inland lakes (stage III–IVa). In this example, the establishment of nonindigenous plants via ballast represents localized (stage III or IVb) populations, whereas the subsequent establishment of populations throughout the basin and in inland lakes produces spreading (stage IVa or V) populations. Note that the difference between III and IVb or

between IVa and V is simply the abundance or dominance of the invader in these habitats. Sometimes the same vector may be responsible for both the introduction and spread. For example, many nonindigenous plants in North America were both introduced from overseas and spread throughout the continent as contaminants of hay and other vegetative material, while other species have multiple vectors including escapes from horticulture or deliberate introduction [22]. It is useful to know whether individual propagules were introduced from overseas or from other established populations, however it is often difficult or impossible to obtain this information (but see [23, 24]). Nevertheless, it is largely the issue of scale that separates establishment from spread, thus where specific sources are not known, spatial scale (i.e., transfer between *versus* within a continent or country) may be an important criterion.

The second problem is that the spread (stage III to IVa and IVb to V) and proliferation (stage III to IVb and IVa to V) transitions are time-dependent and represent gradients rather than distinct stages. A gradient of conditions means that any categorization will necessarily be incomplete, but the key is to use categories that capture the essential components of underlying ecological processes. I suggest that stage IVa refer to both species that are widespread as well as species that are spreading and are likely to become widespread. This is because spread is time-dependent, and because similar ecological processes are likely to be responsible for both cases. However, the precise criteria for transition to stage IVa (spread) will necessarily be system specific. For example, Richardson et al. [6] suggest a criterion of >100 m in <50 years for tree species, but effective criteria will clearly vary with the types of species, ecosystems, and transport vectors involved. A similar problem involves criteria for stage IVb (abundant/dominant), but one solution might lie in comparing the abundance of an invader with similar species already present in the recipient community. One potential approach to operationalize this stage would be to graph the ranked, cumulative abundance of all similar taxa in the community, and choose a threshold, perhaps based on the top 10% of abundant species, or some other percentile based on impacts identified for other species included in the graph. Like 'spread', criteria for 'abundant' will necessarily be system-specific. Note that since many of the stages are time-dependent, the status of a given population may also change through time. However, this is not necessarily bad because understanding the factors responsible for these transitions (both forward and backward) may provide valuable ecological insights [14].

A third problem with the CM model is that additional criteria or stages may be important for some systems but not for others. For example, several models of plant invasion differentiate between the invasion of disturbed and natural areas, while some models of aquatic invaders treat the entire waterbody as a single habitat (e.g., [6, 11]). However, the CM model can address this need for habitat flexibility, if stages are partitioned among habitats – for example, a particular species may be described as forming dominant (stage IVb or V) populations along roadside, but interspersed (stage III or IVa) populations in old-

field habitats, and rarely forming stage III (self-sustaining) populations in forest understory.

One final problem is that there are no obvious criteria to categorize a species' status as nonindigenous. However, interest in invasion ecology is driven primarily by the effect of species that are introduced by human activity to areas where the species has no historical evolutionary history. Thus, status as nonindigenous should be reserved for species introduced by humans, usually over a significant isolating barrier, to an area where the species has no recent evolutionary history with species native to the recipient community. NIS may be further subdivided based on criteria such as geographical distance, purpose of introduction, or time since establishment (e.g., [25]). It seems important to reiterate that while criteria for nonindigenous status may be crucial to the early stages of the model (0–III), processes acting at later stages (III–V) may be similar for both native and NIS.

Application of the CM model

According to the CM model, there are three key categories of 'determinants' affecting successful transition between each stage: propagule pressure, physicochemical requirements of the invader, and competitive or facilitative interactions between the invader and species already in the invaded community (Tab. 1). Here I describe how consideration of these determinants within a stage-based model can help both 1) to develop ecological theory, and 2) to formulate effective management strategies.

Invasion theory – investigating invasion patterns

Current investigations of important processes in invasion ecology generally fall into one of three types of comparisons (see also Chapter 2). First, *inva-*

Table 1. Summary of determinants promoting (+) or impeding (–) successful transition of particular stages of the invasion process (see text and Fig. 1 caption for description of particular stages)

Determinant	Description	Stage transition	Effect
A. Propagule pressure	The number of individuals moving through each transition	0–I, I–II, II–III, III–IVa, IVb–V	+
B. Physicochemical conditions	Interactions between environmental conditions and physiological requirements of invading propagules	I–II, II–III, III–IVb, IVa–V	+ or –
C. Community interactions	Effect of biotic interactions between invading propagules and species already present	II–III, III–IVb, IVa–V	+ or –

siveness studies usually take a taxonomic-based approach and attempt to identify characteristics of species that are particularly 'good' invaders. This strategy is based on the observation that invaders at stages III to V appear to be non-random subsamples of all potential invaders, suggesting something inherently 'invasive' about these species. Second, *invasibility* studies seek to identify characteristics of communities or habitats that render them susceptible or resistant to invasion. Finally, *biogeographical* studies take a population-based approach, whereby differences between native and introduced populations of the same species are investigated. The CM model was developed with these comparisons in mind, as subsampling between stages is crucial to the analysis of both invasiveness and biogeographical studies, while determinants help to identify invasibility characteristics. Thus the model integrates an invader-by-ecosystem approach that may be crucial for making meaningful predictions, and for the development of a cohesive theory of invasion ecology [26–28].

Simply taking a stage-based approach to biological invasions raises an important issue for invasiveness and biogeographical studies – the choice of contrast group. Most taxonomic analyses compare established NIS (at stages III–V) with either 1) a global list of similar species (e.g., from the same genus or family), 2) native species in the invaded community, 3) native species from the same source region as the invader, or iv) introduced species that fail to establish. However, the choice of contrast group may be crucial to the results that are obtained [28, 29]. A simple analysis of the stage-based model reveals why this is so: the choice of contrast group determines the number of stages of separation, and therefore the types of determinants, between contrast groups. In other words, factors affecting successful transition between early stages can confound interpretations of patterns evident at later stages. For example, one might find that stage V (widespread and abundant/dominant) plants in a given ecosystem have a larger flower size than native species in the same community. Despite the temptation to attribute this difference to the invaders' success (via pollinator competition), the focus on stage-based criteria cautions against such an inference because this difference may arise simply by the 'filtering' process that occurs between each stage. In this example, NIS may have larger flowers simply because they were preferentially imported by humans. Indeed, Cassey et al. [29] found that the characteristics of established parrots varied with the contrast group used. Of course, it is possible to test hypotheses based on these characteristics; the CM model simply raises concern over the acceptance of ecological or evolutionary inferences based on species-specific characteristics alone. It would, in fact, be quite easy to test whether the invaders in the example above really did attract more pollinators and whether pollination limitation was an important factor in the establishment or dominance of the invaders. So far, however, such additional studies are rarely carried out.

Conceptually, biogeographical studies are like taxonomic studies in that established (stage III) populations are compared with populations from the native range (stage 0). As with taxonomic studies, established *populations*

(stage III) are also a subset of native populations (stage 0), thus problems may arise in biogeographical analyses as well. One high-profile example involves the currently popular enemy release hypothesis (ERH *sensu* [30]). The ERH posits that invaders successfully proliferate because they are released from the effects of enemies that are lost during the invasion process (see Chapter 2). Evidence for the generality of the ERH is largely dependent upon an observed reduction in the richness of enemies (i.e., number of interacting species) between native (stage 0) and introduced (stages III–V) populations [31, 32]. However, individuals subsampled during transportation (stage I) may include populations from only a small part of the native range. Thus, identification of the proper source (stage 0) population(s) is critical for biologically meaningful results. In the case of enemy release, comparison of populations from the entire native range may artificially inflate measurements of enemy release [33]. This occurs because entire native ranges have been used to estimate enemy release, yet many of these enemies have limited geographic ranges and may have never been transported. Indeed, this seems to be the case for the European starling in North America; after controlling for subsampling of native populations, the starling shows no support for a reduction in enemy richness, despite previous accounts [34]. Referral to the CM model also suggests another avenue of potentially fruitful analysis that, to the best of my knowledge, has yet to be explored – biogeographical studies of stages beyond establishment (i.e., stages IVa, IVb and V). In other words, few, if any studies have compared different introduced populations (of the same species) that vary in their density or abundance. One simple experiment might be to test for a correlation between damage by enemies and the proportional abundance of an introduced species across different populations within its introduced range, rather than focusing on native *versus* introduced populations.

Just as a careful analysis of the stages and their transitions will improve our understanding of patterns evident from taxonomic and biogeographical studies, so will an analysis of determinants improve our understanding of invasibility (Tab. 1). Three broad categories of determinants are identified in the CM model – propagule pressure, biotic or community interactions, and abiotic or environmental conditions. Many invasibility studies have investigated these processes, with particular emphasis on abiotic or environmental conditions, which may themselves result from biotic interactions (see Chapter 2 for some specific references). However, to the best of my knowledge, few predictive efforts have been made to integrate these three classes of determinants for any system, nor has there been any directed attempt to integrate determinants with subsampling processes to develop a comprehensive, quantitative model of invasion for a particular study system. Many of these factors are likely to be system-specific; factors affecting pine tree invasion success are likely quite different than those affecting aquatic benthic invertebrates, for example. However, an integrative approach will be, I suspect, crucial to developing a predictive understanding of the ecological processes underlying biological invasions and a general theory of invasion ecology.

Management efforts – predicting and preventing invasions

Besides the utility of a stage-based approach to the development of ecological theory, as explored above, such an approach also has important implications for the development of policy for the management of invasive species. The most obvious implication is the differentiation between prevention, containment, and control. While these differences may be self-evident without any model of invasion, a focus on invasion stages may improve our understanding of the circumstances under which each approach is likely to be successful.

Prevention focuses solely on the early stages of the invasion process (stages I–III and perhaps IVa), thus an obvious strategy is simply to prevent the introduction of propagules (e.g., [21]). However, it is practically impossible to completely eliminate the number of introduced propagules, for both logistical and economic reasons, perhaps leading some resource managers to question the importance of a vector-management strategy. Nevertheless, an increasing body of literature suggests that successful establishment (stage III) of some species is at least partially contingent upon propagule pressure (e.g., [35, 36]). In other words, NIS that successfully establish tend to be introduced more often and in greater numbers, suggesting that a reduction in propagule pressure to non-zero levels may go a long way towards reducing the rate of invasion. Much work is needed to further explore this determinant for other taxa and other ecosystems, but these results suggest that a focus on reduction of propagules can be an important management strategy. A much less explored strategy for prevention is the management of susceptible habitats. Since both biotic and abiotic determinants may impede the establishment of invaders, consideration of community-level interactions may be an important supplementary strategy to prevent biological invasions. For example, several studies have implicated disturbance, nutrient availability, and a reduction in resident species abundance as factors increasing a community's susceptibility [37, 38] (see also Chapter 2). These factors are by no means universal, and much research is needed to increase understanding of the conditions under which such factors become important *in situ*. Nevertheless, the vast majority of invaders are found in human-altered habitats suggesting an important role for the maintenance of particular communities' properties rather than species diversity *per se*.

Where prevention efforts fail, containment is the next line of defense. As evident from Table 1, reducing propagule pressure (or supply) will be crucial to preventing the spread of species, just as it was for preventing establishment. However, the vectors of spread of an NIS may be quite different than the vectors of introduction, and this has important implications for the efficacy of containment *versus* prevention. For example, many invaders in the Great Lakes have been introduced as contaminants in ballast of transoceanic ships, and have subsequently spread by recreational boating activity. All transoceanic ships entering the Great Lakes must pass through a set of locks, enabling easy access for inspectors. By contrast, it is comparatively impossible to regulate the movement of recreational boats between waterbodies within a country. In

this case it will be far more efficient to focus management efforts on transoceanic ships to prevent the establishment of NIS than to attempt to prevent the spread of a species once it has established in the Great Lakes.

While propagule pressure is important to prevent the establishment and spread of an introduced species, biotic and abiotic factors will be crucial in determining whether an established population persists and/or increases in abundance. Therefore, strategies for the containment or extermination of invaders will necessarily focus on determinants other than propagule pressure. For example, the practice known as 'classical biological control', popular among plant invasions, advocates introducing natural enemies for the control of abundant or dominant species (stage IVb and V) (e.g., [39]). However, this strategy can lead to the formation of stage V (widespread/abundant) populations of the biocontrol agent itself, sometimes with detrimental effects to the native community [40]. Other potentially valuable strategies include the use of native or nonindigenous enemies already present in the introduced range, rather than risk further introductions, or the rehabilitation of communities or habitats to reduce the abundance of invaders [41, 42].

Apart from guiding management strategies, the use of operational categories has important implications for the development of policy and legislation. In the United States, for example, Bill Clinton's Executive Order on Invasive Species (Order 13112, 3 February 1999) attempts to prevent the introduction of 'invasive' species, which it defines as plants and animals that 'cause vast ecological and economic damage, and sometimes human health impacts'. Here the definition of 'invasive' species is independent of the CM model, which does not include impact as a criterion for any of the stages. Nevertheless, the operationalization of the term 'invasive' in this context would go a long way towards improving public policy. For example, what is 'vast ecological and economic damage'? How can ecological damage be measured? Moreover, the intellectual divide over the inclusion of impact in the definition of 'invasive' suggests to me that the only way to arrive at a common dialogue between ecologists and managers will be to drop the term altogether in favor of the more neutral scheme proposed in the CM model.

Uniting theory and management

In addition to the specific benefits that a stage-based approach holds for the development of ecological theory and management strategies, the CM model may help to integrate the two disciplines. The use of a stage-based terminology allows for a common language between ecologists, resource managers and policy makers. This may help reduce disagreement about invasion concepts, as noted earlier for the term 'invasive'. A focus on the invasion process will also allow for better integration of ecological theory with management concerns at a more fundamental level. Ecologists can improve our understanding of the precise determinants affecting transition between the different stages. This has

obvious implications for the prevention, containment and control of non-indigenous populations. In return, careful monitoring of populations at different stages through time will in turn provide invaluable data that will improve the underlying ecological theories. For example, despite the widespread practice of biological control, there are surprisingly few studies of the dynamics of populations managed in this way. Temporal monitoring of populations managed by biocontrol agents as well as of control populations (i.e., those where no biocontrol agents are introduced) is a potential goldmine of data that, to the best of my knowledge, remains virtually untapped.

Conclusion

I have presented here an optimistic view of the CM model and its potential as a unifying framework for both ecological theory and management practices. However, this model is only in an early stage of development, and there is still much work to be done. In particular, it is, I think, largely impossible to come up with a general scheme for the operationalization of invasion terminology. Instead, research is needed to develop specific criteria to apply the CM model to particular systems of study. It is likely that a number of unforeseen difficulties will become apparent during this process. Such problems can only be addressed as they arise, but I am confident that the CM model, as elaborated here, is an important first step in the elimination of ecological phlogiston and the operationalization of invasion concepts. I strongly believe that the use of a stage-based model as an integrative framework will help to unite the rift between invasion ecology and resource management to the benefit of both disciplines.

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Section 1: Ecological aspects

The ecology of biological invasions: past, present and future

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Introduction

The science of invasion ecology has reached a point where we can take stock of its successes and failures, and perhaps formalize the vast quantity of related ideas into a more coherent, conceptual summary. Two recently edited volumes: *Conceptual ecology and invasion biology: reciprocal approaches to nature* [1] and *Species invasions: insights into ecology, evolution and biogeography* [2], are testament to the maturing state of invasion biology. As a developing science, we wish to demonstrate the interplay between theory and observation in the development of modern invasion hypotheses and to assess their potential explanatory power. Well known is the conservation and environmental risk that some nonindigenous species (NIS) pose [3, 4], but what is not always appreciated is that the road from conservation concern to explanatory science is not always easily traversed [5]. This article aims to review the ways in which invasions are currently understood. We begin with a brief overview of invasion ecology as a discipline followed by a broad review of ecological and evolutionary mechanisms that are likely driving observable patterns of invasions.

History of invasion ecology

People have been interested in NIS for as long as human culture has itself 'invaded' new regions. Early human immigrants not only brought language and culture with them, but also plants and animals familiar and useful to these cultures. The earliest European immigrants to North America systematically introduced a wide assortment of agricultural and ornamental species from their homelands. However, at some point this interest in NIS transformed from

purely practical and sentimental utility to a realization of the environmental concerns and scientific interests associated with some NIS [5–8].

Concern over the potential impacts of certain NIS began in the late 18th century. John Bartram, an 18th century botanist, noticed that some introduced plants negatively affected the environment and some were extremely difficult to control [7]. In 1793, the devastating yellow fever outbreak in Philadelphia was blamed on shipments from the West Indies [9], further increasing public awareness of the potential harmful impacts of NIS.

By the mid-to-late 19th century, a number of NIS-focused writings appeared in the literature. Hooker [10] revealed that European plants were rapidly replacing natives in New Zealand. During this period a uniquely American pragmatic approach recognized the economic and agricultural threats from NIS [11–13]. In 1897, Leland Howard, in his address to the American Association for the Advancement of Science, said: "Potentially cosmopolitan forms … have by [human] agency become dispersed over nearly all of the civilized parts of the globe, while thousands of other species have been carried thousands of miles from their native homes, and have established themselves and flourished, often with a new vigor, in a new soil and with a novel environment" [14, p. 4]. Howard and his friend and colleague, Stephen Forbes, published many articles on nonindigenous insects and their agricultural impacts [8].

The environmental concern that developed from the late 18th to late 19th centuries was bound to ignite the interests of pure scientists and natural historians alike. The vigilant Charles Darwin did not let NIS pass his gaze unnoticed. In many instances in the *Origin of the Species* [15], Darwin uses NIS to uncover or support aspects of his theory of natural selection [8]. For example, to highlight the fact that natural selection does not produce absolutely fit species, only species fit relative to those with which it has a history of struggle, he noted the "introduced plants… have become common throughout whole islands in a period of less than ten years" [15, p. 118]. He goes on to say that "The endemic productions of New Zealand, are perfect one compared with another; but they are now rapidly yielding before the advancing legions of plants and animals introduced from Europe" [15, p. 229].

Similarly, many of the most influential early ecology and biogeography texts [16–19] use NIS as examples of their theories, or at a minimum recognized that they needed to be generally explained by their theories, as NIS are real-world observations [8]. Yet these texts did not develop hypotheses or theories to explain how and why NIS can sometimes invade intact communities. Therefore invasion ecology, as an independent school of thought had yet to appear.

It was not until the period from 1936–1958 that a distinct 'proto-invasion ecology' began to emerge, where authors explicitly tried to understand strategies of successful NIS. H.H. Allen [20] gave academic attention to the problem of NIS in New Zealand. Whereas earlier authors like Hooker [10] and Tansley [21] thought that invaders as a group change a plant community with uniform success, Allen [20] showed that the NIS were not a horde of compet-

itive invaders. In fact relatively few NIS (48 of 603 species) became problem species in New Zealand, and these few problem species represented a diverse array of ecologies. Like Allen, Egler [22] thought NIS invaders were not a uniform group changing the ecology of Hawaii. Rather he saw NIS as a diverse group, which made predicting the future of community types nearly impossible. They both thought that after grazing and disturbances were removed, native communities would be much better suited to competing against NIS.

Stewart and Hall [23] clarified the biology of the invasive grass *Bromus tectorum* and how it was affecting the native communities of southern Idaho, USA. Baker [24] used the invasions of *Melandrium album* and *M. dioicum* in Great Britain to study the dynamics of invasion, range expansion and large-scale competition. Finally, the control of problematic NIS was gaining momentum because of famous early instances of successful biological control. These examples would include not only the control of *Opuntia* cacti by *Cactoblastis cactorum* in Australia by 1926 [25] but also the control of *Hypericum perforatum* by *Chrysomela* beetles in western United States [26, 27].

By the 1950s, researchers were explicitly studying NIS to understand the invasion process. Theoreticians around this time were also using their tools to understand invasion dynamics better. Skellam [28] used spatial spread models describing the diffusion of particles to examine the spread of a reproducing population over a two-dimensional landscape. He illustrated this idea using the 1905 introduction and spread of muskrat, *Ondatra zibethica*, in central Europe [28]. D'Ancona [29] showed how Lotka-Volterra equations could be used to understand the dynamics of species invasions.

The science of invasion ecology "as much as one can ever pinpoint the beginning of a field to a single event" was "the publication of Charles Elton's book" [30, p. 806]. Elton [31] fit together disparate ideas and facts and came up with explanatory theories and predictions about how invaders spread and communities are invaded. The single most influential prediction from his book, and one that is still actively researched, was that more diverse communities ought to resist invaders better (see *Biotic resistance hypothesis*, below).

In the decades since Elton [31], several important published works have expanded our understanding of invaders and the invasion process [5]. In 1965, *The genetics of colonizing species* [32] compiled writings from many of the world's leading ecologists and evolutionary biologists. This volume explicitly examined what happens to individual species during and after the invasion process. The most notable ideas from this volume include the notion that traits of invaders can be used to predict impact and the realization that genetics and evolution of invaders could help explain aspects of invasion ecology.

The 1970s and 1980s saw the rise of conservation concern in academic research [5], and out of this concern grew organizations like SCOPE (Scientific Committee on Problems of the Environment). Two important volumes on invasion ecology were published by SCOPE during the 1980s: *Ecology of biological invasions of North America and Hawaii* [33] and *Biological invasions: a global perspective* [34]. The authors contributing to

these volumes explored issues from genetics to species attributes, community assembly to biotic resistance, and disturbance to community attributes encouraging invasions. These two volumes mark the time when invasion ecology became a legitimate academic discipline, metamorphosing from a research interest of a few dedicated practitioners to one of the most frequent interests of ecologists. The editors of these two volumes had the explicit goal of finding a framework that would have allowed ecologists to predict which species become invaders and which communities are likely to be invaded. However, the editors noted in their conclusions that prediction was still some time off. With his aptly-titled book '*Biological invasions*', Williamson [35] contributed the oft-cited 'tens rule', which focused on invasions as a series of stages (transport, introduction, establishment, spread), and his insight into the importance of 'propagule pressure' – the number of individuals or propagules introduced to an area.

This brief history of thinking on NIS reveals that there have been two different interests by ecologists [5]. First, ecologists have tried to understand and explore the processes and dynamics of invasions. In this case the primary interest is the NIS themselves. The second interest is in using NIS as natural experiments to test general ecological theories and concepts. In this case the primary interest is theory. What follows is an expansion on these classic ideas of invasion biology, incorporating an array of current theories and approaches, all of which may lead to a deeper understanding of invasions and toward the ultimate goal of predicting and preventing invasions by harmful NIS. However, the concepts and theories explaining the success of NIS also potentially inform general theories and concepts in ecology [1, 2].

Current ideas

To conceptualize current ideas in invasion ecology better, several authors have proposed a stage-based approach ([35–39]; see also Chapter 2). This framework breaks biological invasions into a series of consecutive stages, beginning with transport and introduction, through the establishment of self-reproducing populations, and ending with spread and abundance (Fig. 1). As first proposed by Carlton [36], each stage entails a sub-sampling of individuals, such that widespread, abundant species are the least likely end-point – many invaders are introduced, but few establish, and even fewer become widespread or abundant. Consistent with this framework, we use the term 'invasion success' in a general sense, to describe success at any stage of the invasion process. We use 'establishment success', 'successful spread', or 'successful proliferation' to refer to success at specific stages.

Much of the modern invasion ecology literature (since c. 1990) has focused on identifying characteristics of successful invaders and habitats more susceptible to invasion; these have been called 'invasiveness' and 'invasibility' characteristics, respectively. Studies of invasiveness characteristics have taken a
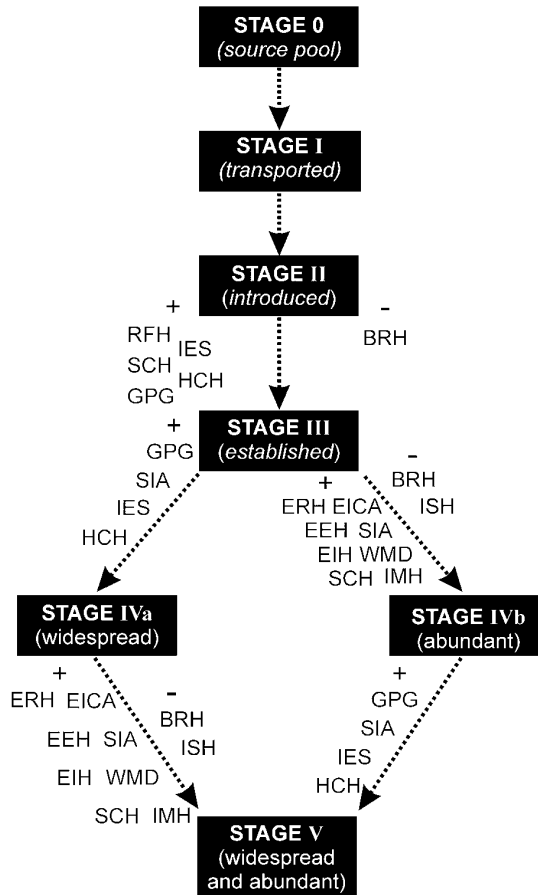
Figure 1. Schematic representation of the invasion process. Under this model, biological invasions are characterized by a series of consecutive stages through which a particular species or individual may pass through. Transition between particular stages may be promoted (+) or inhibited (–) by the hypotheses identified at each transition (acronyms). See Table 1 for hypothesis definitions. Note that the neutral community dynamics (NCD) hypothesis is absent from the figure because under NCD models, species that transit each stage are random selections of the previous stages.

taxonomic approach, that is, they compare characteristics of established invaders with either (1) introduced species that fail to establish persistent, self-perpetuating populations, (2) species from the same source region (usually congeners or confamiliars), (3) species from the global pool, (4) species native to the invaded community [40], or (5) established invaders at other stages of the invasion process (e.g., NIS with widespread *versus* restricted ranges). These taxonomic comparisons constitute a disparate array of studies. On the one hand, some studies compare the distribution of correlated traits across individual species [41], and on the other, some use phylogenetic information

to analyze species patterns [42]. An alternative approach has been to compare native and introduced populations of the same species – a biogeographical approach. Conversely, invasibility studies have taken a community-level, or biotic approach, by examining the species composition (e.g., the number of parasites or predators) of invaded habitats, or an environment-based approach, by examining abiotic characteristics (e.g., physicochemical characteristics) associated with invasibility. Sub-sampling at each stage may therefore occur at either the taxonomic or biogeographical level, and filtering mechanisms may be biotic or abiotic. Table 1 summarizes 15 hypotheses, derived or inferred from the invasion ecology literature, that attempt to explain the success or failure of invaders. These hypotheses are discussed in greater detail below. However, it is important to note that these hypotheses should not be considered mutually exclusive, as the relative importance of each may vary among habitats, invaders, and invasion stage (Fig. 1). Although we often do not explore the matter explicitly, it is worth considering the stage(s) at which each hypothesis is most likely to act, whether each hypothesis predicts success or failure of an invader at that stage, and how the processes underlying these hypotheses may interact with each other in synergistic or antagonistic ways.

Biotic resistance hypothesis (BRH)

The BRH is a widely-cited hypothesis to explain patterns of invasion but ironically does not predict why invaders succeed; rather it describes why they are likely to fail. The late Charles S. Elton of Oxford University first became interested in biological invaders while studying the effects of rodents on England's food supply during World War II [43]. Elton [31] first formalized the idea of invasibility, which is based on niche theory and Lotka-Volterra-type competitive systems. Since its inception [44], the niche has been premised on a supposed inability for ecologically similar species to coexist [45–47]. Niche theory, as formalized by Hutchinson [48], suggests that each species occupies a position in 'niche space' defined by its resource requirements. One key prediction of the BRH then, first noted by Elton [31], is that opportunities for invasion should decrease as the number of resident species increases. This is because niche space becomes filled up as species invade, leaving fewer resources available for future invaders.

Niche-type explanations for invasions are still being promoted today [49], but it is also important to note that such explanations are not universally accepted [50, 51]. Recently, Chase and Leibold [52] have tried to recast the niche concept to include more ecologically complex dynamics than just resource use (see SCH below). Not only has the concept been questioned but so has the pattern. The classic proposition that more diverse communities are less invasible has subsequently been challenged, and remains an area of much debate [53, 54]. More recent reincarnations of the BRH have focused on the role of resident enemies (i.e., predators, parasites, or pathogens), and the def-

Table 1. Non-exclusive hypotheses to explain the successful establishment, spread, or impact of nonindigenous species (NIS). Each hypothesis is described briefly, along with its mechanism (ecological or evolutionary) and interaction scale (population, species, community) of activity. Also shown are references cited in the text that support or do not support each hypothesis.

Hypothesis	Description	Mechanism	Interaction scale	Support	No support
BRH – Biotic resistance hypothesis	Biotic composition of the recipient community repels invaders	Ecological	Community	[31, 45–47, 49]	[50, 51, 53, 54]
RFH – Resource fluctuation hypothesis	Resource availability facilitates invaders	Ecological	Community	[59–65]	
SCH – Superior competitor hypothesis	The invader is a better competitor for limiting resources (R*)	Ecological	Species	[67–70]	[60]
ERH – Enemy release hypothesis	Invaders lose enemies during the invasion process, giving them a competitive advantage	Ecological	Population	[72–80]	[81, 82, 85]
EEH – Enemy of my enemy hypothesis	Co-introduced enemies promote invasion by attacking native competitors	Ecological	Community		
EIH – Enemy inversion hypothesis	Co-introduced enemies have a reduced, or even reversed effect on their hosts	Ecological	Community	[83–85]	
ISH – Increased susceptibility hypothesis	Invaders have reduced genetic variability by founder effects, and are more susceptible to enemies	Ecological/ Evolutionary	Community		
IFH – Invasional facilitation hypothesis	Facilitative interactions promote invasions	Ecological	Community	[86–90]	
EICA – Evolution of increased competitive ability hypothesis	Invaders lose enemies and evolve to invest more into competitive traits (e.g., growth rate)	Evolutionary	Population	[94–98]	[82, 94, 99, 101]

(Continued on next page)

Table 1. (Continued)

Hypothesis	Description	Mechanism	Interaction scale	Support	No support
GPG – General purpose genotype hypothesis	Successful invaders are a genetic subset of native populations that have evolved invasiveness	Evolutionary	Population	[103–105]	[106]
SIA – Selection for invasive ability hypothesis	Humans and human activity, and/or post-establishment evolution have driven the evolution of invasive genotypes in some species	Evolutionary	Population	[93, 111, 112]	[114]
IES – Invasiveness as an evolutionary strategy	Invasiveness is a phylogenetically correlated trait with increased number of successful invaders in certain phylo-groups	Evolutionary	Species or higher	[120]	
HCH – Human commensal hypothesis	Species that are commensal with humans are the most successful	Ecological	Species	[130, 131]	
WMD – Weapons of mass destruction hypothesis	Invaders exclude competitors using allelopathic chemicals	Ecological	Species	[133–135]	[138]
NCD – Neutral community dynamics hypothesis	NIS are subject to neutral processes represented by random birth–death processes and random walks	Ecological	Population/ community	[148]	

inition of 'niche space' has been expanded to include 'enemy-free space'. For example, Maron and Vilà [55] predicted that generalist enemies might offer resistance to invasion, resulting in a form of biotic resistance that is not strictly competition-based. When the number of individuals introduced (inoculum size) is low, heavy generalist pressure can render a community resistant to invasion. However, successful establishment might occur if native enemies do not show a numerical response, and if the abundance of an invader increases above some threshold level. For example, the density of *Sesbania puniea* in South Africa was not reduced by the weevil *Trichapion lativens*, even after 98% its seeds were damaged [56–58]. Although the BRH has been criticized, many of the hypotheses outlined below assume that communities are inherently resistant to invasion, and seek to identify circumstances in which invasions are favored. One key hurdle to testing the BRH, and one that is common to many alternative hypotheses, is that instances of unsuccessful establishment are rarely observed, while successful spread and proliferation are highly time-dependent. Regardless, the fact that modern definitions have switched to stage-based terminology reflects a growing belief that most species are not able to invade new communities successfully.

Resource fluctuation hypothesis (RFH)

A popular explanation for the success of various terrestrial plants is the resource fluctuation hypothesis [59]. According to this model, resource fluctuations promote invasions by creating resource openings for new species, or reducing potential competition from residents at certain times. Davis et al. [59] described two mechanisms for increases in resource availability: (1) if resource use by resident species declined, or (2) resource supply increased. In the first instance, disturbance could reduce the number of resident individuals, thus increasing resource availability [60, 61]. For example, Davis and Pelsor [62] used plant removal to test this hypothesis, and found that the plant *Rudbeckia hirta* flowered at a much higher rate in weeded compared to unweeded plots. Resource increase (e.g., nitrogen addition) has similarly been shown to increase the success of invaders [59, 63, 64].

There are many examples of invasions facilitated by disturbance and/or resource availability [59–61, 65]. *Chromolaena odorata,* a noxious invader from Central and Southern America in the Western Ghats of India, is causing severe damage to plantation crops and inhabits disturbed forest (partial cut and clear-cut) area, forest nurseries and plantations. Western Ghat is the only place in India listed for plant diversity as one of 26 'hot spots' of the world [66]. Disturbance (e.g., forest cutting and fire) plays an important role in *C. odorata* success. After flowering, *C. odorata* shoots dry up and become a highly combustable fire hazard. After fires have freed resources and removed most of the competing vegetation, *C. odorata* quickly re-sprouts and rapidly dominates.

Superior competitor hypothesis (SCH)

David Tilman at the University of Minnesota proposed a mechanistic explanation of species competition [67–69], which can potentially incorporate modern notions of the niche [52]. He suggested that an invader could establish if it was more efficient at obtaining limiting resources (symbolized as R*) than resident species, resulting in suppression or extirpation of the less-fit native species. This type of explanation can be seen as an alternative hypothesis to the RFH, as R* explicitly assumes equilibrium dynamics. According to Grime [60; p. 40], competition determines the addition or exclusion of species in productive communities, while competition is unimportant in highly-infertile soils. Tilman [69, 70], however, believed competition to remain important under infertile conditions. Under these conditions, the competitive success of a species is achieved through the capacity of a species to reduce limiting nutrients in soils to level under which other species cannot grow and reproduce. Grime [60] promoted critical reexamination of Tilman's R* theory under field conditions, because experiments supporting the R* theory could not discriminate between alternative mechanisms, such as nutrient loss via herbivory. Experiments of Wedin and Tilman [71] showed that slow-growing plants in infertile conditions could reduce the level of nitrogen to extremely low levels. However, they were unable to show the extent to which the success of slow-growing plants was due to the capturing of nitrogen at low levels or the ability to retain nitrogen because the plants resisted to herbivores and pathogens [60; p. 43]. Shea and Chesson [49] discussed Tilman's R* rule, predicting that invasion is favored when a resident species' resource requirements (i.e., R*) is greater than an invader's R*. This can happen in two situations: (1) when an invader has a higher resource acquisition rate than that of resident species, and (2) if an invader has lower maintenance requirement than that of resident species. It is important to note that explanations of invader success involving SCH may still require one or more of the other hypotheses presented in this paper. What resource-based explanations often fail to address is why a species is a superior competitor. For example, an NIS escaped from its natural enemies may appear the better competitor, when really the mechanism lies in the release from enemies, not a change in resource dynamics. Chase and Leibold [52] attempt to address this gap by incorporating not only impacts on resource dynamics but also the effects of predation and parasitism. They also extend their discussion to include multi-species systems and evolutionary processes. Nevertheless, the resource dynamics of invaders may be contextual, relying on subsequent explanations that incorporate the impact of the abiotic environment, other organisms and evolutionary dynamics.

Enemy release hypothesis (ERH)

As noted earlier, biological invasions result in a sub-sampling of invaders. Not only does this sub-sampling occur at the level of species and populations, but

it also likely restricts the number of co-introduced species, particularly natural enemies (i.e., parasites, pathogens, herbivores or predators that have an evolutionary history with the invader). Keane and Crawley [72] formalized the ERH as a rapid increase in the distribution and abundance of a plant species (i.e., successful proliferation, stage IVb or stage V (Fig. 1)) in their introduced range owing to a reduction in the number of natural enemies including herbivores. However, the idea that NIS benefit from a reduction of enemies has a long history as a largely untested 'rule of thumb'. Enemies can be *specialists* – defined as a species that is specialized to attack one or a small number of hosts, or *generalists* – enemies that attack a wide range of hosts. Keane and Crawley [72] proposed that the ERH could account for the successful proliferation of NIS if specialist enemies are absent from the introduced range of their host and if generalist enemies present in that range have a greater impact on native resident species. In support of this hypothesis, Mitchell and Power [73] and Torchin et al. [74] found that introduced populations of a variety of plant and animal hosts, respectively, had fewer enemies than populations from the native range [75]. Prati and Bossdorf [76] found that *Senecio inaequidens* was larger in size and had comparatively fewer insect parasites on them in the invaded range than in the native range. Callaway et al. [77] reported that soil biota could promote exotic invasion of *Centaurea maculosa*, which had higher biomass in soil collected from its introduced range. Soil biota in *C. maculosa*'s native Eurasia inhibits its growth, while soil microbes from N. America promoted its growth. Van der Putten [78] suggested two biotic benefits for invaders in the invaded range. These are: (1) invaders escape from enemies such as soil pathogens and do not encounter new species-specific enemies in the naturalized range, while (2) root symbionts are available to the invader to help it to establish in the invaded range. DeWalt et al. [79] tested the ERH with the neotropical shrub *Clidemia hirta* (Melastomataceae), a noxious invader in tropical forest in its introduced range of several islands in the Pacific and Indian oceans. In its native range, i.e., Central and South America and Caribbean, *C. hirta* is found in disturbed, relatively open areas. The absence of *C. hirta* from the forest understory in its native land was due to presence of natural enemies (fungal pathogens and herbivores) and these enemies were absent from Hawaii, where *C. hirta* is invading the forest understory. *Silene latifolia*, a native of Europe, is a serious invader in the USA, where it is considered a problematic weed of disturbed habitat and agricultural land. Wolfe [80] found that specialist enemies (e.g., a seed predator and an anther smut fungus) were absent or present in very low numbers in N. America. The success of *S. latifolia* as an invader in N. America was explained by its release from specialist enemies in its naturalized range.

Contrary to the ERH however, Agrawal and Kotanen [81] found that the level of attack on introduced herbivores was significantly higher than attack on native residents. Colautti et al. [82] reviewed 25 studies that tested the ERH and found that biogeographical studies, which compare enemies (i.e., their effects, abundances or species richness) in native and introduced populations

of the same host species, unfalteringly supported the ERH. However, evidence from community studies, which compared the levels of attack between NIS and native competitors, was much more equivocal. A number of alternate explanations were proposed to help explain this apparent discrepancy: (1) the 'enemy of my enemy hypothesis' (EEH) occurs when a co-introduced enemy does more damage to native competitors than to their co-evolved hosts because of native host naiveté to introduced enemies (see also IFH, below); (2) the 'enemy inversion hypothesis' (EIH) describes a documented situation where a co-introduced enemy may have actually increased the dispersal ability of its host by complex interactions between the host, its natural enemy, and a native species [83–85]; and (3) the 'increased susceptibility hypothesis' (ISH), which predicts that genetic bottlenecks during the invasion process may render a host species more susceptible to the effects of enemies, even though this may be inflicted by a smaller number of species. Colautti et al. [82] also note that biogeographical studies may be biased by a failure to consider the confounding effects of propagule pressure. In other words, many introduced species were likely founded by a small subset of individuals from a restricted part of their native range, and therefore a number of natural enemies had no chance of introduction. Indeed, this seems to be the case for the European starling *Sturnus vulgaris*, as the 'apparent' reduction in the number of enemy species, calculated as a reduction in enemies between its native and introduced ranges, was a gross overestimate of the 'realized' reduction, calculated after accounting for sub-sampling of the source region [85]. It is worth noting the difference between the ERH, which predicts that invaders succeed because they escape natural enemies, and the BRH, which predicts that invaders often fail to establish in the invaded range because of negative effects of enemies native to the introduced range [55]. Indeed, all invaders likely lose enemies during the invasion process, yet only a small proportion of these have appreciable ecological or economic impacts.

Invasional facilitation hypothesis (IFH)

Contrary to the BRH and the ERH, the IFH predicts an increasing rate of invasions through time [86]. The term 'invasional meltdown' was introduced by Dan Simberloff and Betsy Von Holle at the University of Tennessee to describe a process whereby facilitative interactions among NIS may increase invasion rates [86]. Facilitative interactions among invaders have been demonstrated in many systems [63, 87–89]. For example, invasion by the zebra mussel *Dreissena polymorpha* in the Laurentian Great Lakes has drastically altered the ecology of the lakes, including an increase in the diversity of macroinvertebrates, which use zebra mussel shells as refuge from predators [90]. The invasion and subsequent proliferation of *D. polymorpha* in 1988 was closely followed by invasions of three co-evolved species, which are also found in high abundance: in 1994 by *Echinogammarus ischnus*, a macroinvertebrate

that lives among *D. polymorpha* shells, and in 1990 by two fish species (*Neogobius melanostomus* and *Proterorhinus marmoratus*) that feed extensively on *E. ischnus* as juveniles and *D. polymorpha* as adults [89]. In addition to individual accounts of facilitative interactions like these, accelerating invasion rates have been noted in some of the world's best-studied ecosystems [89, 91]. However, it is erroneous to infer invasional meltdown based on invasion rate alone, since a time lag in the discovery of invaders can create the appearance of an increasing invasion rate [92]. Nevertheless, facilitative interactions are increasingly recognized among biological invaders, both with and without a co-evolutionary history, suggesting that the IFH may be more widespread than is currently appreciated.

Evolution of increased competitive ability (EICA) hypothesis

First proposed by Blossey and Nötzold [93], the EICA hypothesis may be thought of as both a variant of the ERH, and a subset of the SIA hypothesis (see below) but one that acts over evolutionary, rather than ecological timescales. The EICA hypothesis predicts that an invader, long released from enemies in its native range, could reallocate resources formerly used for defense to growth, reproduction and other attributes generally increasing competitive abilities [94, 95]. Thus, while the ERH predicts a 'regulatory' release from enemies, the EICA predicts a 'compensatory' release. In support of EICA, Blossey and Nötzold [93] found that introduced individuals of *Lythrum salicaria* had higher biomass than their native genotypes. Siemann and Roger [96] investigated the preference of the grasshopper *Melanoplus angustipennis* for Chinese tallow tree (*Sapium sebiferum*) from native (China) and introduced (Texas) populations. When given the choice between *Sapium* seedlings from China and Texas, *M. angustipennis* preferred Texas *Sapium* foliage compared to foliage from China. Invasive genotypes of *Sapium* exhibited lower resistance to herbivory by Melanopline grasshoppers, suggesting that the success of *Sapium* as an invader in North America could be due to reallocation of resources from defense to growth [97]. EICA is not universally supported. Vilà et al. [94] tested the EICA hypothesis using *Hypericum perforatum*. The competitive ability of native *H. perforatum* from Europe was compared with that of introduced *H. perforatum* from N. America where plants were grown in absence of specialist herbivores. Native species were also compared with *H. perforatum* from western North America where plants are subjected to biological control for more than five decades. Introduced and native *H. perforatum* plants showed no differences, counter to the predictions of the EICA hypothesis. Bossdorf et al. [98] compared native and introduced *Alliaria petiolata* with respect to their palatability and tolerance to simulated herbivory. Higher feeding rates of a specialist weevil (*Centorhynchus scrobicollis*) were observed on introduced *A. petiolata* plants. A generalist caterpillar (*Spodoptera littoralis*) showed no preference, revealing that introduced *A.*

petiolata populations are less resistant to a specialist herbivore but equally resistant to generalists when compared to native *A. petiolata* populations. Willis et al. [99] found no differences in the sizes of biennial species, *Carduus nutans, Digitalis purpurea, Echium vulgare* and *Senecio jacobaea*, from native (United Kingdom and continental Europe) and alien (Australia and New Zealand) habitats. These authors suggested that post invasion evolution of increased size is not common, and observed patterns may be due to a plastic response to the new environment.

Evidence both for and against EICA has been shown, and that evidence supporting EICA is contingent upon much of the evidence questioned for the ERH (above), as the two differ only in the mechanism of increased competitive ability (ecological *versus* evolutionary). However, factors other than the absence of enemies might contribute. Rogers and Siemann [100] investigated the effects of simulated herbivory and resource availability on a native tree, *Celtis laevigata* and an introduced tree, *Sapium sebiferum*. These authors examined the effect of different levels of simulated herbivory on the growth of *S. sebiferum* and *C. laevigata* at different levels of nitrogen and light. It was found that simulated leaf herbivory negatively affected growth of *C. laevigata* and had no effect on growth of *S. sebiferum*. *S. sebiferum* was able to compensate for leaf damage in all resource conditions. They concluded that phenotypic plasticity in combination with low levels of herbivory in the invaded range were likely to have contributed to *S. sebiferum* invasiveness.

Müller-Schärer et al. [101] opined that invaders cannot be completely released from enemies and proposed to revise the EICA hypothesis to include generalist herbivore effects. They argued that shifts in the suite of herbivores to assemblages dominated by generalist enemies should be taken into account. These authors suggested several antagonistic interactions in the native range. First, high concentrations of a toxin may repel generalist herbivore and attract specialist herbivores. Second, plants having lower digestibility-reducing (quantitative defence) defences are more susceptible to specialist herbivores and such a defence strategy is likely to have adverse general impacts on growth. This occurs because, according to Müller-Schärer et al. [101], specialist herbivores are likely to be absent in the introduced range, and plants are more likely to be attacked by generalist herbivores, resulting in an increased toxin concentration. Obviously this logic runs counter to decreases in toxin concentration in introduced ranges as predicted by EICA hypothesis.

General-purpose genotype (GPG) hypothesis

The term 'general-purpose-genotype' was coined by the late Herbert G. Baker working at the University of California, Berkeley. The GPG originally referred to a species possessing characteristics that allowed it to colonize a wide variety of habitats – characteristics such as a plastic growth response, r-selected life-history traits, and tolerance for a variety of environmental conditions

[102]. According to Baker's hypothesis, the colonization ability came at the cost of competitive ability, such that slower colonizing, but competitively superior specialists would eventually displace the general colonizers. More recently, the GPG has been used as a framework to explore the relative importance of phenotypic plasticity and contemporary evolution (see SIA, below) to the successful spread of NIS into new habitats. Van Doninck et al. [103] found that a widespread, asexual ostracod species *Darwinula stevensoni* tolerated salinity and temperature gradients better than the sexual *Vestalenula molopoensis*, which also has a more restricted range. Parker et al. [104] examined the relative importance of phenotypic plasticity and adaptation in an invasive weed *Verbascum thapsus* in California. They found significant phenotypic differences between introduced populations, and phenotypic variance of quantitative traits was largely partitioned among individuals from the same family, suggesting that phenotypic differences are largely plastic, rather than genetic. Genetic evidence suggests that a hybrid invasion by *Phragmites australis* in North America is by a single chloroplast haplotype [105]. However, the GPG hypothesis is not supported in genotypes of the aphid *Myzus persicae* [106]; contrary to predictions of the GPG hypothesis, the mean geometric fitness of obligately parthenogenetic (i.e., asexual) genotypes on different host plants was not significantly higher than that of cyclically parthenogenetic genotypes (i.e., those that reproduce both sexually and asexually, respectively). The importance of a GPG is still largely unexplored.

Selection for invasive ability (SIA) hypothesis

The idea that invaders rapidly adapt to novel environments, or that invasiveness is somehow selected by human activity is certainly not new. In particular, Baker was keenly interested in the effects of humans on plant evolution [107, 108]. These hypotheses have so far received little empirical testing [95, 109]. However, Lee [110] has shown that multiple invasions of freshwater habitats by the copepod *Eurytemora affinis* have occurred from brackish and marine populations that have adapted to freshwater. Several other studies have suggested a change in the mean phenotype of introduced, relative to native populations [93, 111, 112]. However, it is important to consider the relevance of such a finding to the evolution of 'invasiveness'. For example, an 'evolutionary' change could result from a simple founder effect, whereby North American populations are established from a relatively small number of individuals from a relatively restricted area in the native range. This genetic bottleneck is likely to change the mean phenotype of introduced populations, particularly if populations remain relatively small for several generations [113]. Therefore, evolutionary change can result merely from genetic drift, rather than from some sort of selection for invasiveness. Moreover, the generality of the assertion that invaders are more vigorous in their native ranges has recently come into question [114]. Regardless, rapid evolutionary

change in adventive populations has been repeatedly observed [115, 116]. Maron et al. [117] found evidence for adaptation among introduced populations of St. John's wort, *Hypericum perforatum*. Evolution over ecological timescales has also been well demonstrated for *Drosophila* invasions [118]. Studies like these demonstrate that rapid evolution can occur in populations of NIS, but more work is needed to show that adaptation has lead to increased invasiveness.

Invasiveness as an evolutionary strategy (IES) hypothesis

Much of Herbert Baker's career was spent comparing 'weedy' and 'non-weedy' congeners [102] with his eye trained towards developing a synthetic list of the traits influencing invasiveness. The summary of this work [107, 119] includes a popular list of characteristics of the 'ideal weed', which is used in many regulatory frameworks: "the Baker list". However, as studies grew in scale and began comparing hundreds, instead of tens of species, it became apparent that the traits Baker thought to be associated with invasiveness were not independent of phylogeny. A very consistent finding of studies that look for traits associated with large groups of invasive plants is that there is increased invasion risk from plants that are closely related to an invader or that the distribution of invaders is phylogenetically non-random. Scott and Panetta [120] found that species in the same genus as species described as 'weeds' were much more likely to be weedy themselves. Further, Reichard and Hamilton's [121] criteria for rejecting potential plant invaders included having a familial or generic invasive relative.

Along the same vein, many studies have found that nonindigenous invaders are over-represented in relatively few taxonomic groups [122–126]. These types of patterns are not explanations in themselves but reveal that some underlying non-random trait distribution is likely to influence invasiveness. For example, Daehler [125] examined lists of global natural area invaders and found that plant families were over-represented by invasive species when they had high proportions of woody species, contained abiotically-dispersed species, or included climbing species.

The importance of uncovering these types of phylogenetic patterns is twofold. First, the information gained in the above and similar studies has been used to develop methods to predict potential invaders, which have proven invaluable for informing management decisions where a precise mechanistic understanding of the underlying ecology is lacking [121, 127, 128]. However, the accuracy of such methods needs to be very high (e.g., >85%) for general usefulness [129]. Secondly, these large-scale studies allow researchers to uncover patterns, which the various mechanisms outlined in this chapter must ultimately explain.

Human commensal hypothesis (HCH)

The idea that the most successful invaders are commensal with humans and thereby benefit from human disturbance and other activity is perhaps one of the oldest and most cited 'rules of thumb' in invasion ecology. Indeed, many of the most infamous invasive species, such as rats, pigeons, nonindigenous garden and agricultural weeds, and feral populations of domestic animals, are closely associated with humans and have evolved to benefit from human activity. There is no doubt that humans play a significant role in the repeated introduction and spread of particular invaders, along with habitat modification practices (e.g., conversion of old growth forest to agricultural land) much to the benefit of particular invaders. The HCH is becoming regionalized (at least, in North America) due to the fact that the HCH is altering "historical ranges of variability (HRV)" in organizing (disturbance) factors such as fire and floods. By modifying the HRV (via the HCH), species in these systems are no longer adapted to soil/microclimatic conditions, reproduction is vastly affected, and the propagule pressure from invaders is amplified in terms of the success of these propagules (Tim Seastedt, *personal communication*). However, invasion of relatively undisturbed areas is an increasing trend that is poorly explained by the HCH [130, 131]. Moreover, while introductions of NIS are by definition human-mediated, the spread, increase in abundance, and displacement of native species exhibited by some invaders, are often not obviously facilitated by human activity. For example, the overwhelming success of the Argentine ant in North America is likely due to the formation of supercolonies. Supercolonies are a collection of individual colonies that benefit from a decrease in inter-colony aggression owing to a reduction in genetic diversity and thus an increase in relatedness [132].

Environmental manipulation hypothesis (EMH)

Baldwin [133] proposed the weapon of mass destruction (WMD) hypothesis to describe the role of allelochemicals in plant invasions. However, we suggest the less pejorative and more inclusive term 'environmental manipulation hypothesis' (EMH). This hypothesis suggests that invaders succeed because they are able to alter their environment to suit their own needs at the expense of native species. The literature on allelopathy is perhaps the best explored example of this. One such example is the flavonoid (–)-catechin released by *Centaurea maculosa,* which is a potent allelopathic agent against bunchgrass species in North America [134]. Interestingly, the level of (–)-catechin in *C. maculosa* soil from North America was twice the amount detected in soil supporting *C. maculosa* in its native Europe. A related invader, *Centaurea diffusa,* also has inhibitory effects on several grasses (*Festuca ovina, Koeleria laerssenii* and *Agropyron cristatum*) in invaded North American habitats, compared to those from its native Eurasia [135]. Vivanco et al. [136] isolated 8-

hydroxyquinoline from root exudates of *C. diffusa,* and found that levels of 8-hydroxyquinoline were three times higher in N. American soils than in native soils. They concluded that native plants and soil biota might have acquired resistance to 8-hydroxyquinoline while N. American plants and soil biota were highly susceptible, thereby explaining *C. diffusa*'s profound effects in North America. Prati and Bossdorf [137] investigated the allelopathic activities of native and invasive *Alliaria petiolata* against two congeneric species, *Geum urbanum* from Europe and *G. laciniatum* from N. America. Allelopathic suppression of *G. urbanum* germination by invasive *A. petiolata* in N. America was found. The germination of *G. urbanum* therefore depended upon the origin of *A. petiolata.*

Although EMH is a testable hypothesis, it is not yet conclusively shown to play an important role in invasion in field situations. In many allelopathy studies, the significance of larger-scale ecosystem processes is unappreciated [138]. Most allelopathy research is carried out using an autecological approach. Inderjit and Weiner [139] proposed that allelopathy is better conceptualized and investigated in terms of soil chemical ecology. In their view, placing allelopathy in the context of soil ecology can reduce some of the controversy surrounding the phenomenon. It is not ecologically correct to label a species as an 'allelopathic' species, as allelopathy is conditional on species-specific effects [140]. Allelopathy as a potential mechanism of plant invasion needs further study. More recently, Callaway and Ridenour have proposed the 'allelopathic advantage against resident species (AARS) hypothesis' [141], which is conceptually similar to the EMH hypothesis and therefore falls under the more general EMH.

Neutral community dynamics (NCD) hypothesis

One hypothesis that should not be ignored, and indeed might be considered a null hypothesis, is simply that there is no underlying proximate mechanism for invasions, other than random chance. Or, at least, that the outcome of interactions among invaders and resident species are so complex that they can be modeled stochastically. There has been a recent spate of work examining which ecological patterns neutral dynamics can adequately explain [142–144]. Largely inspired by the neutral theory of evolution, neutral dynamics of communities simply describe changes in the composition and abundance of species as the outcome of random birth–death processes, resulting in random walk trajectories [143]. Neutral models may be valuable for developing null models of expected number and relative abundance of NIS, which would have to be rejected before other hypotheses are inferred. However, neutral models may also hold value in their ability to explain some current patterns of invasions more parsimoniously than other hypotheses.

One universal observation of NIS patterns is that most invaders (those that successfully establish) remain relatively rare [35]. For example, Cadotte et al.

[145] show that 68% of nonindigenous plants in Ontario are considered relatively rare. Moreover, the majority of invasions do not seem to result in the direct extinction of native species. Work done by Dov Sax and colleagues [146, 147] revealed that despite global declines in species diversity, local communities are increasing in richness. Further, the construction of the Panama Canal resulted in a faunal interchange between isolated biotas [148]. This interchange has apparently not resulted in any species extinctions. In a review by Davis [149], very few instances of species extinction caused by competition from NIS have been reported. Davis also thought that neutral dynamics may be, in part, an explanation for the lack of competition-induced extinctions.

These observations may point to neutral rather than deterministic processes affecting the persistence and abundances of NIS. Within a neutral framework, one would expect that adding species to a region only increases the source pool in the birth–death probabilities (i.e., more species for the birth part) and that no single species addition should have major impacts on the whole community. However, this is demonstrably false as the most problematic invasive species tend to be problematic in adventive populations elsewhere (see IES, above). Further, one would expect long time lags in increases in abundance, as random walk processes, on average, take many generations for sizable changes in population size. Other processes could potentially explain many of the observations predicted by the NCD hypothesis. Nevertheless, neutral models should be addressed as they may represent null hypotheses and are potentially powerful explanations for some NIS observations at the community level.

Concluding remarks

In this essay, we have provided a brief review of the rapidly expanding literature on biological invasions. Many of the hypotheses explored above are not mutually exclusive, and the processes that underlie them may act simultaneously, in concert or in opposition, to determine the ultimate success or failure of an invader at each invasion stage. Though we have tried to be thorough, experienced researchers in the field will no doubt formulate additional hypotheses that warrant investigation. To date, most experiments have focused on only a single hypothesis for a small subset of invasive species under particular environmental conditions. To arrive at a realistic understanding of the ecological processes underlying biological invasions, a more integrative approach is warranted – one that examines the relative importance of each processes for a variety of species under myriad environmental conditions. This will prove to be a daunting task indeed, but one that will perpetuate the expansion of the field of invasion ecology for years to come, thereby ensuring plenty of fruitful lines of research for the keen investigators of the future.

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Ecological niche models and the geography of biological invasions: a review and a novel application

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Introduction

Invasive species are a threat to Earth's natural ecological systems [1], and increasing global commerce likely will intensify the problem by transporting greater numbers of potential invaders between regions. Preventing the introduction and establishment of invasive species is generally a better strategy than eradication, but to prevent invasions effectively, managers must have *a priori* knowledge of which species are likely to become invasive and which regions are likely to be invaded. Given their high economic and ecological costs, there is an urgent need for a system that accurately can predict invasions. However, despite decades of effort, the desire to develop invasion biology into a truly predictive science remains unrealized [2].

Generally, biologists have used two approaches to predict the invasive potential of species: 1) examination of intrinsic traits, such as life history (e.g., [3]), and 2) analysis of extrinsic factors, such as the environment in which a species exists (e.g., [4, 5]). Within this latter category is ecological niche modeling (ENM), the focus of this chapter. ENM attempts to identify areas prone to invasion by evaluating the degree of environmental similarity between the native and potential ranges of an invader. The first step in this process is the development of a model that relates the current geographic distribution of a species to the environmental conditions within the occupied region. Once developed, the model can be used to identify potentially suitable habitats in other regions.

Typically, ecological niche models consider only the abiotic environment. Thus, this approach is often criticized because both the native and invaded distributions of species also are influenced by biotic factors, such as interactions with other organisms [6, 7]. In addition, limitations to dispersal can prevent a species from occupying all suitable habitats. Therefore, the geographic distribution of a species may not be indicative of the full range of environmental conditions it can tolerate. Furthermore, both species and their ranges

are dynamic entities: species can respond to a changing environment both by local adaptation and by shifting their distributions. Failure to consider these factors when building models can result in misinterpretation of the niche and, consequently, in prediction errors when the model is projected onto a new region.

However, recent enhancements in modeling techniques, and increased availability of fine-resolution climate, topography and landcover datasets, have led to improved predictive capabilities. Yet, despite improvements, ENM always may be criticized for several reasons [2, 8]. First, few exotic species become invasive, even when introduced into suitable environmental conditions [9]. This suggests that other factors also influence the success of invasive species. Secondly, ENM currently cannot incorporate all factors that limit the distribution of species, such as dispersal rates (but see [10]) and biotic influences (yet, the possibility of incorporating geographic representations of biotic factors (e.g., as distributional maps of natural enemies) deserves attention). Therefore, the current geographic distribution of a potential invader, alone, is insufficient to predict whether the factors that govern the native range of the species also will govern its distribution in a new geographic and biological setting.

To validate the ENM approach to predicting invasions, ecologists must answer two questions: 1) Are the distributions of invaders constrained by the same factors that constrain their native distributions? 2) If not, are the differences meaningful at the macro-scales of analysis of ENM? The purpose of this chapter is to investigate these questions. We first briefly review the use of ENM to predict species invasions. Second, we discuss the assumptions and limitations of ENM, investigate why biological invasions may violate these assumptions, and describe how failure to meet these assumptions can result in prediction errors. Third, we describe a new application of ENM, 1) to test whether invasive species are subject to the same distributional constraints in their invaded range as in their native range, and 2) to develop hypotheses as to why constraints on the distribution of a species in its native and invaded ranges may differ. Our new application uses a combination of traditional ENM (which we term "Forward-ENM"), coupled with a unique application of ENM, namely Reverse-ENM. Reverse-ENM uses a niche model based on occurrence points from the *invaded* range to model the potential *native* range (Fig. 1). The predictions from Forward-ENM and Reverse-ENM are then compared. We suggest that differences between the forward and reverse predictions may reveal whether the distribution of an invader is constrained by the same factors that constrain its native distribution. Finally, we analyze the invasion of the red imported fire ant (RIFA, *Solenopsis invicta* Buren) into the United States as an initial demonstration of the Reverse-ENM method.

Predicting invasions with ecological niche models: approach, assumptions, and limitations

Approach

Predicting the distribution of invasive species using ENM has been described elsewhere [8, 11], so here we provide only an overview of the technique and its applications. ENM typically refers to niche modeling approaches that use point occurrence data (in the form of latitude–longitude coordinates) and geographic datasets (in the form of digital maps that describe broad-scale environmental characteristics) to produce an approximation of the ecological niche. The ecological niche is defined as the range of environmental conditions that delineate where a species is able to maintain populations without immigration [12]. At the scales of analysis typical of ENM, modeled niche dimensions are limited to those relevant to geographic ranges (e.g., macro-climate, topography, and landcover). Ecological niche models, when projected onto regions other than the one from which they were developed, can estimate the potential range of an invader or forecast shifts in the distributions of species under scenarios of environmental change. Niche models also have been used to prioritize conservation goals, study the distribution of species, and investigate patterns and mechanisms of biodiversity within the region from which they are based [13].

Assumptions and limitations

ENM relies on a key assumption that the distribution of a species represents a manifestation of the ecological niche. Recall that Hutchinson [14] suggested that the boundaries of the ecological niche are set by the values at which a particular environmental factor becomes limiting and beyond which the species cannot survive. ENM assumes that these limits on the ecological niche determine the geographic boundaries of the range of that species.

Hutchinson further defined the realized niche as the niche that a species actually occupies because of the influence of biotic interactions that exclude the species from parts of its ecological niche. Further, because limitations to dispersal will prevent species from occupying all suitable habitats, they may be absent from locales in addition to those excluded by biotic or environmental limitations. For these reasons, it is unlikely that a species will occupy its entire niche. In terms of geographic ranges, it is unlikely that the current distribution of a species will encompass its entire potential distribution. Therefore, niche models based on the current geographic distribution of a species will reflect only a fraction of the potential conditions in which a species could exist. Because niche models rely almost exclusively on abiotic factors as modeled niche dimensions, the model will not include all parameters pertinent to the distributions of species.

The validity of the predicted distribution that results when the niche model is projected onto a new geographic region depends on the assumption that the niche of the species, as modeled, will be conserved when the species invades this region. In other words, the factors governing the distributional limits of a species in its native range also will govern the distributional limits of the species in its invaded range, and that these factors are included in the model.

Because species can adapt to new environments, its niche may not be conserved when the species invades this region. It has been argued that niche evolution (i.e., evolutionary change in niche dimensions such that ecological niches are not conserved over time) is a primary limitation on the predictability of the geography of invasions. However, in response to this criticism, Peterson [8] argued that empirical and theoretical evidence demonstrates the conservation of ecological niches over evolutionary time, and he concluded that evolution of niche space was not a serious limitation for ENM.

Few ecologists would question that climate is a dominant factor in structuring the distribution of species at macro-scales. Many published niche modeling studies that successfully simulated the current distributions of species support this assertion. Difficulty arises when niche models are used to predict distributions in new settings because biotic interactions and dispersal rates are likely to be different in a new geographic and biological context. These issues could be especially problematic for predicting the distributions of invasive species because invaders may leave behind competitors, pathogens, and other natural enemies. Indeed, release from harmful biotic interactions (i.e., as in the enemy-release hypothesis (ERH) for invasive plants [15]) is a commonly invoked explanation for the observed increases in fecundity, competitive ability or abundance of invasive species in their newly invaded range [15–17]. However, only one study [18] has provided evidence that release from enemies enables an invasive species to exploit a habitat within its invaded range that it could not exploit in its native range. Mack et al. [16] cited several cases in which invaders became established in climatic regions unlike those that would have been predicted based on knowledge of their native range, but mechanisms for the differences were not discussed. To our knowledge, none of these studies have been analyzed using ENM. Therefore, it is unclear if ENM would have failed to predict accurately the potential invaded distributions of these species. Yet, differences in performance and habitat use by invaders in their new ranges suggest that factors other than environmental conditions alone mediate their success and that particular constraints on the distribution of species are not conserved when an invader spreads to a new region. In conclusion, it is not whether ecological niches tend to be conserved, but rather, whether the niche a species *occupies* in its invaded range generally differs from the niche the species *occupies* in its native range.

One potential way to evaluate if an invasive species occupies a different niche in its invaded range than its native range is to compare the predicted invasive distribution with the actual extent of invasion (i.e., *a posteriori* assessment of the accuracy of the prediction). Several such comparisons conducted

to date [5, 11, 19] reported substantial overlap between the predicted distribution in the invaded region and the actual distribution of the invasive species in its new range. This high degree of overlap between the prediction and the actual invaded distribution suggests 1) that abiotic factors play a dominant role in structuring the distribution of species and 2) that particular constraints on the distribution of species are conserved when a species invades a new region.

However, in these retrospective studies, there also were large regions where the predictions and the invaded ranges did not overlap (i.e., where models predicted presence of the invader, but where the invader was absent (commission error) or *vice versa* (omission error)). The interpretation of these errors is problematic, because omission errors may represent a difference in which factors are governing the native and invasive ranges, or may result simply from deficiencies in the model (e.g., the failure to include an important environmental factor). Moreover, commission errors may reflect suitable habitat that is as yet unoccupied (because the invader is still spreading into new habitat), or may again simply reflect deficiencies in the model. Because of these uncertainties, retrospective analyses alone often are inadequate to test fully for differences between native and invaded range constraints on the distribution of a species.

Testing the predictability of invasions: the reverse-ENM approach

Another approach to evaluate differences in which factors govern the native and invaded range of a species is to use the *invaded* distribution essentially to back-predict the *native* distribution. For example, consider the situation where the two key assumptions of ENM are met without exception – occurrence points from the native distribution of a species can be used to model perfectly its ecological niche (i.e., its distribution is not influenced by biotic interactions, and it is not dispersal limited, Forward-ENM in Fig. 1) and the ecological niche of the species is conserved when it invades a new region. If this species is introduced onto a new continent, and is given enough time to spread to all available habitats (i.e., reach a distributional 'equilibrium'), our perfect model should replicate the invaded range of this species. Conversely, because niche occupancy is the same in the invaded and native ranges, an ecological niche model based on the *invaded* range of the invader should duplicate its *native* range (Reverse-ENM in Fig. 1).

Now consider the more realistic case in which a species in its native range occupies only a portion of available habitats because of biotic interactions and limitations to dispersal. As before, we introduce this species onto a new continent, and assuming its ecological niche remains stable, allow it to reach equilibrium. However, this species is limited less by dispersal, or leaves behind pathogens and predators. As a result, the invader is able to survive and reproduce under environmental conditions in its invaded range that were unreachable or unsuitable in its native range. In terms of the niche of the species, this invader occupies a different niche in its invaded range than in its native range.
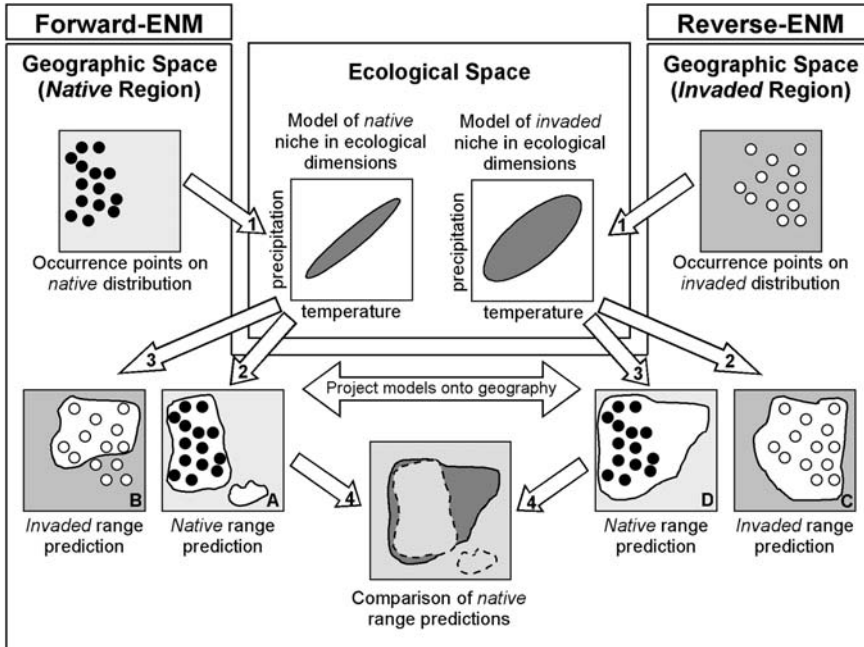
Figure 1. A conceptual model illustrating the use of ecological niche models to investigate differences in native and invasive niche use or occupancy. In Forward-ENM, occurrence points from the native range are used to develop an ecological niche model (1). The niche model is projected into native geographic space, assessed for accuracy (2), and then projected onto another landscape to predict the potential invaded range (3). Reverse-ENM employs an analogous process, differing in that occurrence points from the *invaded* range are used to predict the potential *native* range. In the final step (4), the native range predictions are compared and differences assessed. Bold, uppercase letters correspond to the geographic predictions in Figure 2. Adapted from [8].

In this scenario, a traditional or Forward-ENM model will predict the invader to be absent from areas where it has invaded (i.e., it will under-predict the potential invaded range (omission error)). Conversely, if we build a niche model from the invaded range and project it onto the native region, the model should identify areas where the species does not occur in its native region. The areas that the species does not occupy, but that are predicted to have the species present, should represent portions of its ecological niche that are unexploited in its native range. The evaluation of the differences between the forward and reverse predictions of the native distribution is the basis for the Reverse-ENM process and is a means for assessing differences in invaded and native niche occupancy (step 4, Fig. 1).

Reverse-ENM is directly analogous to Forward-ENM, differing only in the space from which occurrence points are taken and the "direction" of the modeling process. The environmental data layers used as modeled niche dimensions in Forward- and Reverse-ENM are identical. Although an equilibrium

condition simplifies the analysis, Reverse-ENM can suggest, during any stage of the invasion, whether the invader is occupying habitats in its invaded range that it does not occupy in its native range.

Reverse-ENM, if applied across many different taxa and between many different regions, could facilitate a general assessment of the predictability of the geography of biological invasions. Emergent patterns may highlight groups of organisms most likely to follow the same ecological rules in their native and invaded ranges. Fortunately or unfortunately, depending on the perspective, ample study cases now exist involving numerous taxonomic groups and nearly every continent. The following section uses, as an example, the invasion by the red imported fire ant into the United States; limitations to the broader application of Reverse-ENM are discussed at the end of the chapter.

A test case: the red imported fire ant in the US

Introduction

As an initial application of our Reverse-ENM method, we compared the actual and predicted distributions of the red imported fire ant (RIFA) in South America and the continental United States (US). RIFA, which is native to sub-Amazonian South America, was introduced first into the US in the 1930s in Mobile, Alabama [20], and has since spread throughout most of the southeastern United States, as well as parts of Texas, Arizona, Nevada and California. Infestations have been found recently as far north as Maryland and Delaware [21]. In many areas, RIFA persists only in human-modified habitats (e.g., irrigated lawns in the southwestern US). Mortality of colonies by cold winter temperatures is suggested to be the critical factor limiting colony survival [22], and therefore the northern distributional limit. See [23] for a comprehensive review of the natural history of RIFA and its invasion into the US.

RIFA is an ideal invader to evaluate Reverse-ENM because i) its adverse ecological, economical and social impacts have made it one of the most well studied invasive species, ii) its record of introduction and subsequent spread are well documented, and iii) its present native and introduced distributions are known. Consistent with the assumptions of Reverse-ENM described above, the success of RIFA as an invader has been attributed partially to release from natural enemies [24]. In addition, the spread of RIFA in the US appears to be reaching its equilibrium distribution, in that its range expansion has slowed considerably, especially along its northern range limit [22].

Methods

We produced predictions of the distributional potential of RIFA using a desktop computer version of the Genetic Algorithm for Rule-set Production

(GARP) [25–27]. GARP is a genetic algorithm that uses multiple unique niche modeling methods (e.g., logistic regression, bioclimatic rules) and environmental datasets to model various factors that govern distribution potential throughout the range of a species. Genetic algorithms are a solution-optimization technique, loosely akin to evolution by natural selection, wherein a set of possible solutions to a problem is formed, and, through a series of iterations, the solutions are modified and tested until the best solution is found. GARP uses such a process to compose, evaluate and produce a set of rules that approximates the ecological niche of a species. GARP models can be imported into geographic information systems (GIS) and visualized as maps that represent hypotheses for the potential distribution of the organism(s) under study. When projected onto another region, the potential distribution of the species in that location can be estimated. GARP has been used to model the distributions of both native and invasive species, and its predictions are generally more robust than other niche modeling techniques [13, 28, 29]. See [25–27] for a more detailed explanation of GARP and its application.

We confined our analysis to South America and the continental 48 States of the US. We used 12 WorldClim [30] environmental data layers as modeled niche dimensions, including an elevation layer and 11 bioclimatic datasets that summarize temperature and precipitation aspects of climate (Tab. 1). These layers are typical of those commonly used to produce niche models with GARP.

Occurrence data, in the form of state, county and year of infestation for invasive populations of RIFA in the US were provided by the National Agricultural Pest Information System [21]. We obtained 771 distributional points, each defined as the latitude–longitude center-point of counties (determined by ArcGIS 8.3) within which RIFA is established. 71 collection loca-

Table 1. WorldClim v1.2 [30] environmental data layers used to develop ecological niche models for the red imported fire ant (RIFA, *Solenopsis invicta* Buren). All layers had a pixel resolution of 300 km^2

Layer
Elevation
Mean annual temperature
Mean diurnal temperature range (mean of monthly (max temp–min temp))
Isothermality (mean diurnal range/temperature annual range)
Temperature seasonality (σ*100)
Maximum temperature of warmest month
Minimum temperature of coldest month
Temperature annual range (max temp of warmest month–min temp of coldest month)
Annual precipitation
Precipitation of wettest month
Precipitation of driest month
Precipitation seasonality (coefficient of variation)

tions from the native range of RIFA in South America were extracted from primary literature [31–33] and georeferenced as latitude–longitude coordinates.

We used Forward-ENM to develop native-range ecological niche models to predict the potential invaded distribution of RIFA in the US based on the 71 South American occurrence points, divided at random into near-equal sets of training data (used to build models) and test data (used to assess accuracy). Because the process of model development is stochastic, and resultant GARP models vary in quality, we used a procedure described by Anderson et al. [34] to select the best subset of models. In short, we generated (roughly 1,000) Forward-ENM models until GARP produced 100 models with omission errors of zero. We calculated the mean area predicted to have RIFA present from these 100 zero-omission models; then from these 100 models, we selected the ten models closest to this overall mean area. The ten best models were imported into ArcGIS 8.3 and summed to assess the degree of model overlap, which is a measure of model confidence. For example, regions where all ten models predicted presence of RIFA had a value of 10, or maximum model agreement, whereas regions where few models predicted presence of RIFA had low values, or minimum model agreement. The known ranges of RIFA, as determined from published maps [21, 33], were overlaid on the summed predictions for comparison.

Next, using Reverse-ENM and the 771 invaded US county center-points (divided as before into training and test datasets), we developed invaded-range ecological niche models to predict the potential native distribution of RIFA within South America. To select the best subset of Reverse-ENM models, we used a method similar to that employed for Forward-ENM; however, instead of selecting the ten models closest to the overall mean area predicted to have RIFA present, we selected the ten models with the *smallest* area predicted to have RIFA present from 100 Reverse-ENM zero-omission models. By choosing the models with the smallest "presence areas" we ensured, to the largest degree possible, that differences between the Forward- and Reverse-ENM predictions were the result of actual differences in niche occupancy in the US and South America, and not the result of commission errors. The ten smallest Reverse-ENM models were imported into ArcGIS 8.3 and summed, and the known ranges of RIFA were overlaid for comparison.

Results and discussion

The distribution predicted using Forward-ENM closely matched the observed native range of RIFA along the northern, western and southern boundaries (Fig. 2A). The western boundary of RIFA clearly abuts the Andes mountain range, while the northern and southern boundaries appear to coincide with transitional zones into the wetter climates of the Amazon basin to the north and the colder and drier climates of central Argentina to the south. The model suffered from commission error along its eastern boundary. Commission error is
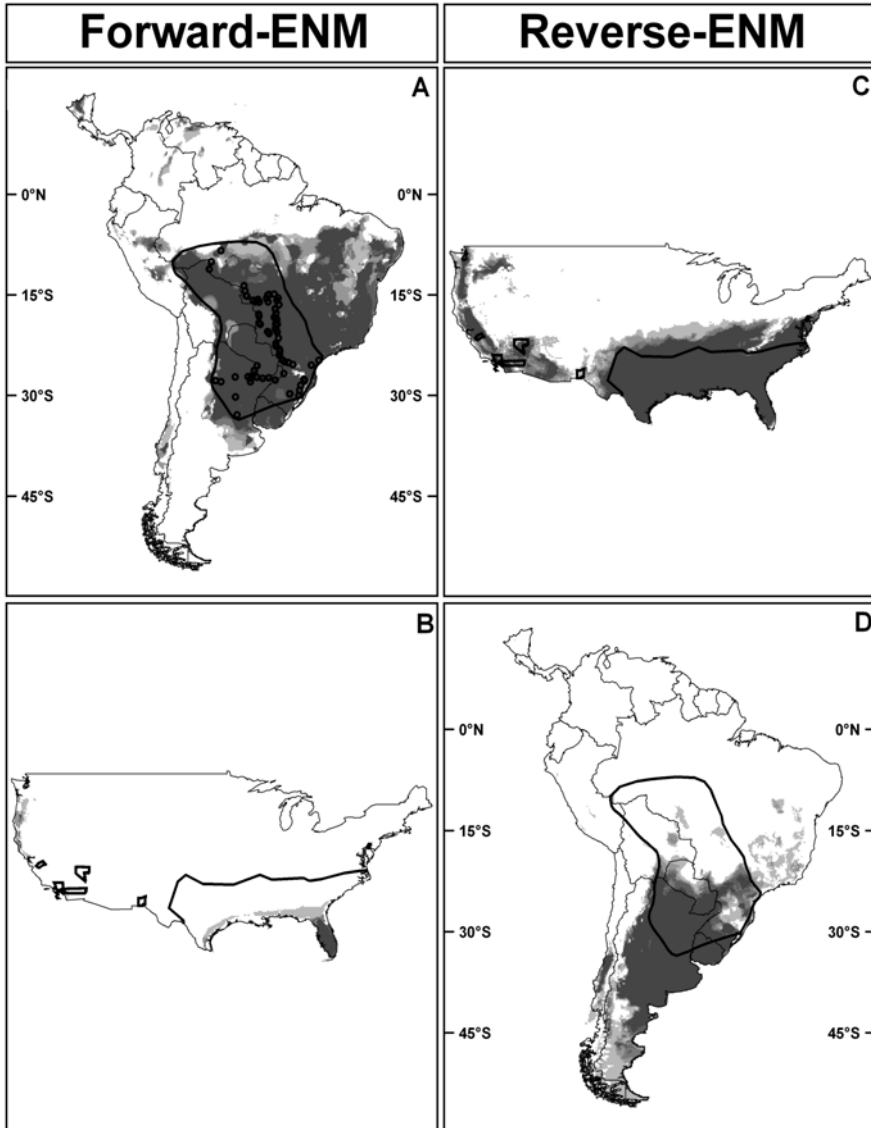
Figure 2. Projections of red imported fire ant (RIFA, *Solenopsis invicta* Buren) ecological niche models. The Forward-ENM projections represent (A) the potential native distribution in South America based on 71 native range points (open circles [31–33]) and (B) the predicted potential invaded range in the US. The Reverse-ENM projections represent (C) the potential *invaded* distribution of RIFA in the US based on 771 invaded range points [21] (not shown for clarity) and (D) the predicted potential *native* range in South America based on the Reverse-ENM model. Bold, solid lines represent (1) regions of the known invasion of RIFA in the US [21] (B, C) and (2) the extent of the range of RIFA in South America [33] (A, D). In all models, darker shading represents greater model agreement in predicting the presence of RIFA.

comprised of two components: 1) true commission error (overprediction) and 2) apparent commission error (correctly predicted areas not verifiable as such). If true commission error caused the overprediction along the eastern boundary of the native range, it suggests that factors that control the eastern range boundary (e.g., competition, landcover) were not included in the model. If the error instead is apparent commission error, this suggests that this region is habitable by RIFA, but that RIFA either has yet to be documented there, or that RIFA is unable to disperse to this region (see below).

In contrast, the Forward-ENM model greatly underpredicted the actual invaded range of RIFA in the US (Fig. 2B). According to this model, Florida is under the greatest threat of invasion by RIFA because it is predicted to be suitable habitat by a majority of the best models (as portrayed by the dark gray regions in Fig. 2B). A minority of the best models (i.e., the light gray regions in Fig. 2B) predicted a narrow band of potentially suitable habitat along the gulf coast of the US (where RIFA was first introduced) and regions of the Pacific Northwest. The Forward-ENM projections suggest that the environmental data layers used to model the native range of RIFA, though able to replicate the native distribution of RIFA fairly well, are poor predictors of the actual invaded range of RIFA in the US.

The niche model developed using Reverse-ENM overlapped the invaded distribution of RIFA in the US, but suffered from commission errors, especially in the Pacific Northwest and north of the distribution boundary in the southeastern US (Fig. 2C). Other research, including physiological-based models [22, 35] and surveys of the timeline of the spread and establishment of RIFA [20, 21], suggests that these commission errors are likely to represent both apparent and true commission error. Northern California and southern Oregon are considered regions where RIFA is likely to invade [22, 35], and thus may represent apparent commission error. Regions where establishment of RIFA is unlikely because of winter kill of colonies caused by minimum winter temperatures (e.g., parts of Tennessee, Kentucky, Virginia and the Snake River valley of Idaho) or insufficient precipitation (e.g., the desert Southwest) may represent model overprediction (true commission error).

The projection of the Reverse-ENM model onto South America suggests that RIFA occupies sites in the US that are colder and drier than habitats currently occupied in its native range; as such, the projection of the native range of RIFA was shifted southward into Argentina. Also, this model predicted that RIFA would not occur in the northern portion of its current native range due to a lack of similar environmental conditions in the US. In terms of niches, these results suggest that the niche RIFA occupies in its invaded range may be different from the niche it occupies in its native range.

Our study is the first published attempt to model the distribution of RIFA using ENM. Two other published studies [22, 35] have attempted to model the distribution of RIFA at scales of analysis similar to the study reported here. However, each used a mechanistic, physiological model of colony growth, based on the invaded range of RIFA, to predict the potential expansion of RIFA

in the US [22] and the world [35]. The results of these models qualitatively were similar to those from our Reverse-ENM model (Figs 2C and 2D).

Mechanism to explain the disparity between the Forward- and Reverse-ENM models

If the distribution of a species is considered representative of the niche of that species, the Forward- and Reverse-ENM analysis suggests that niche occupancy of RIFA differs between its native and invaded ranges. However, differences in predictions may be caused by mechanisms other than differences in niche occupancy. We present several hypotheses to explain the disparity between the Forward- and Reverse-ENM predictions, both involving mechanisms that may and may not bring about differences in niche occupancy.

Hypotheses in opposition to differences in niche occupancy

Inadequate sampling in native range
To our knowledge, the native range occurrence dataset used in this study includes all published records of RIFA in South America. However, RIFA may actually occur south of its known native range, but it has not been observed or collected in that region. Although the exact southern limit of RIFA is admittedly not well known, inadequate sampling seems unlikely given the recent extensive ant surveys in the area of the southern limit of RIFA, which documented ants in the genus *Solenopsis* with the exception of *S. invicta* [33]. RIFA apparently has not been collected south of roughly 34° latitude, well north of the Reverse-ENM predictions (Fig. 2D).

Microhabitat selection in the US
RIFA may occupy natural or disturbed microhabitats in the US that are not indicative of the broader climate. The scale at which organisms select habitat is finer than the resolution of the climate data used to model their distributions. If RIFA inhabits sites that are unlike the broader climate (e.g., irrigated land), the model may predict presence in these regions even though they are climatically unsuitable. For instance, in dry climates in the US, RIFA is associated closely with irrigated areas, such as golf courses and agricultural fields. Neither of these features, nor the degree of anthropogenic disturbance, were included in our models, yet may be good predictors of the local distribution of RIFA. Given the extent of the invasion of RIFA into climates in the US unlike those that it inhabits in South America, it seems unlikely that this mechanism alone accounts for the large difference between the Forward- and Reverse-ENM predictions. If microhabitat selection was responsible for the differences in predictions, it seems plausible that RIFA should occur in disturbed habitats in colder and drier regions in its native range.

Hypotheses supporting differences in niche occupancy

Limitations to dispersal in South America

The southern limit of RIFA may be imposed by limitations to dispersal, which keep RIFA from occupying otherwise suitable habitats. There are no obvious physical barriers that would preclude RIFA from dispersing southward. Rivers pose only a minor obstruction to movement since RIFA can disperse and survive as a floating colony for several weeks and new colonies are established by winged sexual females capable of dispersing several kilometers [23, 36].

Release from natural enemies in the US

RIFA may maintain populations in environmental conditions in its invaded range that it does not in its native range due to release from adverse biotic interactions. This explanation assumes that the ecological niche of RIFA includes habitats found south of its native range, but biotic interactions exclude it from these habitats. At least 30 species of natural enemies (including 18 species of parasitic phorid flies) attack RIFA in South America [24]. Conversely, only two or three natural enemies have been discovered in the US (and phorid flies are being investigated as biological agents). Porter et al. [24] hypothesized that an escape from natural enemies was responsible for observed differences in abundance of RIFA in North *versus* South America, although they did not discuss the ability of RIFA to exploit different environmental conditions in the US. Therefore, we cannot conclude from this study that enemy-release necessarily allows RIFA to exploit different habitats in the US.

Lack of resistance to invasion in the US

Another mechanism akin to enemy-release is a lack of resistance to invasion in the US by native ant faunas. There is evidence that chemical control programs, aimed at reducing the spread of RIFA, also decimated native ant populations, and consequently facilitated the spread of RIFA instead. The pesticide reduced populations of both RIFA and native ants, but native ant populations did not recover to their former dominant levels, while the abundance of RIFA eventually exceeded native populations [23, 37].

Adaptation to new environments in the US

It is possible that the ecological niche of RIFA was not conserved when it invaded the US, and invasive RIFA populations now are adapted to a new environment. The founding populations of RIFA apparently passed through a bottleneck that reduced genetic variation and altered the life history of invasive RIFA relative to native RIFA, and resulted in differences in colony structure between native and invading populations [38, 39].

These hypotheses are not exhaustive or mutually exclusive. Because detailed study would be needed to fully evaluate them, we cannot conclude, based on this study alone, which mechanisms are responsible for the differences in the Forward- and Reverse-ENM predictions. However, the review and case study

presented in this chapter do highlight some of the limitations of using ENM to predict biological invasions.

Reverse-ENM requires similar assumptions and suffers from analogous limitations as Forward-ENM. The invaded range of a species is still likely to be smaller than the geographic extent of its ecological niche, because the distributions of invaders are also subject to biotic influences and limitations to dispersal. Also, for many potential case studies, we found it difficult to find species for which requisite occurrence data existed for both the native and invaded ranges. RIFA was an exception in this regard. Yet, as the RIFA case study demonstrated, Reverse-ENM can be used i) to test for differences in the constraints on the distribution of a species in its native and invaded ranges, and ii) to gain insight into the mechanisms responsible for success of a particular invasive species. Further study, with more species across different regions, generally could determine whether or not the distributions of invaders are governed by the same factors in both their native and invaded ranges, or whether RIFA is an isolated case.

Conclusion

There is an urgent need for a system that accurately can predict which species are likely to become invasive and which regions are likely to be invaded. ENM is a possible solution to predicting the potential geographic extent of biological invasions. However, given the complexity of the invasion process and the inability of ENM to incorporate fully the many factors that influence the distribution of species, ENM-based predictions should be interpreted as only a first evaluation of regions potentially at risk of invasion, and not a prediction of distribution *per se*.

Despite their threat to natural systems, invasive species are unparalleled natural experiments and offer vast opportunity for ecological study. The methodology described in this chapter, Reverse-ENM, attempts to make use of these ongoing natural experiments. By comparing the native and invaded distributions of species, Reverse-ENM can be used to develop hypotheses concerning why invaders may succeed in their new environmental and geographic settings. Given the potential insights that can be obtained from such assessments, it is surprising that there are not more studies that compare the distributions of invasive species in both their native and invaded ranges. However, Reverse-ENM has many of the same limitations as traditional ENM, and the added difficulty of obtaining location data from both the native and invaded ranges.

We used the red imported fire ant as an initial demonstration of Reverse-ENM. By using the invaded distribution of the red imported fire ant to predict its native range, we investigated two questions: 1) Do different factors constrain the native and invaded ranges of an invasive species? 2) If so, are the differences meaningful at the macro-scales of analysis of ENM? Although

Reverse-ENM alone definitively cannot answer the first question, it suggests that the answer to both questions is "yes".

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Importance of species replication in understanding plant invasions into North American grasslands

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Introduction

The global homogenization of the Earth's biota is expected to increase due to the increase in movement of people and goods between regions, and many introduced species are having a negative economic impact. The increase of introduced species can be thought of as a major global change, because ecosystems throughout the world are now impacted by exotics [1, 2]. Grasslands, which cover roughly 25% of the globe, contain perhaps the most disrupted and homogenized communities in the world. Native grasslands have been lost because of land conversion, and native species have been replaced or displaced with introduced grasses and legumes. Many species were intentionally introduced during the early 20th century to prevent erosion or to improve grazing, and many have undoubtedly done so. However, as management objectives for grasslands have expanded to include wildlife habitat, biodiversity, and C sequestration, it has become critical to understand how introduced species are affecting these new objectives as well. For example, Christian and Wilson [3] found that areas in Saskatchewan, Canada, dominated by the introduced forage grass *Agropyron cristatum* are sequestering less C into their soils compared to developing native prairie stands with similar land use histories.

   Exotic species have been planted or have spread to become common or even the dominant species in many grasslands in the US. For example, the grasses *Bromus inermis* and *Agropyron cristatum* are dominant grasses in much of the Northern Plains region (e.g., [3, 4]), species of the genus *Centaurea* dominate some Rocky Mountain grasslands [5, 6], exotic annuals dominate California (e.g., [7]), *Agropyron desertorum* dominates much of the inter-mountain west (e.g., [8–10]), and the grass *Bothriochloa ischaemum* dominates most central Texas grasslands [11]. The spread of these species has occurred within a very short time span. For example, it is stated in the 1979 Flora of Texas that *Bothriochloa ischaemum* was 'not persisting except in cultivation or along roadsides'. The spreading of exotic species, their impact on native communities, and the global homogenization of the flora and fauna makes this an important global issue [1, 12–14].

Several comprehensive reviews exist on invasive plant species [15–21]. Rather than providing another overview of the topic, I will focus on a smaller aspect of the issue, i.e., whether invasive-species conclusions based on single species pairs would differ from conclusions based on means from multiple invasive and native species. I test this hypothesis with a literature review and with data from a common garden experiment.

Are there differences in growth characteristics between natives and exotics?

Two important predictions have been made about exotic species: 1) introduced species have higher growth rates than do natives and 2) introduced species are more tolerant to grazing than are native species, at least in regions where plants evolved with low intensities of grazing. Introduced species are predicted to have higher growth rates because they 1) have been 'released' from their natural enemies (pathogens or herbivores), 2) are able to shift allocation of resources from secondary compounds to growth (reviewed in [22]), or 3) have undergone rapid evolution for high growth rate and increased competitive ability (e.g., [23]). A factor that is seldom mentioned is the possibility that people consciously selected fast growing species (out of a wide distribution of possible species and genotypes) to introduce. Whatever the mechanism, exotics are predicted to have a higher rate of above-ground growth than natives when grown under common conditions.

Several studies have reviewed papers that compared growth rates and competitive abilities between native and exotic plant species (e.g., [24, 25]). Daehler [24], in a literature review, compared natives and exotics for 9 growth related traits, 4 spread related traits, and 3 "composite" traits. He found few differences between natives and exotics. Among the growth related traits, only leaf construction costs and leaf area were significantly different in exotic species. Spread related traits were not significantly different between natives and exotics, except for survival rate, which was higher in natives. Phenotypic plasticity was significantly greater in exotics, and growth generally responded more to nutrients in exotic than in native species. This provides an important link to theory developed by Burke and Grime [26] and Davis et al. [27] that predicts that invasions will be most likely to occur when unused resource pulses occur. Daehler [24] did not analyze tolerance to grazing or clipping, although many of the cited papers contained data on this variable. Daehler concluded that the major difference between exotics and natives is that the former can more rapidly adjust to the fluctuating conditions of disturbed sites. However, Vilá and Weiner [25] found in a meta-analysis that exotics had a higher overall growth rate than natives. They went on to note that differences between natives and exotics may have been influenced by biased choices of investigators, who may have compared highly invasive exotics with "well behaved" native species in at least some cases [25]. The differing conclusions between Daehler [24] and Vilá and Weiner [25], and the large variation in out-

Table 1. Studies that compared native and exotic species (from [24])

Studies that replicated both native and exotic species

Baars R, Kelly D (1996) Survival and growth responses of native and introduced vines in New Zealand to light availability. *New Zealand J Bot* 34: 389–400

Baruch Z, Goldstein G (1999) Leaf construction cost, nutrient concentration, and net CO_2 assimilation of native and invasive species in Hawaii. *Oecologia* 121: 183–192

Blaney CS, Kotanen PM (2001a) Effects of fungal pathogens on seeds of native and exotic plants: A test using congeneric pairs. *J Appl Ecol* 38: 1104–1113

Blaney CS, Kotanen PM (2001b) Post-dispersal losses to seed predators: An experimental comparison of native and exotic old field plants. *Can J Bot* 79: 284–292

Frenot Y, Gloaguen JC (1994) Reproductive performance of native and alien colonizing phanerogams on a glacier foreland, Iles Kerguelen. *Polar Biol* 14: 473–481

Glenn E, Tanner R, Mendez S, Kehret T, Moore D (1998) Growth rates, salt tolerance and water use characteristics of native and invasive riparian plants from the delta of the Colorado River, Mexico. *J Arid Environ* 40: 281–294

Maillet J, Lopez GC (2000) What criteria are relevant for predicting the invasive capacity of a new agricultural weed? The case of invasive American species in France. *Weed Res* 40:11–26

Pattison RR, Goldstein G, Ares A (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* 117: 449–459

Radho TS, Majer JD, Yates C (2001) Impact of fire on leaf nutrients, arthropod fauna and herbivory of native and exotic eucalypts in Kings Park, Perth, Western Australia. *Aust Ecol* 26: 500–506

Smith MD, Knapp AK (2001) Physiological and morphological traits of exotic, invasive exotic, and native plant species in tallgrass prairie. *Int J Pl Sci* 162: 785–792

Studies that replicated native species but not exotics

Black RA, Richards JH, Manwaring JH (1994) Nutrient uptake from enriched soil microsites by three great basin perennials. *Ecology* 75: 110–122

Cleverly JR, Smith SD, Sala A, Devitt DA (1997) Invasive capacity of *Tamarix ramosissima* in a Mojave Desert floodplain: The role of drought. *Oecologia* 111: 12–18

Horn P, Prach K (1994) Aerial biomass of *Reynoutria japonica* and its comparison with that of native species. *Preslia* 66: 345–348

Marler MJ, Zabinski CA, Wojtowicz T, Callaway RM (1999) Mycorrhizae and fine root dynamics of *Centaurea maculosa* and native bunchgrasses in western Montana. *Northwest Sci* 73: 217–224

Nagel JM, Griffin KL (2001) Construction cost and invasive potential: comparing *Lythrum salicaria* (Lythraceae) with co-occurring native species along pond banks. *Am J Bot* 88: 2252–2258

Nernberg D, Dale MRT (1997) Competition of five native prairie grasses with *Bromus inermis* under three moisture regimes. *Can J Bot* 75: 2140–2145

Woo I, Zedler JB (2002) Can nutrients alone shift a sedge meadow towards dominance by the invasive *Typha × glauca*. *Wetlands* 22: 509–521

Yamashita N, Ishida A, Kushima H, Tanaka N (2000) Acclimation to sudden increase in light favoring an invasive over native trees in subtropical islands, Japan. *Oecologia* 125: 412–419

Studies that replicated exotic species but not natives

Fan J, Harris W (1996) Effects of soil fertility level and cutting frequency on interference among *Hieracium pilosella*, *H. praealtum*, *Rumex acetosella*, and *Festuca novae-zelandiae*. *New Zealand J Agric Res* 39: 1–32

McDowell CR, Moll EJ (1981) Studies of seed germination and seedling competition in *Virgilia oroboides* (Berg.) Salter, *Albizia lophantha* (Willd.) Benth. and *Acacia longifolia* (Andr.) Willd. *J South Afr Bot* 47: 653–685

Virgona JM, Bowcher A (2000) Effects of grazing interval on basal cover of four perennial grasses in a summer-dry environment. *Aust J Exp Agric* 40: 299–311

Table 1. (Continued)

Studies that did not replicate exotic or native species

Aptekar R, Rejmanek M (2000) The effect of sea-water submergence on rhizome bud viability of the introduced *Ammophila arenaria* and the native *Leymus mollis* in California. *J Coastal Conser* 6: 107–111

Arenas F, Fernandez C, Rico J, Fernandez E, Haya D (1995) Growth and reproductive strategies of *Sargassum muticum* (Yendo) Fensholt and *Cystoseira nodicaulis* (Whit.) Roberts. *Sciencia Maritima* 59(Suppl. 1): 1–8

Baruch Z, Bilbao B (1999) Effects of fire and defoliation on the life history of native and invader C$_4$ grasses in a neotropical savanna. *Oecologia* 119: 510–520

Baruch Z (1996) Ecophysiological aspects of the invasion by African grasses and their impact on biodiversity and function of neotropical savannas. In: OT Solbrig, E Medina, JF Silva (eds.): *Biodiversity and savanna ecosystem processes*. Springer-Verlag, Berlin, 79–93

Caldwell MM, Richards JH, Johnson DA, Nowak RS, Dzurec RS (1981) Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* 50: 14–24

Callaway JC, Josselyn MN (1992) The introduction and spread of smooth cordgrass (*Spartina alterniflora*) in South San Francisco Bay. *Estuaries* 15: 218–226

Carino DA, Daehler CC (2002) Can inconspicuous legumes facilitate alien grass invasions? Partridge peas and fountain grass in Hawaii. *Ecography* 25: 33–41

Cross JR (1981) The establishment of *Rhododendron ponticum* in the Killarney oakwoods. *J Ecol* 69: 807–824

Goergen E, Daehler CC (2001*a*) Inflorescence damage by insects and fungi in native pili grass (*Heteropogon contortus*) *versus* alien fountain grass (*Pennisetum setaceum*) in Hawaii. *Pacific Sci* 55: 129–136

Goergen E, Daehler CC (2001*b*) Reproductive ecology of a native Hawaiian grass *(Heteropogon contortus*; Poaceae) *versus* its invasive alien competitor (*Pennisetum setaceum*; Poaceae). *Int J Pl Sci* 162: 317–326

Goergen E, Daehler CC (2002) Factors affecting seedling recruitment in an invasive grass (*Pennisetum setaceum*) and a native grass (*Heteropogon contortus*) in the Hawaiian Islands. *Plant Ecol* 161: 147–156

Greenberg CH, Smith LM, Levey DJ (2001) Fruit fate, seed germination and growth of an invasive vine-an experimental test of "sit and wait" strategy. *Biol Inv* 3: 363–372

Gross EM, Johnson RL, Hairston NG Jr (2001) Experimental evidence for changes in submersed macrophyte species composition caused by the herbivore *Acentria ephemerella* (Lepidoptera). *Oecologia* 127: 105–114

Herron GJ, Sheley RL, Maxwell BD, Jacobsen JS (2001) Influence of nutrient availability on the interaction between spotted knapweed and bluebunch wheatgrass. *Restor Ecol* 9: 326–331

Holmgren M, Aviles R, Sierralta L, Segura AM, Fuentes ER (2000) Why have European herbs so successfully invaded the Chilean matorral? Effects of herbivory, soil nutrients, and fire. *J Arid Env* 44: 197–211

Honig MA, Cowling RM, Richardson DM (1992) The invasive potential of Australian *Banksias* in South African fynbos: A comparison of the reproductive potential of *Banksia ericifolia* and *Leucadendron laureolum*. *Aust J Ecol* 17: 305–314

Huenneke LF, Thomson JK (1995) Potential interference between a threatened endemic thistle and an invasive nonnative plant. *Conser Biol* 9: 416–425

Kuhn NL, Zedler JB (1997) Differential effects of salinity and soil saturation on native and exotic plants of a coastal salt marsh. *Estuaries* 20: 391–403

Larson KC (2000) Circumnutation behavior of an exotic honeysuckle vine and its native congener: Influence on clonal mobility. *Am J Bot* 7: 533–538

Lesica P, Miles S (1999) Russian olive invasion into cottonwood forests along a regulated river in north-central Montana. *Can J Bot* 77: 1077–1083

Table 1. (Continued)

Li Y, Norland M (2001) The role of soil fertility in invasion of Brazilian pepper *(Schinus terebinthifolius)* in Everglades National Park, Florida. *Soil Sci* 166:400–405

Luken JO, Kuddes LM, Tholemeier TC, Haller DM (1997) Comparative responses of *Lonicera maackii* (amur honeysuckle) and *Lindera benzoin* (spicebush) to increased light. *Am Midl Natur* 138: 331–343

Marco DE, Paez SA (2000) Invasion of *Gleditsia triacanthos* in *Lithraea ternifolia* montane forests of Central Argentina. *Environ Manage* 26: 409–419

Mesleard F, Ham LT, Boy V, Van Wijck C, Grillas P (1993) Competition between an introduced and an indigenous species: The case of *Paspalum paspalodes* (Michx) Schribner and *Aeluropus littoralis* (Gouan) in the Camargue (southern France). *Oecologia* 94: 204–209

Pavlik BM (1983a) Nutrient and productivity relations of the dune grass *Ammophila arenaria* and *Elymus mollis*. I. Blade photosynthesis and nitrogen use efficiency in the laboratory and field. *Oecologia* 57: 227–232

Pavlik BM (1983b) Nutrient and productivity relations of the dune grass *Ammophila arenaria* and *Elymus mollis*. II. Growth and patterns of dry matter and nitrogen allocation as influenced by nitrogen supply. *Oecologia* 57: 233–238

Pyke DA (1986) Demographic responses of *Bromus tectorum* and seedlings of *Agropyron spicatum* to grazing by small mammals: occurrence. *J Ecol* 74: 739–754

Sallabanks R (1993) Fruiting plant attractiveness to avian seed dispersers: native *versus* invasive *Crataegus* in western Oregon. *Madroño* 40: 108–116

Schierenbeck KA, Mack RN, Sharitz RR (1994) Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology* 75: 1661–1672

Shafroth PB, Auble GT, Scott ML (1995) Germination and establishment of the native plains cottonwood (*Populus deltoides* Marshall subsp. *monilifera*) and the exotic Russian-olive (*Elaeagnus angustifolia* L.). *Conser Biol* 9: 1169–1175

Sher AA, Marshall DL, Gilbert SA (2000) Competition between native *Populus deltoides* and invasive *Tamarix ramosissima* and the implications for reestablishing flooding disturbance. *Conser Biol* 14: 1744–1754

Simoes M, Baruch Z (1991) Responses to simulated herbivory and water stress in two tropical C_4 grasses. *Oecologia* 88: 173–180

Smith MA, Bell DT, Loneragan WA (1999) Comparative seed germination ecology of *Austrostipa compressa* and *Ehrharta calycina* (Poaceae) in a Western Australian Banksia woodlands. *Aust J Ecol* 24: 35–42

Smith RGB, Brock MA (1996) Coexistence of *Juncus articulatus* L. and *Glyceria australis* C.E. Hubb. in a temporary shallow wetland in Australia. *Hydrobiologia* 340: 147–151

Vila M, D'Antonio CM (1998a) Fruit choice and seed dispersal of invasive *versus* noninvasive *Carpobrotus* (Aizoaceae) in coastal California. *Ecology* 79: 1053–1060

Vila M, D'Antonio CM (1998b) Fitness of invasive *Carpobrotus* (Aizoaceae) hybrids in coastal California. *Ecoscience* 5: 191–199

Williams DG, Black RA (1994) Drought response of a native and introduced Hawaiian grass. *Oecologia* 97: 512–519

Witkowski ETF (1991) Growth and competition between seedlings of *Protea repens* (L.) L. and the alien invasive, *Acacia saligna* (Labill.) Wendl. in relation to nutrient availability. *Func Ecol* 5: 101–110

Zedler JB, Paling E, McComb A (1990) Differential responses to salinity help explain the replacement of native *Juncus kraussii* by *Typha orientalis* in Western Australian salt marshes. *Aust J Ecol* 15: 57–72

Studies included in Daehler (2003) that confound differences in lifespan (annual or perennial) and native or exotic origin (and did not replicate species)

Claassen VP, Marler M (1998) Annual and perennial grass growth on nitrogen-depleted decomposed granite. *Restor Ecol* 6: 175–180

Zink TA, Allen MF (1998) The effects of organic amendments on the restoration of a disturbed coastal sage scrub habitat. *Restor Ecol* 6: 52–58

comes among studies, suggests that differences in sampling design (e.g., vote counting *versus* meta-analysis) might have affected the conclusions reached.

Problems with generalizing from studies of exotic-native pairs

Most land managers deal with large multi-species communities that contain multiple exotic species (salt marsh dominated by *Spartina* spp is the exception, e.g., [28]). They are commonly interested in knowing, in general, how all of the exotic species in their area are affecting community and ecosystem processes. The literature that compares exotic and native species growth characteristics (e.g., [24, 25]) is highly relevant to these management issues. However, because species are not replicated in most comparisons of native and exotic species within a given site, results may not provide the best information for management. Results and conclusions will be as highly variable as the variation among species. As any basic statistics book will explain, a greater number of replicates will lead to more precise estimates that approach the actual mean. Using few or no replicates may be leading to the widely varying results, with some results falling well above the actual mean and some falling well below the actual mean. Among-species variation in morphological or physiological traits is enormous among both native and exotic species. Picking one species out of a large distribution will give much greater weight to outlier species and lead to widely varying conclusions among studies. Thus, I hypothesize that conclusions about exotic-native differences by Daehler [24] may have been different if species had been replicated within sites.

Another, but less common problem with exotic-native species comparisons is that growth form (e.g., annual *versus* perennial) is sometimes confounded with native-exotic status [29, 30]. In many cases, the objective of the researcher is to test hypotheses associated with how to restore native species dominance [29, 30]. In these cases, researchers sometimes choose a perennial native species to compare to an annual exotic. In this case, annual-perennial (i.e., successional stage) and native-exotic status are confounded. This makes sense in the context of restoration ecology, but it makes less sense in comparisons of natives to exotics (Tab. 1).

Literature review of native and exotic species comparisons

Here, I analyze data from papers cited in the review by Daehler [24] as well as a few more recent studies, and break down the analysis into two data sets: those that compare a single pair of native and exotic species and those that replicate either native or exotic species, or both (Tab. 1). My prediction is that studies that replicate species within their study areas will give a more accurate estimate of the overall effect of exotic species, and will be less variable than studies that use single pairs within sites. Furthermore, I analyze a variable that

was not measured by Daehler [24], but that is important to grazed grasslands: tolerance to either real or simulated defoliation by grazers. There are few studies with replicated species responses to grazing or clipping, so this variable was analyzed with the combined data set (pooling replicated and non-replicated studies).

A total of 61 studies were analyzed. Of those 61 studies, only 10 replicated both native and exotic species (16%). Seven studies replicated natives only and 3 replicated exotics only, for another 16%. Most studies (41 out of 61, 67%) did not replicate either species type, i.e., they compared a single exotic species to a single native species (Tab. 1).

I found that results differed between studies that did and did not replicate native and exotic species (Fig. 1). I used a vote count technique [24] and classified studies into categories of 1) exotic mean > native mean, 2) no significant difference between exotic and native species means and 3) native mean > exotic mean. In contrast to Daehler [24], who classified studies as exotic = native if any of the natives equaled the exotic (which biases the results towards
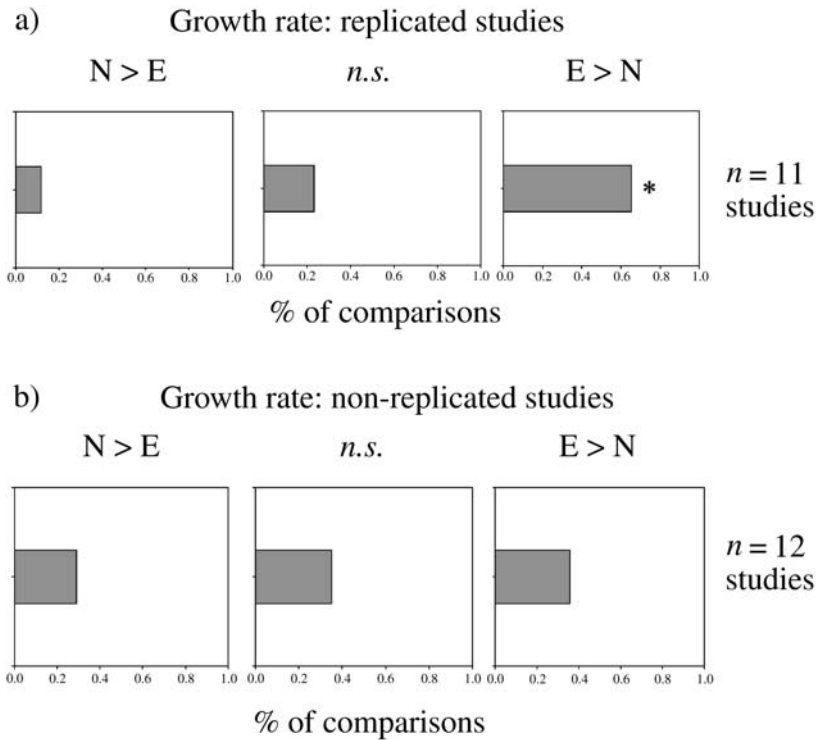

Figure 1. Proportion of studies cited by Daehler [24] that found higher growth rates in exotics than natives (E > N), no significant difference (n.s.), or higher rates in natives than exotics (N > E) among studies that replicated either native or exotic species identity, or both (a) or among studies that did not replicate species (b).

not finding overall differences), I based differences on the means for all native or exotic species. I only had enough data to test for above-ground growth rate variables because of the small number of studies that replicated species. In 11 studies that replicated either native or exotic species or both (Fig. 1a), I found a significant difference among outcomes (chi-squared exact test, $\chi^2 = 6.3$, 2 d.f., $P < 0.05$). Majority of studies (65%) found that exotic species had higher growth rates than natives (Fig. 1). Only 12% of studies found that native species had higher growth rates than exotics. Thus, this analysis supports the hypothesis that growth rate overall is higher in exotics than it is in natives. When I analyzed the data set that included studies that did not replicate species (Fig. 1b), I found no significant difference among the three outcomes (chi-squared exact test, $\chi^2 = 0.1$, 2 d.f., $P > 0.10$), which does not support the hypothesis that exotics differ from natives. Taken together, the difference between these two data sets suggests that conclusions about exotic species may change depending on whether species are replicated within groups. If multiple species were used, the (correct?) generalization reached was that exotics had higher growth rates than natives. If un-replicated species pairs were used, the (incorrect?) generalization is that there was no overall effect. This result is not entirely surprising. By using species pairs, one is less likely to find a difference between natives and exotics because of the very high variability among species. Replicating species leads to a more precise estimate of mean differences between native and exotic species within sites, which is an important variable to managers.

Grazing tolerance in exotic species

Many plant species were introduced into North and South America, Australasia and elsewhere to improve grazing lands. In many cases, introductions were made of species that tolerate grazing well. For example, grasses from East Africa were introduced to many places because they evolved with large populations of grazing mammals [31, 32]. Tolerance is defined as having a smaller reduction (or even an increase) in relative growth rate due to compensatory growth after grazing or simulated grazing (i.e., clipping) [33–35]. An intolerant plant would have larger reductions in relative growth rate. A few influential early studies found that a native species was less tolerant of defoliation than an invading exotic species [8, 32]. Again, both of these studies used only a single native and exotic species. Based on these studies, the authors concluded that an exotic *Agropyron* (now *Pseudogneria* sp.) species was spreading in grazed grasslands of the inter-mountain western USA and an African grass was spreading across South America due their greater tolerance to grazing [8, 32].

   I reviewed studies cited by Daehler [24] that included data on grazing or clipping tolerance in exotic and native species. By including several studies in my analysis, I could test the generality of the hypotheses of Caldwell et al. [8]

and Simoes and Baruch [32]. I found that out of seven studies, all but one found support for the hypothesis that exotics are more tolerant of grazing or clipping than native species (Fig. 2). Support of the hypothesis was found by Caldwell et al. [8], Pyke [10], Fan and Harris [36], Simoes and Baruch [32], Schierenbeck et al. [37], and Holmgren et al. [38]. Only one study [39] reported inconsistent results, with exotics being more tolerant to grazing only in situations where water availability was high. Thus, the overall data set seemed to support the hypothesis that exotics have higher grazing tolerance than natives. The higher tolerance of exotics to grazing may be important in their spread in grasslands, which could be due to the commonness of grazing by native and domestic animals throughout grasslands of the world. The processes underlying this phenomenon deserve much further research.
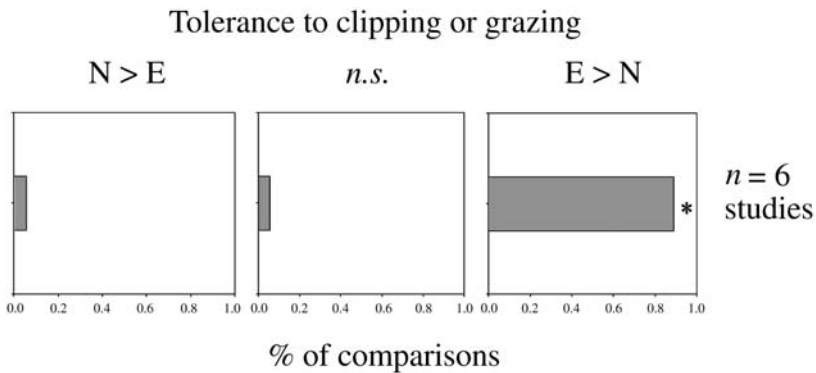

Figure 2. Proportion of studies cited by Daehler [24] that found higher tolerance to grazing or clipping in exotics than natives (E > N), no significant difference (n.s.), or higher rates in natives than exotics (N > E). Studies that either did or did not replicate species were combined due to small sample sizes.

An experimental example on the importance of replication

In an ongoing experiment in the Texas Blackland Prairie region [40], we are comparing growth characteristics of the common exotic and native C_4 grasses in the region. Plants are being compared in common garden monoculture plots, as well as in 2, 4, and 8 species mixtures. Small equal-sized transplants were planted into monoculture 1 m^2 plots (96 transplants per plot) in spring 2001 within three blocks (block term, $F_{1,15} = 2.4$, $P = 0.143$) and allowed to grow for two growing seasons before harvest. Plots were weeded when necessary. An estimate of average difference between exotics and natives is possible because species identity is replicated, with 3 exotic and 5 native species being represented (Fig. 3). A fixed effects model (that uses plots as the error term) is appropriate here because we have all the major native and exotic species in this system, and therefore, the choice of species would not change if we were to
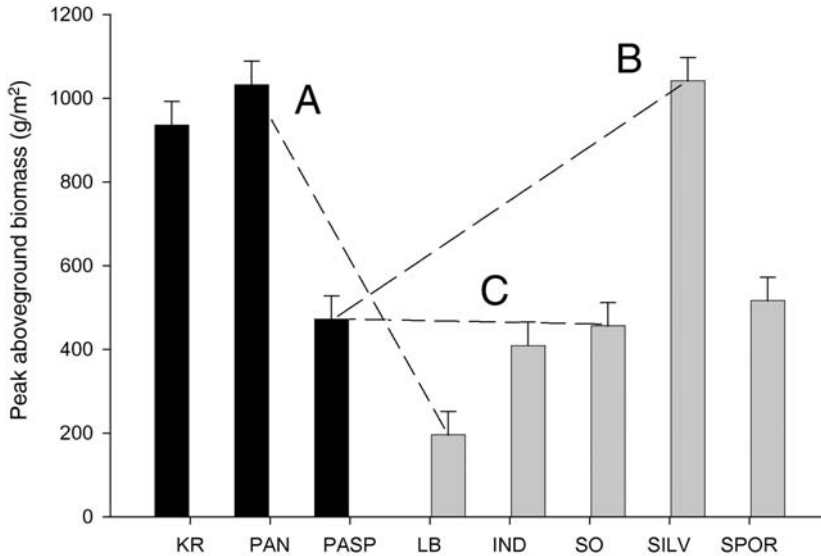
Figure 3. Peak biomass of exotic and native C_4 grass species grown in a common garden through two growing seasons. Exotic species, which are denoted by black bars, are KR = King ranch bluestem, *Bothriochloa ischaemum*, PAN = Kleingrass, *Panicum coloratum*, and PASP = Dallisgrass, *Paspalum dilatatum*. Native species, which are denoted by gray bars, are LB = little bluestem, *Schizachyrium scoparium*, IND = indian grass, *Sorghastrum nutans*, SO = side-oats grama, *Bouteloua curtipendula*, SILV = silver bluestem, *Bothriochloa laguroides*, and SPOR = tall dropseed, *Sporobolus asper*. A, B, and C denotes the varying results that would have been found if species were not replicated and conclusions were based on comparisons of single exotic-native species pairs.

conduct the experiment a second time. Thus, we are attempting to determine if exotics differ from natives, but only at this site. Mean aboveground productivity (peak biomass) was 813 g/m^2 for exotics and 524 g/m^2 for natives, and this represents a highly significant difference ($F_{1,15} = 49.1$, $P < 0.001$). This represents a 55% increase in growth overall in exotics over natives. There was also a large amount of variation among species within native-exotic type ($F_{6,15} = 29.8$, $P < 0.001$). In order to compare our overall results with what would have been found if we had not replicated species, we back selected several species pairs to point out how variable results could have been. A, B and C in Figure 3 denote single species pairs, which might have been chosen for comparison. In scenario A, if these two species were pre-chosen for comparison, we would have made the correct qualitative generalization (exotic > native), but would have hugely overestimated the difference, i.e., a 428% increase in growth in the exotic. If the species pair in scenario B had been used, an incorrect generalization would have been reached: that exotic species had a 55% *decrease* in growth compared to the native species due the use of a non-representative native species, *Bothriochloa laguroides*. In scenario C, virtually no difference (3%) would have been found between the exotic and native species.

Thus, widely different conclusions would have been reached at this site if we had not replicated species in this study. By including the major native and exotic species from this system in our design, we were able to more accurately estimate the overall impact of exotic species in this system. Exotic species ecology will greatly benefit by developing a more community-level approach that replicates species [24].

Do exotic species affect species diversity-NPP relationships?

There has been much recent interest in whether exotic species are lowering species diversity, and in turn, whether lowered species diversity will affect ecosystem process rates. Although 25% of the earth's surface is reported to be grassland, much of it is human-derived grassland, or grassland that assembled from previously farmed areas. Classical succession theory would predict that a high diversity native system would develop in these systems given enough time. However, this has not been the case. Many areas no longer have an adequate seed source of native species, or even if a seed source is available, native species have a multitude of exotic species to contend with during early community development. A few studies have shown that exotic grasslands tend to have lower diversity than do native grasslands, even many years after abandonment from agriculture [3, 11, 41]. However, in many cases, it is unknown whether this low diversity is caused solely by higher resource availabilities due to fertilizer carry-over [42–45], or if part of the effect is due to characteristics of the species themselves. Christian and Wilson [3] found that former Saskatchewan croplands planted with *Agropyron cristatum* had lower species diversity than adjacent unplanted areas even after many years of abandonment. Foster et al. [41] found that 34 species were largely unable to establish from seed in low diversity grassland patches with strong dominance by exotic grasses such as *Bromus inermis* in Kansas. I have found essentially zero seedling emergence in *Bromus inermis* plots within western Iowa (unpublished data). Less interest has been focused on whether exotic species affect species diversity-ecosystem functioning relationships [46, 47].

   Although most researchers focus on the individual plant or population levels, invasive species establish and grow in communities. Higher aboveground growth rates by exotic species might lead not only to higher productivity, but to a greater rate of local species extinctions [40]. Loreau and Hector [48] outlined a powerful technique for partitioning the net biodiversity effect (i.e., yield of a plant species in mixtures compared to expectations from monocultures) into a selection and complementarity effect. The overall net biodiversity effect compares yield in mixtures to yield in monocultures. The partitioning method then breaks this overall effect into a selection and complementarity effect. These two effects can hypothetically range from negative to positive, and are combined to account for the net biodiversity effect. The complementarity effect combines the effects of niche differentiation and facilitation [48].

A positive selection effect occurs when species that are highly productive in monoculture are the ones over-yielding in mixture. Taken together, these two processes can increase the growth of mixtures above that which would be expected based on that expected from monocultures [48]. Loreau and Hector [48] used this technique on native species assemblages in Europe and found that the complementarity effect accounted for the higher yields in mixtures. The selection effect varied from negative to positive across sites and was less important than complementarity.

In contrast to the results of Loreau and Hector [48], we have found strong selection effects in native-exotic mixtures that are caused by exotic grasses. Polley et al. [49] found that both the selection and "complementarity" effects were negative in three species mixtures with annuals. The exotic *Lolium perenne* was the most important species in explaining negative selection effects. Wilsey and Polley [40] found a large positive selection effect that increased with species richness; a smaller complementarity effect was found only when mixtures were planted with high evenness. The strong selection effect, especially during the first year, was driven mostly by the exotic grass *Panicum coloratum*. Local species extinctions, which started in the second year of the study, were highest in species with low aboveground growth rates and in plots planted with low species evenness [40]. Taken together, these studies suggest that the dynamics of native-exotic mixtures may differ from mixtures with only native species. However, further research with a greater number of study systems is needed to determine how general this phenomenon is. Further monitoring of our experimental plots over many years will be helpful in determining whether local extinction rates are higher in plots as a function of the proportion of exotic species.

Conclusions

I found that results from exotic-native comparisons differed depending on whether a single exotic-native species pair was compared or if replicated groups of exotics and native species were compared. Comparing groups of exotics to natives gave more consistent results, and supported the hypothesis that exotic species have higher aboveground growth rates than natives. Comparing single species gave more widely varying results because of the large amount of variation that exists among species. Of course, this variation among species is important and should be taken into account by land managers dealing with a new invasive species. Management plans will have to be somewhat species-specific in these cases. However, if the goal of a manager or policy maker is to develop a comprehensive general management plan for exotic species at a given site, or to develop ecological theories on exotic species effects, studies with replicated species will be highly useful.

There are other problems with studies that focus on native-exotic species pairs. For one, native species are not always picked randomly. Introduced spe-

cies are often selected for research studies because they are highly invasive and problematic in their area [25]. This is not surprising, but it makes it difficult to decide which native species should be chosen for comparison. Should the exotic be compared to an equally aggressive native species, or to a nonaggressive native? These choices have the potential to greatly impact the conclusions that are reached [25]. By focusing on the overall effects (i.e., mean of several species responses) of exotic species, the biases from individual ("outlier") species are likely to be lessened. Thus, by replicating species, we may be able to increase the predictive power of invasive species ecology.

Finally, in addition to finding mean growth rate was higher in exotics than in natives in monocultures at our study site, we also found that exotic species can have especially large effects on productivity in mixture [40]. The higher growth rate of exotics in mixture [40] is potentially very important because it 1) may partially explain why exotic species are commonly associated with lower species diversity (i.e., exotics are causing diversity loss), and 2) could lead to altered ecosystem process rates. These issues deserve further study.

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Residence time determines the distribution of alien plants

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Introduction

Determining which biological traits enable a species to become invasive has been a major objective in invasion ecology [1–5]. Part of the theory relies on comparisons of large species sets; such studies attempt to identify the factors that contribute to the probability that a species will be introduced to a region [6] and become naturalized or invasive [7–9]. It has been shown that different factors are of different importance at particular stages of the invasion process [6, 10]. Recently, sophisticated data on alien floras from around the world have become available in the scientific literature [8, 11–16]. Some biological and ecological traits of invading species were identified as contributing to the success of invasive species, e.g., high fecundity [17], efficient dispersal [18], ability to utilize generalist mutualists [19], ability to evade specific natural enemies [20], small genome size [3], relative growth rate [5] or specific leaf area [5, 20].

However, not only species' biological traits are important. Cultural influence has been recognized as an important factor co-determining the fate of species subsequent to their first introduction to a new area [21, 22]. Recently, it has been emphasized that stochastic effects, which depend on initial inoculum size, residence time, and the number of introduction events (propagule pressure) and their spatial distribution [23] co-determine whether a species becomes invasive. One of the robust emerging generalizations of invasion biology is that the probability of invasion success increases with residence time [24], i.e., the time since the introduction of a taxon to a new area. Residence time represents another dimension of propagule pressure: the longer the species is present in the region, the more propagules are spread and the probability of founding new populations increases [25]. As it is usually not known exactly when a taxon was introduced, the term 'minimum residence time' (MRT) has been suggested and used in the literature [24–27].

Herein, we utilize available data to determine the effect of residence time in plant invasions in detail at two temporal scales. First, the phenomenon is ana-

lyzed for recent invaders, to explore how species reaching the target areas at different times over the last 2–4 centuries perform as current invaders. Second, a question is raised whether the residence time still affects the current distribution of species that were introduced millennia ago. The results are then discussed in the context of available literature dealing with temporal aspects of plant invasion.

The data

Four data sets representing alien floras or their subsets and containing information on the first record of each species in the area and some measure of their present occurrence were collated: the Azores (38.00 N, 28.00 W; [28]), Czech Republic (49.30 N, 17.00 W; [29, 30]), Hawaiian Islands (22.00 N, 160.00 W; [31]), and New Zealand (41.00 S, 174.00 E; [32]). They were used to assess the effect of minimum residence time (MRT) on the distribution and frequency of species that invaded in the last 2–4 centuries (see Tab. 1 for characteristics of data and how the primary sources were standardized to provide comparable information). In Europe, these species are termed neophytes and defined as aliens that arrived after the year 1500 [33–35].

In addition, information on historical invaders introduced to a target region between the beginning of the Neolithic up to the year c. 1500 (termed archaeophytes, see [35] for definitions) was obtained for two regions: Czech Republic [29] and Great Britain (54.00 N, 2.00 W; [36, 37]). In the New World, a concept analogous to archaeophytes and neophytes is not being consistently used, although early plant introductions are recognized, e.g., by Polynesians to Pacific Islands [31, 38, 39]. These introductions are of minor importance in terms of species number because the vast majority of modern invaders arrived after the discovery of America [40]. In the Mediterranean, the concept of archaeophytes is rather blurred as species that are archaeophytes in other parts of Europe originated in the Mediterranean. Hence in the Azores, Hawaiian Island and New Zealand, all alien species reported in the respective primary sources were considered in analyses, with the exception of early plant introductions to Hawaiian Islands [31].

The present distribution of alien species in studied regions was expressed using two measures: 1) the first measure (termed "range") is related to geographical distribution, expressed by the number of occupied geographical units (mapping squares, islands or regions, Tab. 1) and 2) the second measure (termed "frequency") is related to how frequent the species is in the region regardless of how widespread it is in geographical terms. In original datasets, frequency scales are based on qualitative assessment or estimates of the number of localities (Tab. 1). The number of herbarium specimens given for the New Zealand data was also taken as a measure of frequency as it reflects the number of localities (see [41] for discussion on biases associated with herbarium specimens as sources of data).

Table 1. Summary statistics for regressions of the current distribution of alien plants on minimum residence time (MRT) compiled from the literature. Period indicates MRT of the earliest species' record in the data set. Both the measures of range/frequency and MRT are standardized to zero mean and variance one so that all regression slopes are mutually comparable. For regression slopes, 95% confidence intervals (CI: lower limit – upper limit) are shown; if these overlap, the slopes do not differ significantly at $p = 0.05$. Invasion status follows the definition in Richardson et al. [42] and Pyšek et al. [35]

Region	Measure	Invasion status	n	R^2 (%)	slope	95% CI	F	P	Period (yrs)	Data	Species set	Source
Azores	frequency	casual [1]	210	4.8	0.073	0.029–0.12	10.58	<0.01	414	frequency scale [2]	complete flora	[28]
Azores	frequency	naturalized	700	15.9	0.42	0.35–0.49	131.99	<0.0001	414	frequency scale [2]	complete flora	[28]
Azores	range	casual	210	14.6	0.22	0.15–0.30	35.61	<0.0001	414	number of islands [3]	complete flora	[28]
Azores	range	naturalized	700	34.9	0.61	0.55–0.67	373.89	<0.0001	414	number of islands [3]	complete flora	[28]
Azores	frequency	all aliens	910	18.7	0.43	0.37–0.49	208.6	<0.0001	414	frequency scale [2]	complete flora	[28]
Azores	range	all aliens	910	35.5	0.60	0.54–0.65	500.58	<0.0001	414	number of islands [3]	complete flora	[28]
Czech Republic	frequency	all aliens [4]	691	29.4	0.54	0.48–0.60	286.7	<0.0001	202	frequency scale [5]	complete flora	[29]
Czech Republic	frequency	casual [4]	523	18.0	0.28	0.23–0.33	114.6	<0.0001	202	frequency scale [5]	complete flora	[29]
Czech Republic	frequency	naturalized [4]	168	11.8	0.42	0.25–0.60	22.33	<0.0001	202	frequency scale [5]	complete flora	[29]
Czech Republic	range	naturalized [6]	52	23.6	0.49	0.24–0.73	15.47	<0.001	257	number of quadrats	sample of successful aliens	[30]
New Zealand	range	naturalized [7]	32	39.6	0.63	0.35–0.91	19.68	<0.0001	174	number of regions	sample of woody plants	[32]
Hawaiian Islands	frequency	naturalized [8]	786	28.4	0.66	0.58–0.73	310.38	<0.0001	181	number of herbarium specimens	complete flora	[31]

(Continued on next page)

Table 1. (Continued)

Region	Measure	Invasion status	n	R² (%)	slope	95% CI	F	P	Period (yrs)	Data	Species set	Source
Hawaiian Islands	range	naturalized	786	30.4	0.55	0.49–0.61	341.9	<0.0001	181	number of islands [9]	complete flora	[31]
Great Britain	range	archaeophytes[10]	98	8.3	0.28	0.096–0.48	8.64	0.0041	8000	number of quadrats [11]	complete flora	[36, 37]
Czech Republic	frequency	archaeophytes[10]	136	4.1	0.20	0.038–0.37	5.8	0.0174	7300	frequency scale [5]	complete flora	[29]

1 Species classified as subspontaneous, casual, and very rare relicts from cultivation by Schäfer [28] where classified as casual, others as naturalized.
2 Original qualitative frequency scale was transformed as follows: 1 – very rare, 2 – rare, 3 – scattered, 4 – common, 5 – very common. Mean value was used for species with different frequencies on particular islands.
3 Number of islands on which the species was recorded (n = 9).
4 Neophytes.
5 Estimated on a five degree frequency scale of Clement and Foster [60]: 1 = 1–4 localities; 2 = 5–14; 3 = 15–49; 4 = 50–499; 5 = over 500 localities.
6 A subset of naturalized neophytes with available information on the cumulative number of phytogeographical mapping units (quadrats of 11 × 12 km), from which the species was reported.
7 One species with zero rate of spread was excluded from the original data.
8 Species with the first record dated at 1000 A.D. (n = 24) were excluded from the data of Wester [31].
9 Number of islands on which the species was recorded (n = 9).
10 Residence time of particular species was taken as the middle of the period from which it is first reported in Great Britain [37] and Czech Republic [29].
11 Cumulative number of hectads (phytogeographical mapping quadrats of 10 × 10 km) from which the species was reported.

The two measures may be supposed to be closely related because common species tend to be more widespread; this is supported by data from the Azores where both range and frequency are available for the same set of species and they are significantly correlated (F = 831.6, df 1, 908, P < 0.0001, R^2 = 47.8%). However, they reflect different aspects of the distribution of alien plants: a species may be present in a low number of localities but occupying a large area, or it may be very frequent locally but with restricted overall distribution. For that reason, the two distribution measures were analyzed separately for those regions where data were available. Indeed, the results reported below indicate that using range and frequency, as defined for the purpose of the present paper, provides different results with respect to MRT.

Where information on the invasion status [35] was given or could have been inferred from unequivocal criteria (Tab. 1), alien species were classified into naturalized and casual, using the approach of Richardson et al. [42] and Pyšek et al. [35].

Statistical analysis

Where appropriate, the effect of minimum residence time (MRT) was evaluated by ANCOVAs, using a standardized measure of distribution or frequency (Tab. 1) as the response variable, standardized MRT as a covariate, and region or species group classified according to invasion status (Tab. 1) as factors.

For the Czech flora, where the effect of species traits together with the effect of MRT on the occurrence of alien species was evaluated, the standardized frequency was regressed on four standardized covariates (MRT, maximum plant height, start of flowering and propagule size) and five factors (introduction mode with three levels: accidental and deliberate either for ornamental or utilitary reasons; origin with three levels: America, Asia or Europe; life history with four levels: annual, biennial, perennial or woody plants; Grime's strategy with eight combinations; predominant dispersal mode with four levels: no special vector, water, wind or animals; data taken from [29]). In these analyses, minimal adequate models (MAMs) were determined, where all explanatory variables (factors and covariates) were significantly (P < 0.05) different from zero and from one another and all non-significant explanatory variables were removed. This was achieved by a step-wise process of model simplification, beginning with the maximal model (containing all factors, interactions and covariates that might be of interest), then proceeding by the elimination of non-significant terms (using deletion tests from the maximal model), and retention of significant terms [43]. To prevent biases to the model structures caused by correlation between variables, model simplifications were made by backward elimination from the maximal models by using step-wise analysis of deviance tables [44]. The results obtained were thus not affected by the order in which the explanatory variables were removed in the step-wise process of model simplification. The

appropriateness of the models was checked by plotting standardized residuals against fitted values, and by normal probability plots.

Path analysis [45] was used to explore the inter-relationship between the species distribution, MRT, and the rate of spread. This enabled an assessment of relative direct and indirect effects by which the MRT contributed to the current distribution of alien species through the rate of spread. An appropriate path model was suggested by the regression analysis of the species distribution measures, MRT, and the rate of spread. To achieve a comparable influence in absolute values, as with the minimal adequate models, each parameter was standardized to have a zero mean and variance of one.

Distribution of recent invaders is largely determined by residence time

For the three regions where data on complete alien floras were available (Azores, Czech Republic and Hawaiian Islands), there was a steady influx of alien species over the last two centuries (Fig. 1). Fluctuations in the pattern of increase in species numbers over time among regions usually reflect changes in research intensity or publication of important floral works [31] but sometimes can be interpreted by historical circumstances. That historical events markedly influence the immigration of alien plants into a region was
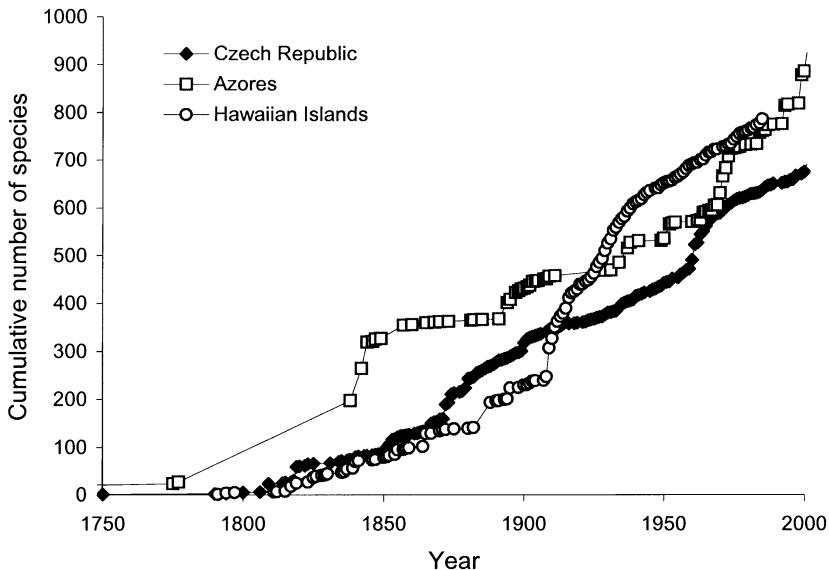
Figure 1. Temporal pattern of invasion into the three regions analyzed in the present study. Cumulative number of species reported up to a given year is shown for the Czech Republic (n = 691; time scale: 1750–2001, data: [27]), Azores (n = 910; 1589–2001; [26]) and Hawaii (n = 786; 1791–1985; [29]). See Table 1 for details on data sets.

documented for Taiwan. In this country, there was a clear acceleration of records of alien species about ten years after political events in 1940s to 1960s, which were associated with massive immigration of Chinese from the mainland [27].

Of the three regions shown in Figure 1, the increase in records of alien species is most regular for the Czech Republic. A previous paper [6] showed that the record of cumulative species numbers over time in this country was not significantly affected by research intensity which has been quite high since the beginning of the 19th century and fairly steady over the last 50 years or so [29, 46]. In any case, Figure 1 documents that alien species differ in their residence time and that the three data sets provide a reasonable basis for evaluating the effects of residence time on the current distribution of alien species in these regions.

Range and frequency

For all data sets, a significant relationship between the range/frequency of aliens and their MRT was found, and most models are highly significant. The percentage of variation in the data explained by MRT varies between 4.1 and 39.6, with higher values reached where complete data sets including both groups of aliens, i.e., naturalized and casual, were considered (Tab. 1). This can be regarded as strong evidence that residence time is an important factor affecting the range and frequency of alien species in various regions, including examples of continental (Czech Republic) and island floras (Azores, New Zealand, Hawaii) from Old (Azores, Czech Republic) and New World (Hawaii, New Zealand). The same relationships are indicated for complete alien floras and their subsets (Tab. 1). Additional evidence for a close relationship between the number of reported localities of alien species and MRT comes from literature data on naturalized grasses in Venezuela ($R^2 = 63\%$, n = 111, P < 0.001; [23]) and naturalized taxa of Fabaceae in Taiwan ($R^2 = 23\%$, n = 48, P < 0.01; [26]). The latter result can be compared with those obtained for alien representatives of the same family in the Czech Republic, where the number of current localities is also significantly related to MRT ($R^2 = 50\%$, n = 56, P < 0.0001; data from Pyšek et al. [29]). Rejmánek et al. [23]), using the data on alien plant species recorded in five north-western states of the USA, also found a significant dependence of the number of occupied counties on the minimum residence time ($R^2 = 18\%$, n = 132, P < 0.001). Finally, even for as few as seven invading plants in Kenya [47], the number of herbarium specimens highly significantly depended on the species' residence time ($R^2 = 82\%$, n = 7, P < 0.01).

Available data are too scarce to allow a rigorous statistical analysis of detailed patterns, but some conclusions can be drawn from comparing the statistical parameters of regressions summarized in Table 1. Before this can be done, some theoretical considerations need to be outlined, that is what can be

inferred from the statistical regression relationships and how do they relate to residence time? Three parameters of the regression can be used for comparisons. First, the slope of the regression line indicates how suitable the recipient region is for invasions; the higher the slope, the more distributed alien species with the same MRT will be. Since all slopes were standardized (zero mean, variance one; Tab. 1), the slopes obtained for different group of taxa and regions are mutually comparable. Second, the proportion of explained variation (R^2) is another parameter and indicates how important MRT is in determining the outcome of invasions. R^2 parameters from linear regression models with the same number of explanatory variables and the same transformation can be directly compared with each other [48]. Whether an invading species will be successful in a new region depends on a complex interplay of numerous factors, that include traits of invading species, interaction with native biota, constraints imposed by existing communities, environmental variables such as climate and disturbances, but also chance and timing [19, 49–51]. The more important MRT is relative to other factors, the higher the proportion of variation it explains. A non-significant effect of MRT would indicate the completely overwhelming effect of the other factors, hence when the species was introduced would not affect its chances to become naturalized or invade. Third, the intercept with y axis for MRT = 0 refers to the start of the spread; the higher it is, the earlier the invasion started.

The data summarized in Table 1 allow for comparison with respect to the invasion status (Pyšek et al. [35]) and invaded region. First, it is plausible to compare the subsets of naturalized and casual species within each data set as the measures used to express the species' occurrence are the same. In the Azores using the range as a measure (Fig. 2), naturalized species invaded earlier than casuals, as indicated by a significant difference (F = 114.0; df = 1, 907; P < 0.001) between intercepts, and their range increased with MRT at a faster rate than that of casuals since the slopes were significantly higher for naturalized than casual species (F = 36.62; df = 1, 907; P < 0.001). Minimum adequate model (MAM) describing this pattern explained 43.1% of variance (F = 228.7; df = 3, 906; P < 0.001). Lower values of regression slopes for casuals compared to naturalized species reflect the fact that the latter generally occupy a wider range. If frequency is used as a measure, the results are the same, i.e., naturalized species invading earlier (F = 190.4; df = 1, 908; P < 0.001) and increasing their frequency with increasing MRT faster (F = 117.1; df = 1, 908; P < 0.001) than casuals (MAM: 29.7%; F = 192.1; df = 2, 907; P < 0.001). However, unlike the former model, casuals do not increase their frequency with MRT, as indicated by the slope from this relationship not being significantly different from zero (F = 1.34; df = 1, 907; NS). Comparison of the two measures available for the Azores, i.e., the number of occupied islands (as a proxy for range) and species frequencies, seems to indicate that while in naturalized species both range and frequency increase with MRT, for casual aliens this is true only for range but not for frequency. This is in accordance with the characteristics of both species groups; casuals are often
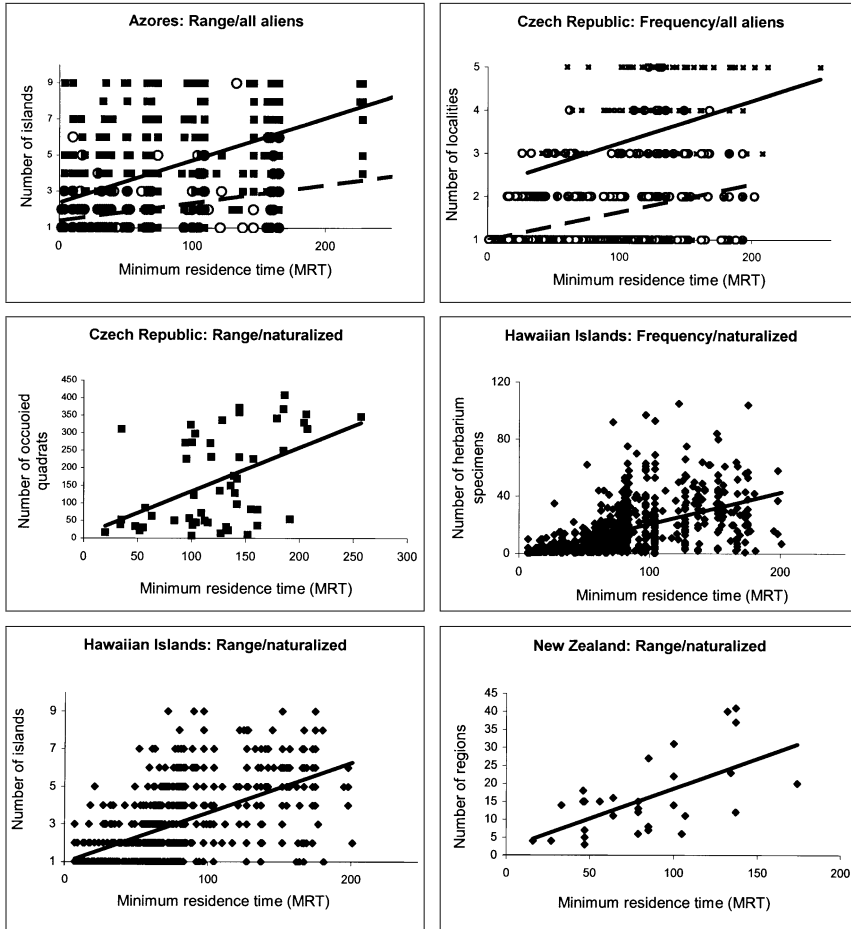
Figure 2. Examples of relationships between frequency and distribution range of alien species and minimum residence time (MRT, in yrs). See Table 1 for parameters of standardized relationships. Empty circles and dashed line refers to casual, solid squares and solid line to naturalized species on figures referring to all aliens.

rare species that do not persist in the wild without repeated input of diaspores by human activities [42]. Obviously, the longer the casuals are present the more islands they colonize but the propagule pressure might have been too low to ensure simultaneous increase in frequency; regardless of how long they have been present, their frequency is on average the same. This suggests that for casuals "being at the right place at the right time", i.e., earlier than others, manifests primarily into a better chance to achieve a wide range but not to become more frequent.

The pattern is different in the Czech Republic, where only frequency is available as a measure. Naturalized species again invaded significantly earlier

than casuals (F = 250.9; df = 1, 688; P < 0.001) and the number of localities they occupy increased with MRT at a faster rate than that of casuals (F = 250.9; df = 1, 688; P < 0.001). In total, 54.6% of variance is explained by MAM (F = 275.0; df = 3, 687; P < 0.001). Unlike in the Azores, casual species that are present for a long time have higher frequencies than those that arrived early. As the measures of frequency are very similar for both regions (Tab. 1), the difference does not seem to be an artefact of the way the data were recorded. It may be hypothesized that differences between both regions, namely in propagule pressure, which is higher in a densely populated mainland region with intensively managed landscape and developed industry [46], are responsible for the observed difference. That might explain why casuals increased their frequency with increasing MRT in the Czech Republic but not in the Azores.

Second, two comparisons are possible *among regions*. Four data sets provide information on the range of naturalized taxa (Tab. 1), which significantly increased with increasing MRT (MAM: 32.9%, F = 872.0; df 1, 1778; P < 0.001). In the Azores, Czech Republic, Hawaii and New Zealand (the latter based on a subset of woody plants only), neither the start of invasion (F < 0.01; df = 3; 1775; NS) nor the rate of increase in range with MRT (F = 0.67; df = 3, 1778; NS) significantly differed among these regions.

Measures of frequency are available for complete alien floras (including casual species) of the Azores and the Czech Republic (Tab. 1). Both regions were invaded at the same time (F < 0.01; df = 1, 1598 P < 0.001) but the rate of increase in frequency was significantly (F = 6.09; df = 1, 1599; P < 0.05) higher for the Czech Republic than the Azores.

Invasion status

Residence time affects not only the range and frequency of an alien species but also its invasion status, i.e., whether it persists as casual or becomes naturalized or invasive [42]. These two measures, distribution and status, are closely related (naturalized and invasive species are usually distributed over a wider range and exhibit higher frequencies than casuals) but not necessarily; many alien species are naturalized only locally [29, 52] and some casuals may be quite distributed, but still relying on repeated input of diaspores [35]. Table 2 shows the difference in the mean MRT between alien species classified with respect to invasion status. The pattern is consistent for the three floras (Azores, Czech Republic and New Zealand) and corresponds to that found for the range/frequency. Casual species have significantly shorter mean MRT than naturalized aliens in both the Azores and the Czech Republic, and within the latter region, invasive species have a tendency for a longer MRT than those that are classified as naturalized but not invasive (Richardson et al. [42] and Pyšek et al. [35]). The same holds for New Zealand, where the difference between naturalized and invasive species appears significant (Tab. 2).

Table 2. Mean minimum residence time (MRT) for species with different invasion status in regional floras. Means bearing the same letter within a region are not significantly different at $p = 0.05$ in ANOVA or LSD test. Invasion status follows the definition in Richardson et al. [42] and Pyšek et al. [35].

Region	Invasion status	Minimum residence time			Source
		Mean	S.D.	n	
Azores	casual	57.5 a	65.1	210	[28]
Azores	naturalized	102.8 b	69.8	700	[28]
Czech Republic	casual	76.3 b	51.4	523	[29]
Czech Republic	invasive	140.0 a	41.5	54	[29]
Czech Republic	naturalized (excl. invasive)	126.3 a	47.8	114	[29]
Czech Republic	naturalized	130.7 a	46.2	168	[29]
New Zealand	invasive	106.1 a	31.3	11	[32]
New Zealand	naturalized	63.0 b	37.3	22	[32]

Importance of the residence time relative to other factors

The probability of invasion success increases with residence time [24] but in particular floras, a long minimum residence time does not always correlate with more localities. For example, among Fabaceae in Taiwan several genera have more than one naturalized species with similar MRTs and these species differ in invasion success; some occupy many habitats whereas others have never spread out. Four of the six naturalized species of the genus *Crotalaria* have similar MRTs but the numbers of recorded localities range from four to 70. Wu et al. [26] suggested two explanations: i) the species with more localities might have been spread more efficiently by human activities or, ii) they differ in their invasiveness. As pointed out above, the higher the variation in invasiveness of individual species and the more important the effect of local conditions and recipient vegetation, the less important residence time will be for determining the result of invasion.

To obtain an insight into the role residence time plays relative to other factors, current frequency of alien species in the Czech Republic was related to several life history characteristics that were used as explanatory variables and so was MRT of each species in the data set. The minimal adequate model explained 52% of variance in the frequency of alien species (F = 7.40; df = 28, 197; P < 0.001). Grime's life strategy, area of origin and dispersal mode had a direct effect on the number of localities, while life history and height significantly contributed to the explained variation in interactions with other variables (Tab. 3). MRT did not exhibit a direct effect on the number of localities but significantly interacted with both life strategy and life history. Compared to other factors, the effect of MRT was very strong. Its interaction with Grime's life strategy and species' life history explained 35.9% of variance

Table 3. Significance (F, df, P) of explanatory variables in the minimal adequate model of the frequency of alien species in the Czech Republic when regressed on the minimum residence time together with other species traits (factors are in *italics*, other traits are standardized covariates).

Explanatory variable	F	df	P
Grime life strategy	2.47	6, 203	<0.05
Origin	5.18	2, 199	<0.01
Dispersal mode	3.59	3, 200	<0.05
(*Grime life strategy*) × (minimum residence time)	2.49	6, 203	<0.05
(*Life history*) × (minimum residence time)	4.03	3, 200	<0.01
(*Grime life strategy*) × (height)	2.86	7, 204	<0.01

(F = 14.52; df = 10, 207; P < 0.001), while all species traits not including MRT together explained only 16.1% of variance (F = 3.62; df = 18, 215; P < 0.001). This can be considered as a robust evidence of the overwhelming effect of the residence time on current pattern in the distribution of alien species. It must be kept in mind that the results reported here concern a single region, but given that the simple regression of frequency on MRT for this data set is well within the range of values found for other models summarized in Table 1, it might be of general validity.

Data on naturalized aliens of the Czech Republic allow another view on the relative importance of MRT. Williamson et al. [30] give the maximum rate of spread for a subset of species that were found to have a straight section on a logarithmic plot of the cumulative number of quadrats over time. The rate of spread of an alien species in the invaded region is constrained by environmental factors, biological and ecological barriers as well as the resistance of local plant communities to invasion; hence the variation in this parameter reflects the relative importance of these factors. Multiple regressions, relating the distribution range to both explanatory variables yielded a significant relationship (F = 7.39; df = 2, 24; P < 0.01) and explained 38.1% of the variance. Both explanatory variables, i.e., the MRT (F = 14.16; df = 1, 25; P < 0.001; R^2 = 36.5%) and the rate of spread (F = 8.87; df = 1, 25; P < 0.01; R^2 = 22.9%) were significant and contributed to the current distribution range of naturalized aliens. Path analysis, a convenient tool for evaluating the relative effect of these two factors (Tab. 4), revealed strong direct effects of MRT, a positive one on range (b_2) and negative on the rate of spread (a_1). The earlier the species arrived, the wider range it occupies, and the later it arrived, the more slowly it has been spreading. When summing the positive direct and negative indirect effect of MRT (the latter manifested via the rate of spread) on range ($b_2 + a_1b_1$), the total effect of MRT on the current distribution appears to be weaker than the total effect of the rate of spread (Tab. 4).

Residence time is therefore less important than the rate of spread in determining the present distribution range of naturalized Czech aliens. This result

Table 4. Path and effect coefficients of the path model of the distribution range of naturalized aliens in the Czech Republic (expressed as the number of phytogeographical mapping quadrats) as a function of MRT and rate of spread (data from [30]). Path coefficients a_1, b_1 and b_2 represent direct effects; a_1 is the regression slope for standardized variables rate of spread and MRT; b_1 and b_2 are standardized regression slopes from multiple regression of range as a function of MRT and rate of spread. Indirect effects are calculated as a product of path coefficients along the links between causal variables and the response variable through other causal variables. Effect coefficients are the sum of direct and indirect effects.

Path coefficients:	
a_1, effect of MRT on the rate of spread (direct)	−0.63
b_1, effect of the rate of spread on range (direct)	0.62
b_2, effect of MRT on range (direct)	0.78
a_1b_1, effect of MRT on range (indirect)	−0.39
Effect coefficients:	
$b_2 + a_1b_1$, MRT on range (total)	0.39
b_1, rate of spread on range (total)	0.62

is in a seeming contradiction with the results provided by the minimal adequate model using species traits, discussed above (Tab. 3). A comparison of these two models indirectly indicates the importance of landscape features and recipient communities [30]. In the minimal adequate model, including species characteristics, some proportion of variation remains unexplained – a part that can be related to environmental variables. Residence time therefore seems to be more important than species traits on their own but if the rate of spread, which can be viewed as a proxy for the complex effect of all factors related to invasions, is included, those factors explain the distribution range of aliens better than the time of their arrival.

Residence time not only represents another dimension of propagule pressure [25] but also integrates culturally-determined processes [53]. With increasing time since the first introduction, the probability also increases that safe sites for establishment appear as a result of natural disturbances and human-made changes in site conditions that both may facilitate invasions. For example, *Ailanthus altissima* in central Europe started to spread vigorously only after rubble sites appeared in destroyed cities after World War II. With increasing time since the first introduction, the probability also increases that the introduced species is propagated by various modes of secondary releases by humans (e.g., deliberate planting or sowings in the wild) that may overbridge gaps between suitable, but not accessible sites [54]. It should be therefore borne in mind that the rate of spread also integrates spreading resulting from ongoing human activities.

Historical invaders: the effect of residence time still detectable

One might expect that in archaeophytes, historical invaders that were arriving for several millennia since the beginning of Neolithic agriculture until the end of Medieval, the effect of the time of arrival would be no longer obvious. The opposite is true: for both data sets providing the information on approximate dates of the first records ([29, 37]; Tab. 1), the current frequency or range of archaeophytes in the region increases with MRT, indicating that the earliest new-comers are more common than those that arrived later (Fig. 3). The rather low proportion of explained variation (4.1 and 8.3%, Tab. 1) reflects that residence time is, compared to other factors affecting the present distribution, of lower importance in archaeophytes than in most data sets covering recent newcomers.

Archaeophytes in the Czech Republic and Great Britain do not differ in the rate at which their distribution increases with MRT (F = 0.41; df = 1, 232; NS). This means that in both regions, MRT has the same effect on the invasion by archaeophytes and neither of the regions appears to have been more suitable for invasion by this group of species. The reason might be that arable land, a typical habitat of archaeophytes [33, 37, 55], is to a large extent similar in different regions and so it is the management that affects the occurrence of archaeophytes [43].

Interestingly, the mean MRT for British archaeophytes is highly significantly lower than that of Czech archaeophytes. On average, the invasion of
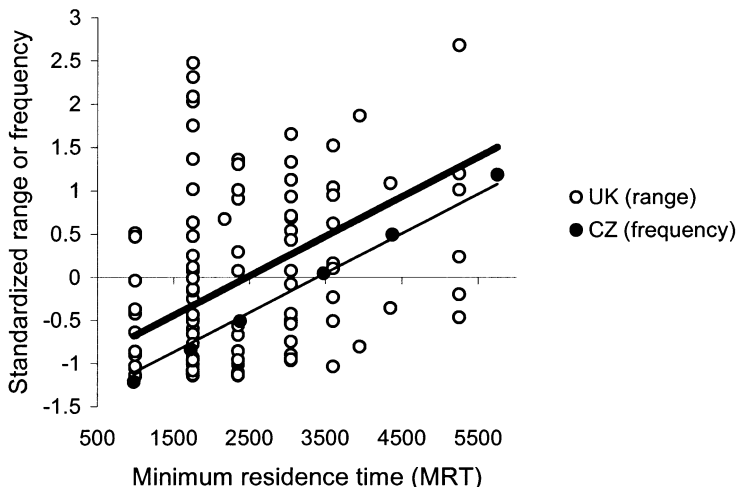
Figure 3. The relationship between standardized current range (UK) and frequency (Czech Republic) of archaeophytes and their non-standardized MRT (yrs). Note that for the average standardized range and frequency (having a zero mean) the MRT is 2,461 years for UK but 3,388 years for the Czech republic; this difference is statistically significant (F = 23.25; df = 1, 232; P < 0.001). The slopes are not statistically different (F = 0.42; df = 1, 232; NS); their values for both range (UK) or frequency (CZ) and MRT standardized are in Table 1.

archaeophytes reached the area of the present Czech Republic by nearly thousand years earlier than that of Great Britain (Fig. 3). This primarily reflects that the onset of Neolithic agriculture in Great Britain (c. 6,000 yrs B.P. [37]) was postponed compared to Central Europe (c. 7,300 yrs B.P. [29]). One might expect the different geographical distances of these regions from the Mediterranean, the area where archaeophytes originated, to play a role. Britain is located further to the northwest, i.e., more distant, but the results do not suggest that there was a delay in invasion by archaeophytes in this region due to the time needed for reaching it. They rather indicate that as Neolithic people brought about not only crops but also weeds [43], the invasion by archaeophytes in both regions started immediately with the beginning of agriculture.

Discussion

The data analyzed above provide firm evidence that residence time is an important factor that should be considered in studies on plant invasions. Our study confirms the conclusions of previous papers; so far, the effect of residence time was highlighted in the literature namely by papers of Rejmánek and his collaborators [23–27]. More evidence is available from New Zealand, where the most widespread invaders are those which were introduced early [24], and Tasmania [23]. Rejmánek et al. [23] concluded that the suggestions made recently by some ecologists, that there is some constant proportion of invasive taxa recruiting from the pool of introduced taxa [40, 56, 57] is unlikely to hold. Rejmánek et al. [23] suggest that the reasonably constant proportion of alien taxa that invade across a wide range of systems is, at least partly, a result of the similar mean residence times of species in alien floras.

It should be noted that the dates of first species records are not in fact the exact dates of invasion, i.e., time at which the species first occurred in the wild after it has been unintentionally introduced or escaped from cultivation. That it is usually not known exactly when this happened is why the term of "minimum" residence time was suggested [24–26]. Nevertheless, this approach is justified: It can be reasonably expected that the more common a species is the more often it is recorded by floristic surveys, hence that common species were first recorded earlier than less common species. For multi-species analyses, the comparability increases if the information on all species in the set is derived from the same primary sources [30, 46]. In general, potential for generalization based on floristic records increases if biases associated with such data are taken into account. In some papers attempts have been made to control for the increasing intensity of floristic research over analyzed periods by involving the information on the dynamics of native species under the same scenario [41, 47] or on the increasing quantity of herbarium collections [57].

The present overview extends the view that residence time is important. We showed that in modern invasions on the time scale of centuries, the longer the alien species are present in the territory the higher their chance 1) to pass suc-

cessfully through the stage of casual occurrence and become naturalized, and 2) to become more distributed and invade over a larger range. The former is documented by higher mean MRT found in naturalized than in casual species (see also [25]), the latter by a significant positive relationships between measures of invasive species distribution and MRT.

In Europe, the effect of residence time is still obvious after several millennia of plant invasions. Not surprisingly, it is less pronounced in archaeophytes than in neophytes but statistically detectable, even though the data used to reconstruct the history of invasions on a time scale of millennia must be necessarily less precise and more biased than reconstructions based on herbaria and published records that are available for neophytes.

Can we compare the effect of residence time between these two distinct groups of European alien species, i.e., archaeophytes and neophytes (historical invaders *versus* recent newcomers)? Simple comparison along the lines of the present paper would suggest investigation of the current distribution of both groups. That archaeophytes are more common than neophytes has been repeatedly documented using the Czech flora [29, 55] and the same can be shown for Great Britain. Number of quadrats (hectads) from which the species is reported from the period 1987–1999 in Preston et al. [36] is significantly higher ($F = 173.3$; $df = 1, 1751$; $P < 0.001$) for archaeophytes (as classified in Preston et al. [37], $n = 231$) than for neophytes ($n = 836$). However, this pattern cannot be interpreted as a consequence of different residence times only. Archaeophytes, mostly weeds of arable land recruited from the Mediterranean area, represent an ecologically distinct group with specific features and differ from neophytes in many respects: life form and strategy and habitat requirements in particular [55]. That they are more common than neophytes is certainly, at least in part, associated with their long-term presence in invaded regions – there is no reason to expect that the principles valid for archaeophytes and neophytes separately, on two different time scales, do not apply for the entire history of plant invasions in Europe. However, given the pronounced difference in habitat affinities of both groups, to decouple the effect that residence time might have had on archaeophytes and neophytes from other factors, both groups should be compared in a habitat where their occurrence overlaps, i.e., arable land. Such analysis is available and shows that the historical associations are very subtle, yet clearly detectable at present: Pyšek et al. [43] found that archaeophytes are common in old crops introduced with the beginning of agriculture, such as cereals, but poorly represented in relatively recently introduced crops (rape, maize), where neophytes are most numerous. These patterns reflect the history of plant invasions in Central Europe. Neolithic agriculture, introduced from the Near East in the 6th millennium BC, brought archaeophytes with crops and, by creating intense and continuous propagule pressure and imposing new agricultural management, facilitated their invasion. By contrast, the crops introduced during the past five centuries and their specific agrotechnical management has supported spreading of other weed species, mainly invaders from overseas. In addition,

archaeophytes respond like neophytes to some variables (climate, seasonal development of crop) and, alternatively, like native species to other variables (increasing agricultural intensification through time, human population density). This indicates that the identity of crop and its introduction history are important factors determining the current distribution of archaeophytic weeds and acting in concert with the residence time of associated weeds.

Finally, a question may be raised: what is the effect of residence time at spatial scales other than those considered in the present paper? For individual invading species residence time is usually not known at local scale. An exception is the study of Müllerová et al. (Institute of Borany, Průhonice, Czech Republic; unpublished observation), who documented, by using historical aerial photographs, 40 years of invasion by *Heracleum mantegazzianum* in the Czech Republic. Knowing when this species appeared in particular localities allowed quantification of the relative importance of the rate of spread and residence time for the outcome of invasion. Both residence time and the rate of spread significantly contributed to the resulting size of invading populations, and the direct effect of the residence time was four times smaller than that of the rate of invasion. However, since the residence time affected the rate of invasion (which was faster in sites where the invasion started later), it exerted an indirect effect on the size of invading populations. Consequently, the total effect of the residence time was about the same as that of the rate of spread (Müllerová et al., unpublished observation).

This is different from the results of path analysis performed on a number of naturalized species of the Czech flora discussed above (Tab. 4) where the rate of spread turned out to be more important than residence time. Both analyses can be only compared with the awareness of the differences in data in mind. Nevertheless, the higher relative importance of residence time found in the study on *H. mantegazzianum* might reflect that 1) the rate of spread is closely associated with a species' invasion potential and *H. mantegazzianum* is one of the most successful European invaders [59]. It is likely that other, less competitive alien species would be more limited by local constraints which would accordingly increase the average importance of the rate of spread on behalf of the residence time. 2) For *H. mantegazzianum*, the rate of invasion was directly measured from aerial photographs capturing the area invaded at particular time intervals which is a more exact measure of the rate of spread than estimation from cumulative increase in distribution over time [30, 32]. Unfortunately, data that would make it possible to compare the patterns at different scales and among species are not available.

Lack of data is a major obstacle to disentangling the intriguing phenomenon of residence time in plant invasions. High quality data sets, using the same classification criteria of the species' invasion status [35] and based on detailed historical information are unfortunately rare. To proceed further, more data are needed to allow for analyses that would make it possible to relate the effect of residence time to environmental characteristics and local conditions of invaded regions.

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The relationship between community diversity and exotic plants: cause or consequence of invasion?

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Introduction

Biological diversity is the modern unifying metric by which the health and status of communities and ecosystems are assessed throughout the world. Diversity is used to identify areas of special conservation concern while threats to biodiversity are the focus of remediation and legal action. Although the greatest threats to biodiversity are typically thought of as being the direct or indirect result of habitat loss and fragmentation, biological invasions follow closely behind. Despite this high priority position, our knowledge of the relationship between invasions and diversity remains relatively early in its development.

The invasion of terrestrial communities by exotic plant species is a major concern for ecologists and natural resource managers. With the increased speed of planned and unplanned movement of species throughout the world and greater rates of disturbance, exotic plants are becoming a larger component of regional floras [1–4]. Furthermore, exotic species already cover vast areas of many community types and sometimes dominate local plant communities. Invasions affect both natural and agricultural systems and cause financial, as well as biological problems in areas of heavy invasion. While there has been an increase in awareness of the problem of exotic invasive plant species, their community-level impacts remain relatively unknown [5–8].

A frequently observed pattern within plant communities is a negative relationship between diversity, typically expressed as species richness, and the cover of exotic plants (Fig. 1A). This simple pattern has been explained by two community-level mechanisms that differ in the cause/consequence relationship between diversity and invasion. In the first mechanism, diversity regulates the invasibility of the local plant community, causing the diversity/invasion relationship. This view comes from theoretical and experimental community ecologists over the past several decades starting with Elton [9] and continues with empirical work (e.g., [10–12]). In the second mechanism, plant invasion results in the reduction of community diversity by driving other species from
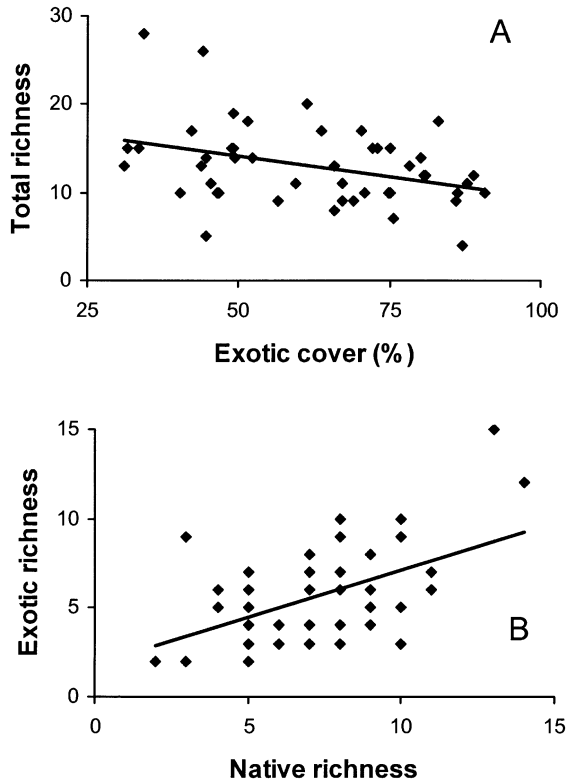
Figure 1. The relationship between invasion and species richness. (A) Total species richness as a function of the proportion exotic plant cover (Spearman rank-sum correlation R = –0.42; P = 0.003) (B) Exotic species richness as a function of native species richness (Spearman rank-sum correlation R = 0.40; P = 0.005). Data were collected as percent cover in 1 m^2 plots as part of the BSS.

the local community. Changes in diversity in this context are a consequence of invasion. Conservationists largely present this view as justification for the control and regulation of exotic plant species [13, 14].

Unfortunately, most studies have only addressed invasions from the cause or consequence perspective, leaving the true nature of the relationship unresolved. Currently, it is unknown whether the relationship between exotic plant invasion and diversity is caused by the local displacement of species by plant invaders, differential invasibilities of areas of varying diversity, or some combination of both. In this chapter, we specifically identify limitations of the current perspective on invasion and propose a conceptual framework from which to address the nature of the relationship between diversity and invasion. The framework aims to abstract the components of this relationship to allow generalization across systems and invaders, thereby enhancing ecological understanding of the causes and consequences of invasion. Several case studies are provided to illustrate the necessity of separating these two disparate perspectives of plant invasions.

Scale and the invasion of plant communities

Before directly addressing the relationship between diversity and invasion, it is first necessary to deal with the issue of scale. A hierarchical perspective of biological invasions reveals three nested scales which interact to determine invasions and their impacts in communities [15]. The coarsest scale, the regional scale, determines the species pool of invaders and residents, setting the potential range of species interactions. The intermediate scale, that of the landscape, determines which species within that larger regional pool will be able to colonize a given habitat based on their presence within the landscape, their vagility and physiological tolerances. The finest scale of interest is that of the neighborhood; the scale at which species interacts. Interactions lead to differential performance of the species, resulting in the realized composition of the neighborhood. At this fine scale, individuals may interact to influence invasion success or to generate the impacts of an invasion. Therefore, the most appropriate scale for studying the diversity/invasion relationship should match the scale at which organisms interact within a system.

The scale of interaction varies widely with the type of system being studied and with the specific interaction involved. Within experimental microcosms or modeling studies of community invasibility, all species within the community interact, or at least have the potential to interact [16, 17]. This is in marked contrast to the condition in terrestrial plant communities, where interactions occur at neighborhood scales [18, 19]. Typically, only plants with canopy or root overlap have the potential to interact. For example, two herbaceous plant species may compete strongly when in close proximity, but would have no effect on each other when separated by even a few meters. For this reason, the total number of plant species in an entire community should have no bearing on the overall invasibility of that community. Rather, fine-scale, within-community patterns of diversity may determine neighborhood invasibility. What constitutes a neighborhood in a particular system should parallel the scale at which organisms interact, probably from 10 cm^2 or less for small plants and emerging seedlings to 50 m^2 or more for large canopy trees.

Plants in terrestrial ecosystems are immobile and compete locally for largely immobile resources such as light and soil nutrients. This leads to the development of heterogeneity in local competitive environments, even within sites heavily invaded by an aggressive exotic species. This interaction heterogeneity explains why plant invasions rarely, if ever, directly lead to the loss of a species from an entire community. Species may be lost from areas directly impacted by an invasion, but will persist in spatial refugia not dominated by the invader (e.g., [20–22]).

While competitive interactions dominate the ecological literature on invasions [23], there are several other direct and indirect mechanisms through which plant invaders could interact with the resident community. These include allelopathic interactions [24–26], associational defenses [27], influences on nutrient dynamics [28, 29] and alterations of soil biotas [30]. Similar

to competitive interactions, all of these interactions function at relatively fine scales.

Scale emerges as a critical variable when assessing apparent conflicting relationships of diversity and invasion published in the literature. At regional scales, the relationship between exotic and native species richness is often a positive one [4, 31–34], while at fine scales within sites, the same communities may show a negative correlation between exotics plants and native species richness [32, 33, 35]. Diversity at regional scales is less determined by species interactions and more the result of changes in abiotic factors such as disturbance rate or productivity [36, 37] or variation in historical, evolutionary and biogeographical influences [38]. Native and exotic species appear to respond to this regional variation in abiotic conditions in a similar manner [4, 19, 34, 39, 40], resulting in the positive spatial associations at coarser scales.

Overall, community-level controls on invasion must function through local processes of interaction with the resident community. Likewise, the majority of impacts on the community would be expected to be manifested at fine scales that match the scale of species interactions. These local dynamics are nested within the regional context that determines the pool of native and exotic species and the availability of species to colonize a particular site (i.e., propagule pressure). Throughout the remainder of this paper, we will focus only on fine-scale causes and consequences of plant invasion.

Cause: diversity and the regulation of community invasibility

Interactions between invading species, the existing plant community and microhabitat conditions influence the ability of an exotic plant species to invade a site. Within plant communities, areas with lower diversity are often thought to be more susceptible to invasion than relatively species-rich areas [9, 39, 41–44]. This is because species-poor microsites may have more available resources, or vacant niches, allowing a specific exotic plant species to become established [9, 10, 45]. Experimental evidence suggests that higher diversity areas use resources more completely, leaving few colonizable niches [10, 12, 19, 45]. Local resource availability has been found to be critical in determining neighborhood invasibility in many studies [12, 46–49], and may represent a general explanation for fine-scale invasibility patterns [48, 50]. Alternatively, it may not be the diversity, but the composition of the neighborhood that regulates invasibility [11, 22, 51, 52]. Higher diversity areas would be more likely to contain competitively dominant species through sampling from a limited species pool [10, 11, 53] and are thus more likely to resist invasion. This is commonly referred to as an ecological sampling effect [53].

The diversity-invasibility hypothesis has been tested in herbaceous communities with contrasting results. Neighborhoods of higher diversity were more resistant to invasion in some studies [10–12, 19, 52] while other studies found higher diversity plots to have equal or greater invasibilities [4, 32,

33, 51, 54–56]. Positive associations between diversity and invasion suggest that the same basic factors which make a microsite able to support many native species also make them able to support a diverse group of exotic species [4].

The quantity of evidence currently available on the diversity–invasibility hypothesis shows that diversity can regulate neighborhood invasibility in some systems, but that the directionality of this relationship appears to vary. The more important research themes now become the determination of the conditions under which diversity regulates community invasibility and the development of conceptual models that explain the variation in the direction of this relationship. Neighborhood diversity appears to limit the establishment of invading plant species in communities dominated by equilibrium dynamics, particularly in those communities strongly structured by competitive interactions such as in the nutrient limited sites studied by Tilman and colleagues [10, 45, 57–59]. Sites dominated by non-equilibrial dynamics, such as successional sites or those with otherwise high species turnover, appear to have a positive association between invasion and fine-scale diversity [19, 32, 35, 55]. However, this dichotomy may be artificial, as invasibility has been predicted to respond unimodally along diversity gradients when both facilitative and competitive interactions structure the community [23, 55]. The directional responses seen in many systems may therefore represent the extremes of the gradient, or situations where either positive or negative interactions dominate.

The variation in the diversity–invasibility relationship across systems may also reflect the short-term nature of the majority of studies. Our ability to make reliable predictions about ecological systems is often limited by the temporal extent of available data [60]. The lack of predictive models in invasion biology may therefore be linked with the lack of sufficient long-term data.

Consequence: invasion impacts on diversity

While exotic plant invasions alter plant community composition and structure, the direct effects on diversity patterns are largely unquantified. Unfortunately, the vast majority of studies are observational, with little ability to assess the direct impacts of plant invasion on diversity [8]. It appears that exotic plant invasions are associated with a decrease in the number of species in natural communities [6, 61–64]. However, this pattern is clearly not ubiquitous across all plant communities [65–68].

Differences among studies in the measure of invasion complicate attempts at generalization. Studies that relate richness of exotics to native diversity often find a positive correlation [66] while studies that assess invasion by cover or dominance tend to find negative associations [61, 69, 70]. Within a single community, it is possible to have both a positive association between native and exotic species richness and a negative association between total richness and exotic plant cover (Figs 1A and 1B).

Negative associations between exotic plant cover and community diversity have been used to suggest that invading exotic species do not merely fill vacant niches in natural communities [10], or replace native species one-for-one, but that they displace species disproportionately from the community, lowering diversity. Field studies of invasive exotic plants often cite this hypothesis, either as a correlation or as anecdotal information. However, this direct interaction has rarely been experimentally tested.

The competitive displacement of native plant species is often used as justification for the eradication of individual exotic species, although the perceived relationship with diversity may not exist [13, 67, 68, 71]. Many, if not most exotic species have only trivial impacts on community structure, becoming minor components of the plant community that increase regional species diversity [5, 72]. Problematic exotic species, those which become widespread and locally dominant, are generally found to be competitively superior to native species in two-species competition experiments [73–75]. However, it is not known whether exotic species are, on average, competitively superior to native plant species, which would be necessary to result in lowered diversity across a community. Increases in richness or species performance following invasive species removal suggest that competitive displacement may result from some invasions [76–83].

An excellent example of exotic plant invasion impacts is that of *Lonicera maackii*. This species, a bird-dispersed shrub native to Asia, has become widespread throughout the eastern United States [84]. It has become a problematic invader of deciduous forests, particularly second growth and disturbed forests [85–87] and often dominates the forest understory in heavily invaded sites. Observational data show that this invader is associated with declines in tree seedling abundance and in the abundance and diversity of the herbaceous understory [63, 83, 87]. The mechanisms behind this association have been tested experimentally, showing that *L. maackii* directly reduces the growth and fecundity of herbaceous annual and perennial understory plants [77, 78, 83] and competes with tree seedlings [88, 89]. Indirect impacts of *L. maackii* include protection of tree seedlings from deer browse [88] and increased tree seed predation by rodents (S. J. Meiners, unpublished data). Taken together, this suite of studies documents both patterns indicative of invasion impacts and documents direct and indirect interactions that generate these patterns. This is one of the few species invasions whose community-level impacts have been characterized mechanistically. However, beyond this species' connection to relatively open forest stands and gaps [85, 87], community-level controls on invasion success are unknown.

Cause *versus* consequence: invasibility *versus* impacts

Clearly, the mechanism(s) that result in the often-observed relationships between exotic plant invasion and community diversity are unclear in current

ecological literature. Associations between diversity and exotic plant cover have been used as evidence for both the regulation of neighborhood invasibility by diversity and the impacts of exotic plants on resident species. These two pathways of interaction must be separated conceptually to assess the relationship between exotic plant invasion and community diversity. These contrasting mechanisms can be formalized into two hypotheses, the *invasibility hypothesis* and the *impact hypothesis* (Fig. 2). The hypotheses differ in the role of diversity – as a regulator of exotic plant invasion or as a response to invasion. These two mechanisms also function at significantly different ecological stages, one at the establishment phase of the invader, the other once an invasion has successfully occurred and the species begins to spread within a site.

In the invasibility hypothesis, the diversity of the neighborhood serves as an ecological filter that determines the invasion success of an exotic species. While there is no *a priori* reason to expect a single direction for the outcome of this interaction, most studies have focused on the inhibition of invasion by diversity. This reflects the overwhelming focus on competitive or other nega-
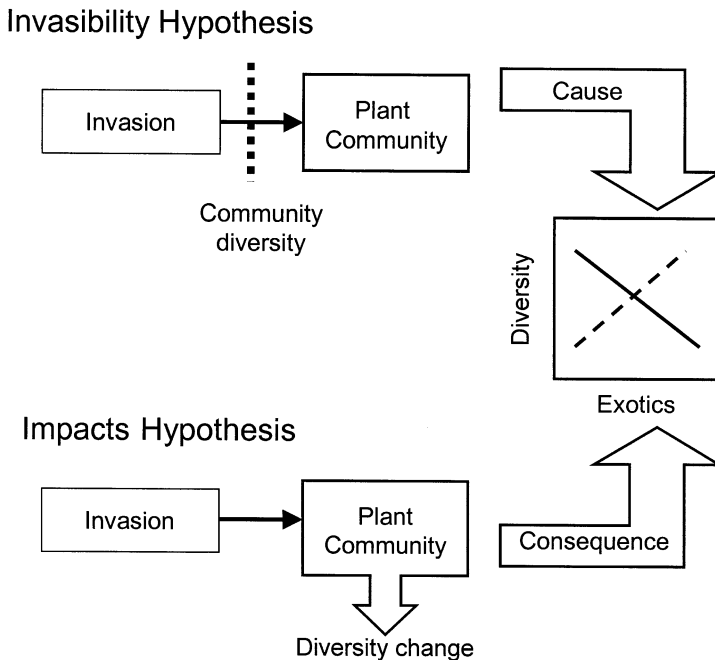
Figure 2. Schematic model of the two major hypotheses explaining the relationship between community diversity and exotic plant invasion. The invasibility hypothesis states that community diversity regulates the invasion of exotic species into a community, generating a relationship between diversity and exotic plant invasion. The impact hypothesis states that following invasion by exotic species, interaction between the resident community and the invader lead to changes in community diversity. As there is no *a priori* assumption of directionality for this relationship, both positive and negative diversity/invasion relationships are shown.

tive interactions in the exotic species literature [23]. Under this hypothesis, early seedling establishment and performance of the exotic species would be expected to vary with neighborhood diversity.

In the impact hypothesis, exotic species invade a neighborhood and subsequently interact with species residing within the community, resulting in altered diversity. This is typically thought to occur via the invader competitively displacing species currently in the area [8, 64, 77], or by preventing the establishment of other species [11, 22]. Species displacement would result in a reduction in neighborhood diversity if individual exotic species, on average, displaced more than one resident species. While positive interactions between invaders and other species have rarely been documented, the invasion of a species that facilitates the growth or establishment of other species may directly increase neighborhood species richness.

Both invasibility and impacts processes may generate similar changes in neighborhood diversity in association with exotic plant species, but would differ mechanistically. The diversity/invasion relationship of different exotic species may be explained by different mechanisms, or both may simultaneously operate to determine the relationship of an invader to community structure. The diversity/invasion pattern exhibited by the plant community will be the net effect of these two independent processes. It is also possible that species that exhibit no associations with neighborhood diversity may actually have counteracting invasibility and impact relationships.

Finally, as null a hypothesis, there may be no mechanistic relationship between exotic species and diversity. Diversity and invasion may both respond to similar extrinsic factors that generate associations without direct interaction. For example, microsite conditions that generate spatial patterning in diversity may also favor the establishment of an exotic plant species. However, this would probably lead to fine-scale variation in dominance of individual exotic species with variation in microsite conditions. Since many exotic species tend to be problematic across many community types and at regional scales, this alternative seems unlikely. Variation in local seed input may also generate positive associations between exotic and native species, even when higher diversity results in lower invasibility [19]. Because most plant communities are seed-limited [10, 90, 91], and exotic plant species tend to be extremely vagile [44, 92, 93], exotic species may be the first plants to invade a disturbed area, resulting in low diversity with high invasion. In this situation, the relationship between invasion and diversity would disappear as the less vagile native species invade [94].

The variation in the direction and strength of the relationship between exotic plant invasion and diversity in the ecological literature may partly result from the lack of a useful conceptual framework that separates out the invasion process from subsequent species interactions. Most observational and experimental studies artificially integrate both mechanisms into a single assessment of invasion, therefore obscuring the species interactions underlying the community dynamics associated with the invasion.

Case-studies: *Lonicera japonica* and *Rosa multiflora*

The limited temporal duration of most studies constrains our understanding of the causes and consequences of exotic plant invasions [5, 8, 66, 95–97]. While most plant invasions occur over time periods of decades or longer, most experimental studies of invasions are brief, lasting only 1–2 years. Similarly, observational sampling studies frequently only capture a single snapshot of community associations, yielding little information on how these associations developed. Even studies that have incorporated time spans matching the scale of invasions frequently have only a few sample periods, typically only before and after invasion [65, 97–99] and do not capture the complex dynamics during the intervening period.

To explore the utility of our conceptual framework for understanding the community dynamics that shape the relationship between exotic species and diversity, we use long-term data of species invasions in abandoned agricultural land from the Buell-Small Succession Study (BSS). This study has recorded the presence and percent cover of all species occurring within permanent plots in 10 abandoned agricultural fields since 1958 [100]. The fields vary in crop prior to abandonment (hay *versus* row crops) and in the year of abandonment (1958–1966). Each field contains 48, 0.5×2.0 m plots that were sampled annually from 1958–1976 and in alternate years since 1976. This long-term data has provided a unique opportunity to study the function of exotic plant species within dynamic communities [22, 72, 94]. Individual plots can be followed over the course of an invasion to simultaneously determine the factors that regulate community invasibility and the community impacts of the invasion [72].

The two most common and abundant exotic species within the study are *Lonicera japonica* and *Rosa multiflora*. We use these two species to examine patterns of invasion and impacts on species richness over the course of the invasions. Both of these species are problematic at a regional scale and are typical of the plant species that are the focus of diversity/invasion studies in that they are widely believed to be detrimental to native ecosystems [14]. *Lonicera japonica* is a bird-dispersed liana that is native to Asia and has become widespread throughout the eastern United States [101]. This species has been shown to compete strongly with native tree species [74]. *Rosa multiflora*, a bird-dispersed shrub, also native to Asia, was purposefully introduced as a living fence and as erosion control [102].

We analyzed data from years 5–15 and 10–20 post-abandonment for *L. japonica* and *R. multiflora*, respectively. These periods represent the beginning and midpoint of the species invasions within the study (Fig. 3). We documented three basic patterns for each species to assess the relationship between invasion and diversity: 1) the relationship between invader cover and species richness as a general pattern at a single point in time, 2) the relationship between species richness and invasibility, and 3) the relationship between invasion and subsequent species loss.
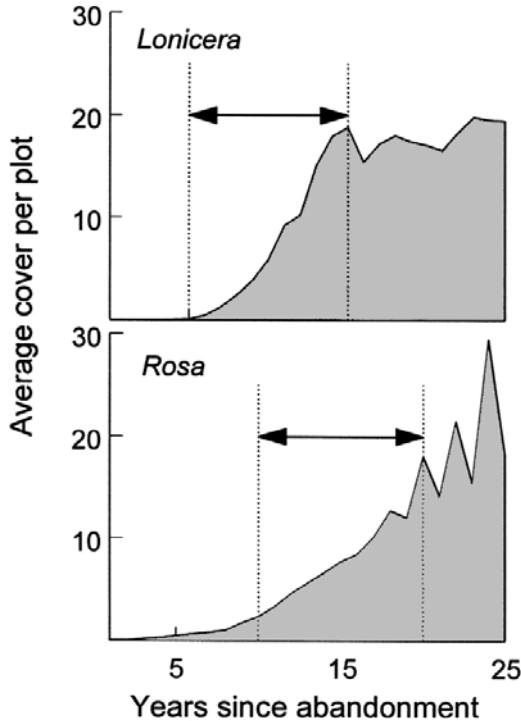
Figure 3. Temporal patterns of cover for *Lonicera japonica* and *Rosa multiflora* during succession within the BSS data. Arrows indicate the time span over which community dynamics in association with each invasion were assessed.

We determined the associations between total species richness and *R. multiflora* and *L. japonica* cover within plots at the midpoint of each invasion. This analysis is analogous to the one-time community sampling studies frequently conducted to assess the impacts of exotic plant invasion. For both species, there was a significant, negative relationship between the cover of the invading species and the total species richness of each plot (Fig. 4). This relationship by itself does not elucidate any mechanisms that generate the observed pattern, but suggests interaction between the community and the invader.

For all plots that were uninvaded at the beginning of the observation period, we determined the relationship between initial species richness and the probability of subsequent invasion during the observation period for each species. This determines whether the invasibility of plots changes with species richness. For both species, plots with higher initial species richness were more likely to become invaded over the observation period than were plots with lower species richness (Fig. 5). The dynamics demonstrated by these species are in the opposite direction of most theoretical and experimental results, which show negative associations between invasibility and diversity. The
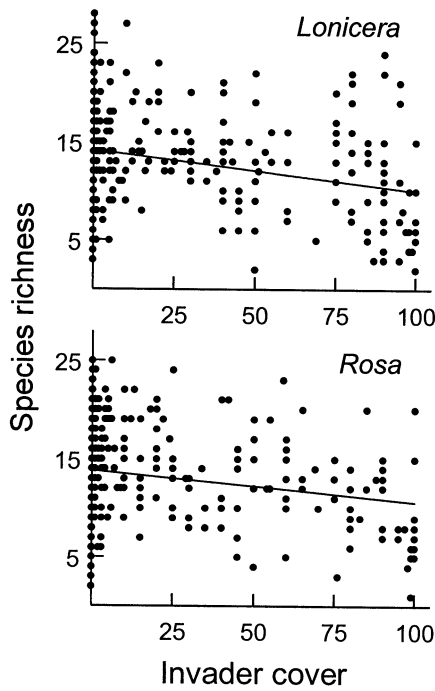
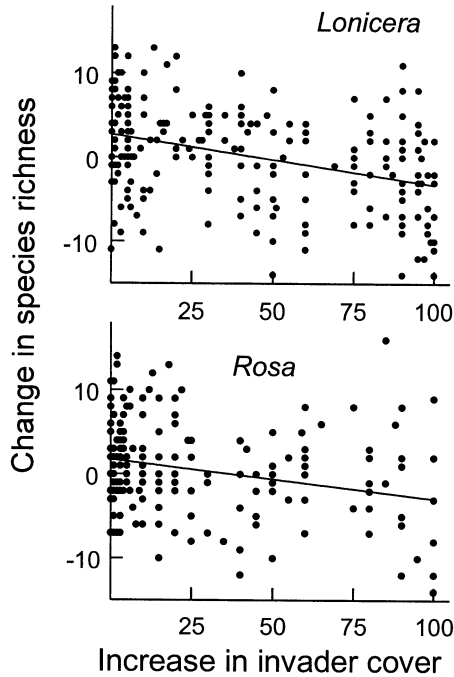Figure 4. General association between invader cover and species richness for *Lonicera japonica* and *Rosa multiflora*. Regression analysis: *Lonicera* – $F_{1,478} = 40.84$; $P = 0.0001$; $R^2 = 0.08$; *Rosa* – $F_{1,478} = 16.86$; $P = 0.0001$; $R^2 = 0.03$.

selective invasion of high richness plots by these two species would tend to generate a positive association between invasion and diversity. Patterns of diversity are transient within the BSS, suggesting that there are no inherent differences between high and low richness plots that may influence invasibility. Invasibility at the neighborhood scale appears to be influenced primarily by stochastic events that generate opportunities for establishment [103], neighborhood species richness, and positive and negative interactions with resident species [55]. Once invasion had occurred, initial species richness did not influence the increase in cover of either species.

Finally, we determined the association between the increase in cover of the invading species and the change in species richness for those plots that were invaded during the observation periods. Change in cover for these two invaders represents increased cover of established individuals and, to a lesser extent, the recruitment of new individuals. This analysis assesses the ability of the invading plant to influence other species within the neighborhood [72]. As the cover of both invaders increased, the change in total species richness of the plot changed from a slight increase in richness over time to a net loss of species (Fig. 6). This shows that species were disproportionately lost from plots that
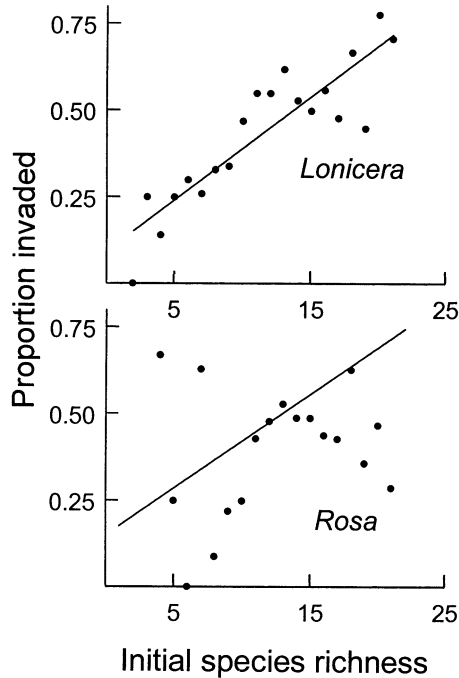
Figure 5. Influence of initial species richness on plot invasibility for *Lonicera japonica* and *Rosa multiflora*. Line represents logistic model predictions, points represent actual proportion of plots invaded where N = 3. Logistic regression analysis: *Lonicera* – $\chi^2 = 7.51$, df = 1; P < 0.01; *Rosa* – $\chi^2 = 4.62$, df = 1; P < 0.05

were heavily invaded, strongly suggesting that both invaders were displacing resident species.

Both invasibility and impact processes interact to generate community structure and dynamics associated with the invasion of these two species. The overall negative association seen in the single-sample data is the net combination of both of these factors. Interestingly, these two processes are antagonistic to each other, as selective invasibility would generate a positive association while invader impacts would generate a negative association. Invader impacts are clearly stronger in both of these cases, leading to the overall negative association even though invasibility partially obscures the impacts of invasion at the community level.

Extensions of separating cause from consequence

There are some interesting extensions of our conceptual framework that suggest invasion may alter community structure at a broader scale under certain circumstances. In cases where invasibility and impacts of an invader are both

Figure 6. Impacts of invasion on species richness for *Lonicera japonica* and *Rosa multiflora*. Regression analysis: *Lonicera* – $F_{1,218} = 34.88$; $P = 0.0001$; $R^2 = 0.14$; *Rosa* – $F_{1,186} = 13.53$; $P = 0.0001$; $R^2 = 0.07$. Analyses were conducted only on invaded plots only to avoid confounding effects of richness on invasibilty.

in the same direction (e.g., low diversity areas are more invaded and invasion leads to species displacement), we would expect to see increased variance in neighborhood diversity across the site. Similarly, in cases where these two processes function antagonistically towards each other (e.g., high diversity areas are more likely to be invaded and there is subsequent species displacement), we would predict an overall decrease in the variance of neighborhood diversity as invasion intensity increases.

Of the three species within the BSS data that show significant species displacement and a positive association between invasion and species richness (*Elytrigia repens*, *Lonicera japonica* and *Rosa multiflora*), only *E. repens* (a grass) had decreased variance with invasion intensity as predicted. Thus, invaded systems may become more homogeneous during the course of invasion. The variation seen among invaders may represent the intensity of interaction between the invader and resident community and the time scale over which these interactions occur. The two species that did not exhibit a relationship dominate systems for much longer and may generate a response as the invasion proceeds. This relationship should be explored in other systems to see whether it is a common consequence of plant invasions.

The value of long-term monitoring of natural plant communities is clearly evident in the above case studies. The non-experimental nature of this and similar studies actually increases the range and breadth of questions that can be addressed with the resulting data, although direct experimental control has been sacrificed. In unmanipulated systems, the types of relationships and interactions that can be addressed are not limited by experimental protocols designed to separate out a small suite of effects. For this simple reason, a study began to document successional dynamics has been very useful in addressing plant invasions and their impacts.

Conclusions

Invasion ecology has suffered from the artificial separation of invasibility and impact processes in understanding the relationship between diversity and plant invasion. By studying these independently functioning stages of invasion in concert, we can gain great insight into the biological causes and consequences of invasions, and develop crucial information for the generation of adequate management strategies. Our conceptual framework provides a structure to synthesize the current body of research, suggests research needed to fill the gaps in understanding and to organize results from future research. The framework is a powerful tool to guide ecological understanding of the relationship between invasion and diversity across systems, species, and scales.

The case studies discussed here clearly show how both the cause and consequence of diversity may operate simultaneously within an invasion to generate the community associations often noted in static studies. Currently, it is not possible to make generalizations about which mechanism is the most important because of the extreme lack of information for most plant invasions. To understand the nature of the relationship between diversity and invasion, both of these processes must be assessed to determine their relative contribution.

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Invasive plants: the process within wetland ecosystems

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Invasion as a process

Expansion of the biogeographic range of organisms is a fundamental reproductive strategy. Clearly expansion occurs where essential energetic resources and environmental conditions and their dynamics lie within the physiological ranges of the organisms and their capacities to adapt and reproduce. An immediate consequence of such spatial expansion is competition for resources among other organisms. Obviously interactions among invasive species can lead to various degrees of competition, depending on the niche requirements of the organisms, and result in displacement of indigenous organisms.

Such diffusion of biological propagules, as Hengeweld [1] puts it, can be radically altered by the activities of humans. Certainly the rates of natural invasion have been advanced spatially and accelerated temporally by human activities. Although the rates and efficacy of introduction of invasive species are altered by human activities, invasions are an integral part of evolutionary processes and will continue regardless of fortuitous or intentional interventions of animals, including humans.

Invasive interactions and competition

The acceleration of invasive species with human activities has raised great concerns because of a multitude of negative biological and economic effects among many different types of ecosystems (see reviews of Cronk and Fuller [2]; Vitousek et al. [3]; Pimental et al. [4, 5]; Mack et al. [6]; and Ehrenfeld [7]). Some 20–30% of introduced species are economic pests and cause major environmental problems. Many accidental and deliberate introductions of agricultural species were imported and cultivated by human immigrants for food, forage, seasonings, medicine, or ornamentals (e.g., [8–10]). Many species escaped from areas of intended use. Growth of naturalized flora and the number of invasive taxa were facilitated by a marked acceleration and increased efficiency of human transportation both inter- and intra-nationally.

Numerous ecological factors encourage or allow invasive species to succeed. Introduced species commonly lack appreciable natural competitors, as is the case with the wetland emergent purple loosestrife (*Lythrum salicaria*). Often artificially or naturally disturbed habitats create altered environmental conditions that favor alien species. Invasion of some highly adaptable alien species can easily out-compete indigenous species. Among wetlands, the water hyacinth (*Eichhornia crassipes*), hydrilla (*Hydrilla verticillata*), and water lettuce (*Pistia straiotes*) possess remarkably efficient physiological and reproductive capacities that facilitate exclusion of competing species [11–15].

Many species have major ecosystem-level impacts. For example, the growth of the wetland tree *Melaleuca quinquenervia* can rapidly alter the topography, hydrology, and water budgets, and these environmental modifications exclude many native species. The zebra mussel, such as *Dreissena polymorpha*, and similar species can decrease biogenic turbidity of shallow waters, greatly increase habitat for aquatic plant growth, and thereby strengthen the linkages between pelagic and benthic processes by their intensive filter feeding activities [16–19]. In spite of many successful invasions, however, most (90–95%) introductions of non-indigenous species fail [20, 21] because environmental variability is too great for existing physiological tolerances of the invasive species.

Major economic repercussions occur and societal values have been lost as a result of species invasions. Aside from wetland crop losses (e.g., rice), invasive species can alter nutrient cycles, alter fish and other aquatic animal community structure, and reduce the recreational and commercial uses of rivers and lakes [11, 22, 23]. Many physical problems emerge from excessive development of invasive species, including increased sedimentation by production and by trapping of particles, interference of water movements, navigational transport, and recreational uses. Excessive developments of invasive aquatic plants have often increased habitats conducive to the development of vectors of human diseases [24]. Among wetland and littoral plants, hundreds of millions of dollars are devoted annually to aquatic plant control of non-indigenous species [4, 5, 25, 26].

Introduction of alien species in wetlands

Discussion here is directed toward the processes that enhance the effectiveness of invasive success. One observes, as has been often described, that about two-thirds of all invaders established in natural wetland vegetation occur in small water-courses, particularly in plant communities of the *Bidens* and *Convolvulus* groups, and in *Azolla, Hydrilla,* and *Elodea* mats. Among aquatic plants and wetland species, the primary means by which habitat expansion occurs is via physical plant fragmentation and clonal vegetative reproduction. The observed pattern of invasion is first of population expansion, then contraction and consolidation of the invasive species, followed by fragmentation of the population and integration within indigenous biota [1, 27–34]. The

expansion is from a high-density core surrounded by peripheral, low-density zones. Expansion from this highly reproductive (sexual or clonal) core is often constrained by resource limitations, such as topography and other biota.

Exotic species are not necessarily superior competitors; they are usually separated by physiological requirements (e.g., deep soil water, nitrate, and light) and could depress abundance and fecundity of exotic annual plants after overcoming recruitment limitations. Exotics may dominate not because they are physiologically better competitors, but rather as a result of prior disturbance and low dispersal abilities [35].

Effects on biological diversity

Major alterations and loss of biodiversity have occurred as invasive species competitively suppress native species populations and alter habitats and ecosystems [36–40]. Invasive species have been involved, often by influencing habitat conditions and availability, among about half of the species now considered rare, threatened, endangered, or extinct [41]. More species diverse ecosystems have greater temporal stability and exhibit positive diversity-productivity relationships with less susceptibility to success of invasive species [40]. Invasion rates increase markedly, however, once invasion progresses and species diversity decreases.

Establishment of non-native species with the expansions of the ranges of a species results in many ecological effects. Suppression of native species occurs through predation, parasitism, disease, and especially competition. Invasive species may hybridize with congeneric native species and thereby alter the gene pool of the native species. Resulting hybrids and the invasive species can displace native species (e.g., *Spartina alterniflora* [42]). Hybridization or altering of selection pressures by changes in habitat can be powerful drivers of evolutionary change. In particular, hybrids can be isolated reproductively from native species, such as by polyploidy, and be highly competitive [42–43].

Competitive interactions

The effects of invasive plants on native species are enormously complex because of the many interactive pathways that can and do occur [7, 44]. Usually exploitative competition (i.e., negative interactions resulting from utilization of resources by a consumer and subsequent limitation of those resources to other consumers) is given as a primary interactive mechanism [45–46]. However, exploitative competition among plants is only one of many interactive mechanisms. Non-exploitative mechanisms (i.e., not involving resource consumption) can occur simultaneously [47–51]. For example, certain invasive species can release chemical compounds that have allelopathic effects on selective species of the indigenous plant community [52]. The native

species may not have had previous exposure to, and sufficient time to develop defensive mechanisms to cope with, the allelochemicals.

One observes at any given time a balance of multiple processes among both positive and negative non-exploitative mechanisms that often can enhance plant growth and competition. In contrast, exploitative interactions are by definition negative. Some parameters, such as increased concentrations of atmospheric CO_2, can impose both exploitative and non-exploitative interactive mechanisms simultaneously, and certainly these interactions vary physiologically among species within the same communities. The balance between these competing processes results in the net direction of effects of invasive species in the receiving ecosystem. The relative magnitudes of these processes are dynamic and constantly changing – as a result, the regulating mechanisms controlling the dynamics and net balance are difficult to quantify [44]. That complexity of shifting dominance of interactive mechanisms in regulating competitive success makes it difficult to develop predictive models to account for variations in the strength of impacts of invasive species on the indigenous communities.

Invasive species clearly impact processes at the ecosystem level. Alterations are induced in nutrient cycling [53–56], hydrology [57], and other processes. Competitive exploitation for light is often a dominant mechanism of interaction, particularly at high fertility and high plant densities. Among aggressive invasive wetland plants (e.g., *Typha, Juncus, Phragmites*, and similar emergent plants), severe shading of incident light (70–90%) is a most effective competitive strategy against native species [58–61]. However, in the early stages of colonization by such invasive plants, shading is not the dominant contributor to the negative effects on the indigenous community. Other factors, such as exploitation of limiting nutrients, can dominate competition [61]. Hence, dominance of exploitative competitive interactions can shift very rapidly spatially and temporally as the dynamics of the species invasion proceeds in a new environment.

A relatively large area of ignorance centers on competitive belowground interactions of invasive plant species with indigenous species. Complex interactions occur among rooting tissues and rhizospheric microflora. The relatively rapid rates of fine root turnover (hours to days) results in both active release of root exudates as well as release of rooting tissue by fragmentation in various stages of degradation with the release of inorganic and largely dissolved organic carbon and nutrients. These nutrients and organic substrates are rapidly assimilated and recycled by soil microflora to inorganic forms more readily assimilable by mycorrhizae and active roots. These two sources of potentially important nutrient regeneration and repeated recycling are very poorly understood and rarely quantified, particularly among wetland plants [7, 49]. It is probable that accelerated aggressive growth of invasive plants owes part of their competitive success to simultaneous active growth of roots with high fine root turnover, root expansions, and efficient nutrient recycling.

A number of studies indicate marked variability in the types and periodicities of organic exudates from fine roots. In the immediate rhizosphere of the soil, plants perceive and respond to the chemical environment of the soil par-

ticles and associated microbes. Although a large range of organic and inorganic substances are exchanged between the roots and soil, plants can quickly modify their rhizosphere in response to environmental signals and stresses [62, 63]. For example, certain plants are capable of rapidly synthesizing, in response to organic elicitors from pathogens, increasing concentrations of soluble and wall-bound phenolic polymer organic acids and esters that function as anti-microbial defenses in the root tissues [64]. Variance in defensive capabilities certainly exists among species, and it is suggested that highly successful invasive plant species potentially have superior capabilities in relation to those of indigenous species.

It should also be noted that anthropogenically altered environmental factors can induce changes in rates of the release and chemical composition of leachates and root exudates from living and senescent tissues. Differences among plant species in growth and biochemical responses to these climatic changes likely confer advantages to many invasive plants that are highly successful in competitive interactions with other species. For example, under elevated atmospheric CO_2 (e.g., double ambient, 720 ppm) growth of many plants can be accelerated, often leading to nitrogen limitation [65]. Increased carbon uptake is utilized in secondary compound synthesis, and lignin and related phenolic compounds often increase appreciably (double). C:N ratios and percentage lignin and total phenolic compounds were 15–100% higher in live and senescent plant tissues in some wetland plants grown on elevated than in ambient CO_2 conditions [66–68]. As these plants senesce and slowly degrade, leachates from those tissues grown on elevated CO_2 concentrations with more recalcitrant organic compounds are degraded more slowly than those grown at ambient concentrations. Similarly, there are indications that the stimulation of growth by elevated CO_2 alters and enhances releases of root exudates and, as a result, the metabolic activities of rhizospheric microbes and coupled nutrient recycling rates. For example, elevated CO_2-grown grasses effected a shift from metabolism of older soluble carbon compounds to more easily degraded exudate compounds [69] or reduced utilization rates of carbohydrates, amides, amines, carboxylic acids, and phenolic compounds [70, 71]. Similarly reduced oxidation of polymers and more rapid utilization of carbohydrates, amino acids and carboxylic acids occurred in soils of the rhizosphere of a shrub grown under elevated CO_2 [72]. The findings are inconsistent, and suggest considerable variability, even if one assumes the methodology employed allows direct comparisons. In general, however, one would anticipate that highly productive species, particularly growing in nutrient-rich habitats, would allocate less carbon to rooting tissues. These plants, which include many successful invasive species, can exhibit a greater intensity of CO_2 assimilation and higher efficiency of conversion of CO_2 to organic carbon, with smaller carbon losses to root respiration and exudates (see [73]). It is important to note, however, that although the direct root inputs to the hydrosoils may be reduced with enhanced aboveground growth, the total organic matter of aboveground tissues of the invasive species is often much increased which in turn will result in

greatly increased loading of organic carbon to the soils both in particulate detrital matter and in dissolved organic matter. Microbial utilization of that increased organic matter will in turn increase recycling of nutrients and enhance the competitive advantage of the invasive species.

Many successfully invasive emergent wetland plants exhibit rapid clonal growth through rhizomes and large structural roots that have slower turnover rates in comparison to fine roots. Nonetheless, detailed seasonal field studies of growth of two species of *Typha* demonstrated that most of its new growth occurs in the roots and that carbon allocation to the roots increased markedly in nutrient-insufficient hydrosoils [74–78]. Not only was biomass of roots at any given time considerably larger than that of rhizomes, but the much higher turnover rates of roots in comparison to rhizomes led to at least an order of magnitude, likely two, higher carbon allocation to roots than to rhizomes.

Many of the most aggressive and successful invasive plant species are those exhibiting clonal reproduction and rapid growth, often under nutrient sufficient (eutrophic) conditions. Additionally most of these plants exhibit continuous population growth with the constant growth of new cohorts or with a number of overlapping cohorts (e.g., [79] for *Typha latifolia*; [80] for *Juncus effusus*). Accompanying such productive growth strategies is constant senescence of tissues with large amounts of 'standing dead' tissues and accumulated litter of tissues relatively resistant to rapid degradation. For example, the leaves (culms) of the emergent rush *Juncus effusus*, a plant common to many littoral areas and wetlands of lakes and streams, senesce from the leaf tip to the base at an exponential rate (over 90–225 days), the rate of which is greater with increasing temperatures seasonally [81]. The leaves of *Juncus* remain standing while dead, a feature common among emergent wetland plants. Although fungal biomass constituted 3–8% of the total detrital mass, decomposition was slow ($k = 0.40$ yr^{-1}), and senescent leaves lost about half of their biomass in two years. Availability of water was a major factor affecting rates of fungal respiration [82–83]. CO_2 evolution from the senescent tissues increased precipitously in the evening with increasing relative humidity (>90%) and plant water potentials (> −1.0 Mpa). Fungal respiratory rates were manifold higher during night and early morning hours than during daytime on clear days. Throughout this long period of aerial degradation of senescent tissues, appreciable recycling of nutrients occurs by leaching of nutrients with rainfall and transport to the hydrosoils for utilization and recycling by microbes and living plants (e.g., [84–85]).

Similarly, with the greater intensive growth of the invasive plant species, and the common multiple, overlapping cohort production that is found among many of these aggressive invasive plants, accumulations of senescent litter is often greater than is the case among native vegetation. If wet or submersed, fungal production is often reduced and supplanted by bacterial production [86, 87]. Here again, diurnal fluctuations of environmental conditions within the litter detrital organic matter can be very great, largely keyed to the periodicity of insolation and photosynthesis of both the macrophytes and the algal/cyanobacterial photosynthesis. For example, the redox conditions often rapidly fluctuate

from anoxic reducing conditions in darkness to highly oxidized supersaturated conditions within the sediments and detrital masses by photosynthetic activity of attached microalgae. These changes can occur very rapidly upon receiving light (shifting from anoxia to dissolved oxygen supersaturation and increase several pH units within minutes) and result in marked alterations of rates of sorbed nutrient releases and fluxes [88–90]. Beneath the understory of emergent aquatic plants, the rates of decomposition of the detrital plant are markedly influenced by redox conditions and fluctuating water levels [91]. As these recycling processes increase, the capacity of the dominating invasive species to increase was directly correlated, and presumably these processes enhance invasive expansion and ability to compete with indigenous species.

Defensive mechanisms

Selection pressure from competition among wetland plants has led to the development of numerous competitive adaptations. Submersed, verticillate macrophytes, such as *Hydrilla, Elodea* and *Myriophyllum* spp, are capable of rapid shoot elongation and sloughing of shaded leaves in response to reduced light intensity [12, 92–94], adaptations that concentrate photosynthetic tissues within the photic zone of water bodies. High rates of aboveground production provide a competitive advantage through shading of nearby competitor species (e.g., *Typha latifolia, Juncus effuses* and *Hydrilla verticillata* [59, 78, 95]). Vegetative growth strategies often rely upon vegetative clonal growth with reduction of sexual reproduction [96]. Many of these clonal methods of propagation also function in perenniation or supplemental resource exploitation (e.g., adventitious root formation and fragmentation in *Myriophyllum*; [97]).

Wetland and aquatic macrophytes not only compete with other macrophytes, but also face competition from attached epiphytic microbial communities for both light and nutrients. There is some indication that various allelopathic interactions exist between macrophytes and epiphytic microbial communities, but only in a few cases is the chemical evidence compelling (see reviews of Gross [98] and Ervin and Wetzel [94]).

Aggressive chemical mechanisms function effectively as well. For example, certain invasive species can release chemical compounds that have allelopathic effects on selective species of the indigenous plant community [52]. The native species may not have had previous exposure to, and sufficient time to develop defensive mechanisms to cope with, the allelochemical compounds and rapidly capitulate to the invasive species.

Herbivory

Various toxic metabolites (phenolic compounds, terpenoids, alkaloids) are well known to deter herbivory upon aquatic plants [94]. Some hormonal

sesquiterpenoid and glucosinolate compounds function both as anti-herbivore defenses as well as allelopathic agents in suppressing growth of competitive plants (e.g., [99–103]. Sulfur-containing compounds (trithianes) are known among aquatic plants and macroalgae (Characeae) that have both antimicrobial and anti-herbivore properties [98, 104]. Some elegant studies have isolated specific polyphenolic and lignan compounds from specific aquatic plants that confer anti-herbivory properties against the crayfish [105, 106]. Glucosinolate compounds are produced by watercress (*Nasturtium officinale*) that functions in both allelopathic and anti-herbivory properties [107–109].

Such studies support the hypotheses of Lodge [110] and Newman [111] that aquatic and wetland macrophytes may be well defended chemically against herbivory. Evidence suggests that phenolic compounds are more likely responsible for herbivory deterrence than are alkaloids. Plant damage, as via herbivore feeding activities, can result in immediate induction of phenolic production and suppression of feeding by a variety of invertebrate herbivores.

Less toxic chemical defenses are more widespread among plant species than are more narrowly distributed highly toxic compounds. Herbivores can adapt to novel, more toxic chemical defenses of plants by becoming specialists. Alternatively, herbivores can become generalists but at the cost of reduced feeding success on any particular plant species [112]. The limited literature on phytochemical defense mechanisms among aquatic plant and wetland communities provide support for a co-evolutionary model. Herbivory responses are sufficiently distinct, however, to indicate diffuse co-evolution. Microorganisms may select for plant defense compounds. As plant species diversify, novel defense chemicals will become widespread. The tendency then would be for herbivores to adapt to it and eventually develop mechanisms to disable such compounds.

Conclusions

Scientific understanding of the competitive capacities of invasive species is critical to effecting prevention, detection and rapid management responses to invasive species introductions. Many of the changes being imposed upon indigenous communities by invasive species offer direct evidence for the capacities of these advantaged plants to compete with native species. In some cases, anthropogenic alterations of environmental parameters, such as changes in atmospheric concentrations of CO_2 and related climatic and hydrological changes, have both direct and indirect effects on facilitation of biological invasions [113–117]. Truly effective management skills emerge, however, when the underlying physiological and genetic control mechanisms are understood. In many cases, the inadvertent invasions of exotic species into natural communities provide useful experiments – their rigorous analyses and interpretations can effectively augment controlled experimental analyses at specific biochemical and genetic levels that are so essential to gain needed understanding.

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Understanding invasions: the rise and fall of diffuse knapweed (*Centaurea diffusa*) in North America

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Introduction

Diffuse knapweed (*Centaurea diffusa* Lam.) is an aster of Eurasian origin that has colonized 1.4 million hectares of semiarid grasslands in western North America over the last century [1, 2]. The species can be found from Washington to Michigan and from British Columbia to New Mexico. This species is a short-lived perennial that often produces a rosette in the first year and in the second year will flower, set seed, and die. The senesced adult plant can function as a tumbleweed to disperse seeds. The weed reduces grassland forage and has the potential to exhibit negative effects on other ecosystem services of these rangelands [3–5].

Midway through the last century *C. diffusa* was sufficiently widespread to implement biological control efforts. The first species of biological control insects (gall flies, *Urophora* spp) were released in North America in 1970, followed by the release of about 10 additional species of insects over the next two decades [6]. By 2000, 13 insects had been released [7]. In spite of these efforts, diffuse knapweed continued to spread, and through the 1990s, biological control efforts appeared unsuccessful. As summarized by Carpenter and Murray [8] "At least nine biological control agents that attack *Centaurea diffusa* are established in parts of the United States. Unfortunately, it appears that none of these agents, alone or in combination, effectively controls diffuse knapweed populations."

While evidence was accumulating indicating that top-down controls were not affecting dominance for this and related species of *Centaurea*, the importance of bottom-up controls (competitive and resource acquisition mechanisms) were being documented. Gerlach and Rice [9] indicated that a relative of diffuse knapweed, *C. solstitialis*, was successful as an invader due to its abilities to persist within a community and exploit resource opportunities. Research on diffuse knapweed at our site [5] indicated that the characteristics

of persistence and opportunism also described the invasiveness and dominance of *C. diffusa* as well. Suding et al. [10] demonstrated that rosettes of diffuse knapweed were strong competitors under ambient nutrient conditions, but were less competitive under lower nutrient conditions that may have characterized North American grasslands until recently. Elsewhere, the role of soil biota – collectively the benefits provided by mycorrhizae and the absence of soil pathogens – has also been indicated in the success of invasive species of *Centaurea*. Mycorrhizae fungi provide a competitive advantage to invasive spotted knapweed *C. maculosa* [11, 12]. Callaway et al. [13] demonstrated that mycorrhizal interactions allowed *C. melitensis* to exhibit compensation to grazing damage. Those findings added to the work showing that overcompensation to root herbivory occurred in *C. maculosa* [14].

Allelopathy was also identified as a competitive mechanism used by *Centaurea* species. Spotted knapweed was found to possess an allelopathic agent, (–)-catechin [15]. Another allelopathic chemical, 8-hydroxyquinoline, was subsequently identified for diffuse knapweed [16], supporting the contention of Hierro and Callaway [17] that *C. diffusa* used allelopathy to achieve a competitive advantage. This particular chemical contains nitrogen, an element that is generally more available in many areas of North America due to increased atmospheric nitrogen deposition and chronic fire suppression [18]. Callaway and Ridenour [19] suggested that the relatively high production of allelopathic compounds could explain the dominance of invasive *Centaurea* species.

While specific findings were being reported for *Centaurea* spp, Klironomos [20] demonstrated that invasive plant species with strong dominance (high abundance in their respective communities) often exhibit positive feedbacks with soil biota. Mitchell and Power [21] found that those invasive species that exhibited dominance and were identified as noxious and invasive tended to be those that had escaped their native fungal pathogens and viruses. These same species had yet to accumulate an equivalent number of pathogens in their introduced environments. Not surprisingly, Callaway et al. [22] subsequently showed that *C. diffusa* growth exhibited positive feedbacks in soils of invaded communities. Collectively, these results argue that the combination of traits – persistence and opportunism, allelopathy, and potential positive feedbacks from soil biota – allow for *Centaurea* species, including diffuse knapweed, to function as something we might call "super-invaders" [23]. Such plants appear to be superior competitors and capable of dominance across a broad range of ecological conditions.

By 2003, however, evidence suggested that certain insects were having a strong influence on diffuse knapweed densities in Colorado [24]. Subsequent reports from Montana [25] and British Columbia [26] indicated that this response was widespread. The common factor in this reduction was the addition, to the existing suite of herbivores, of a weevil that consumed both seeds and maturing plants. Differences in nutrient availability and plant competition have the potential to mediate weed responses to herbivory (e.g., [27, 28]).

Accordingly, tests at multiple sites and under multiple climatic regimes are warranted to establish the generality of top-down controls on diffuse knapweed.

Here, we use results from studies of insect herbivory on diffuse knapweed populations in the Colorado Front Range to make inferences about factors controlling invasiveness of diffuse knapweed and its relatives in North America. We show that top-down controls negate the characteristics that made knapweed successful as an invader in Colorado. We also hypothesize that these controls, as represented by the current list of biological control insect species released in North America, may not be uniformly effective for all of the invasive *Centaurea* species.

Monitoring effects of herbivores on knapweed populations and seed production

A monitoring site dominated by diffuse knapweed (25–30% of plant cover) was established in Boulder County, Colorado, USA in 1997. In that year small numbers of *Sphenoptera jugoslavica* Obenb., (Coleoptera: Buprestidae), *Cyphocleonus achates* Fahraeus (Coleoptera: Curculionidae), both root feeders of rosettes, and *Larinus minutus* Gyllenhal (Coleoptera: Curculionidae), the lesser knapweed flower weevil, were released at the site. In addition, there were existing populations of *Urophora quadrifasciata* Meigen, (the knapweed seed head fly, Diptera: Tephritidae). A second species of fly, *Urophora affinis* Frauenfeld, the banded gall fly, invaded the site from unknown sources by 1999.

Knapweed abundance and reproduction was obtained by counting rosettes, flowering stems, seed heads per plant, and seeds per seed head. The abundance of *Larinus minutus*, which reproduces by placing eggs in flowers of the knapweed, was also obtained during the inventory of seed heads. Details on data collection procedures at the Boulder site are reported in Seastedt et al. [24].

In addition to quantifying seed production and weevil abundance at the above site, additional areas containing large densities of knapweed were sampled for seeds and weevils. Sites included three mountain meadow sites and eight additional grasslands at distances up to 100 km from the original study site. Insects were released at these sites in the late 1990s or insects from other sites eventually colonized the areas. Data on seed and weevil densities in seed heads reported here were collected during the 2001–2004 interval. With one exception, counts were based on inspection of 180 seed heads from 30 different plants at each site collected in the mid August to mid September interval. At one site this analysis was limited to 108 seed heads from 18 plants.

The patterns observed for knapweed stem densities at our 1997 release site show that about four years were required for insect populations to build up to levels where knapweed densities were significantly reduced (Fig. 1). In contrast to the sharp decline in densities observed at this site, other sites not experiencing these levels of insect herbivory continued to maintain high densities
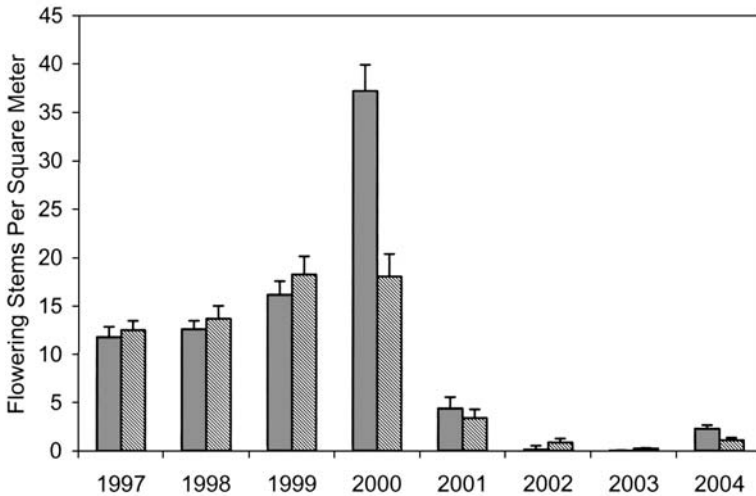
Figure 1. Flowering stem densities of diffuse knapweed at two monitoring sites where insects were released in 1997. Seed head weevils were relatively uncommon until 2000. Each bar represents the mean and one standard error of 30 samples taken from 1 m^2 quadrats at two sites over the eight year period. Data for the 1997–2001 interval were reported in [24].

and cover of knapweed [24]. By 2004, the seed head weevils had expanded to almost all remnant grasslands in the area, and two plots that had substantial knapweed when first censused in 2001 had no flowering stems or rosettes of this species in 2004.

Summer precipitation during the study interval was variable and typical of semiarid grassland found in a continental climate. During the last five years rainfall was average or above average in 2001, 2003, and 2004. The year 2000 was moderately dry and the autumn and winter of 2001 and all of 2002 were extremely dry. Knapweed rosettes may have refrained from flowering in 2002 but persisted through the drought. Seeds germinated by substantial rains in 2003 produced a modest increase in knapweed in 2004, but at levels well below those observed prior to 2001. Rosette densities of knapweed were about 50 plants m^{-2} in 1997 [24], but ranged from 1–3 plants m^{-2} at the release site in 2004 (data not shown). Given the potential persistence of a seed bank for this species [29] the decline in rosettes likely reflected both the reduction in seed production as well as substantial mortality of seedlings.

A single *Larinus* weevil larva will consume all of the seeds found in a diffuse knapweed seed head. Thus, the average seed production of knapweed impacted by this insect is determined by the number of seed heads with weevils (all contributing zero seeds) as well as the seeds produced in those seed heads not containing weevils. The relationship is 'triangular', i.e., when weevil abundance is high, seed production is uniformly low, but when weevil
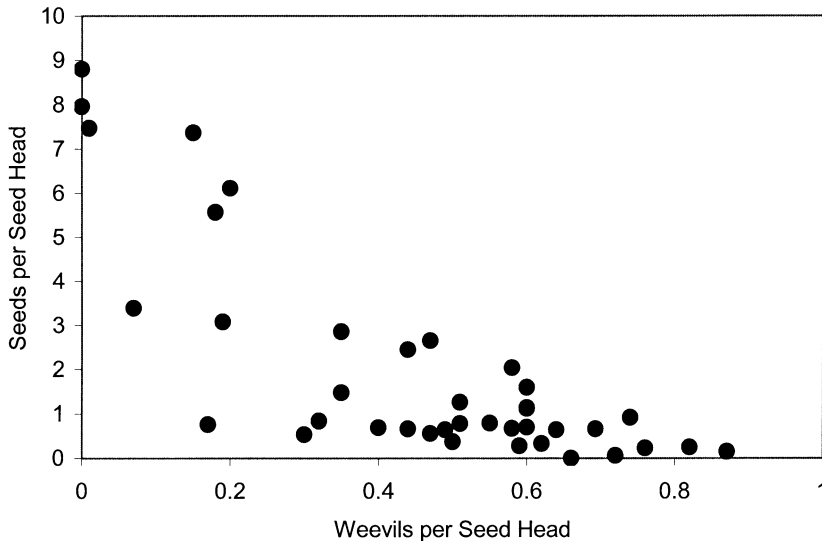
Figure 2. Relationship between seed and weevil production in seed heads of diffuse knapweed. Each point represents the mean value of seeds per seed head and weevils per seed head for 12 sites in the Colorado Front Range area collected during the 2001–2004 interval. (n = 38; not all sites were sampled in all years.)

abundance is moderate-to-low, seed production can be low, moderate or high (Fig. 2). The difference in seed production likely relates to the amount of defoliation experienced by the flowering plants. *Larinus minutus* over-winters as adults beneath the knapweed, and they tend to defoliate plants in the spring following their emergence from the soil. If sufficient defoliation occurs, the vigor of flowering is suppressed, and weevils apparently lay few eggs on stressed plants. Such plants produce few seeds and contain few weevils, providing the low seed–low weevil results seen in Figure 2. The weevils that defoliate flowering plants disperse to healthy plants that do produce seeds in those seed heads not fed upon by the weevil larvae. Those plants produce the moderate seed-low weevil points seen in Figure 2.

Knapweed not subjected to significant weevil herbivory generally produced 4–8 seeds per seed head (Fig. 3). Once weevil populations become established, seed production is greatly reduced, both by the direct consumption of seeds and the reduction in plant vigor caused by the feeding activities of the adults. While the summer of 2004 was spectacular in terms of rainfall and plant growth, weevil damage on a seed head basis was about the same as that seen in previous years (Fig. 3). Seed rain, the amount of seed produced per m^2, was initially above 4,000 seeds per m^2 in 1997, declined to about 700 seeds per m^2 in 2000 (the year before the large population decline shown in Fig. 1), and was estimated below 200 seeds per m^2 in 2004 (Fig. 3). The failure for knapweed to maintain its flowering stem densities, given these seed inputs, argues
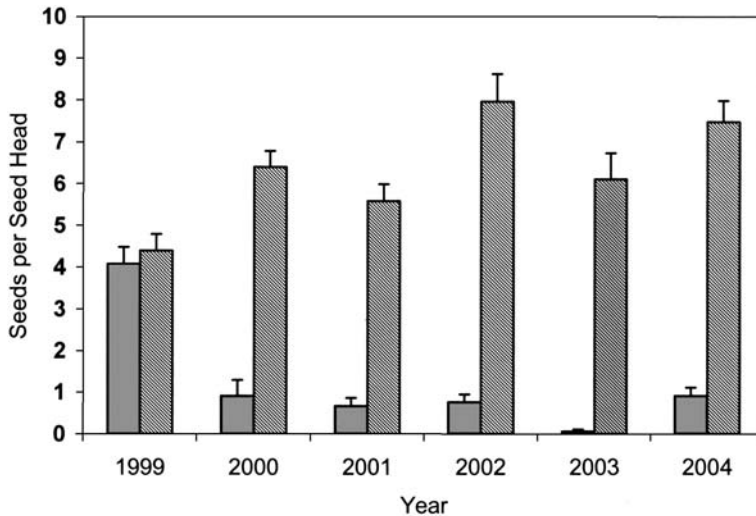
Figure 3. Seed production from the insect release site (shaded bars) compared with sites experiencing little or no herbivory by the seed head weevil, *Larinus minutus* (hatched bars). Weevil densities at the release site were estimated to be below 0.1 weevil per seed head in 1999, but were above 0.5 per seed head in subsequent years. Values are means and standard errors of a minimum of 180 seed heads sampled from 30 plants at each site for each of the six years.

for substantial mortality of seeds, seedlings, and rosettes. We do not know the extent to which that mortality results from plant competition *versus* direct mortality from herbivory and pathogens, but we believe this mortality is likely important in the sustained low densities of the knapweed. Interestingly, 'weevil rain' (number of adult weevils emerging from seed heads) has been as high as 2,000 weevils per m^2. Unless an effective predator or parasite for this species appears, knapweed experiencing these densities of herbivores is doomed to either an early death or very low reproduction.

Harris [30] suggested that the objective of knapweed control should be to achieve less than 5% cover by the weed on rangelands. This has been accomplished in Colorado, and similar results are underway in other regions (e.g., [25, 26] and unpublished results). Myers and Bazely [31] make the strong case that this decline is likely due to the combination of effects that the insects have on multiple stages of the knapweed lifecycle.

The reduction in knapweed densities in Colorado is attributed largely to activities of the lesser knapweed flower weevil, *Larinus minutus*. The other insects present in this study have not been able to control the weed [31], or, as in the case of *Cyphocleonus achates*, were not particularly abundant during intervals of knapweed decline (Seastedt, unpublished results). However, these observations do not exclude the possibility that the addition of the other species collectively have more impact on the rate and extent of knapweed decline than *L. minutus* operating alone. Seedling mortality appears to be a significant

part of the reduction in plant densities, because densities decline when seed production is still moderately high [24]. Since root feeders have been observed to cause mortality in immature plants [31], these species in particular likely do assist in the speed of the decline in knapweed densities. Myers and Bazely [31] indicate that seed predators should only be effective when host plants are poor competitors and have low rosette survival. In Colorado, seedling survival appears to be a vulnerable stage for this plant, and soil nutrient availability and plant competition influence survival ([5, 10] and unpublished results). Thus, similar to findings of McEvoy et al. [27] and research summarized by Muller-Scharer and Schroeder [6], we believe that resource competition, generated by low soil resource availability or through plant competition, mediates the exotic plant response to herbivorous insects. Accordingly, we predict that in spite of large reductions of knapweed in grassland areas, knapweed will remain common in areas of soil disturbance with high nutrients and little plant competition. To date, our observations match this prediction.

The relationship between biotic controls and 'super invaders'

Our findings do not negate the studies that show *Centaurea* species to possess allelopathic chemicals, to maximize mutualistic associations with mycorrhizae, or to benefit from positive feedbacks with soil biota. Further, *Centaurea* species may have escaped pathogens found in soils of their native habitat, thereby conferring additional advantage. These mechanisms, however, operate most strongly at high population densities. These factors are relatively ineffective at maintaining dominance if propagule pressure (seed production) and survivorship of juvenile plants are insufficient to maintain high densities of the invader. Our data suggest that the combination of herbivore stress to flowering plants and direct seed consumption by weevil larvae in undisturbed vegetation can reduce the abundance of this species to relatively low densities. Therefore, top-down controls (i.e., the components of classical biological control) are capable of negating or overriding 'novel weapons' or other mechanisms that confer competitive advantage to this species. Demonstration of top-down controls in North America does not prove that these insects controlled knapweed in their native lands (e.g., [32, 33]), but these results do show that this negative feedback is sufficient to deter dominance in the invaded areas studied here.

The *Centaurea* species that have invaded North America possess numerous traits that have interacted with the invaded communities in ways that have enhanced the dominance of these species. However, allelopathy may be the equivalent of "bringing a knife to a gun fight" as a mechanism for maintaining dominance. The ability to acquire and preempt limiting resources is a requirement for plant dominance. When that ability is precluded by the absence of propagules or the absence of tissues necessary to obtain those resources in an efficient manner, then dominance is unobtainable. Knapweed's ability to grow

and produce seeds is often limited by nitrogen availability [5]. Since the allelopathic agent of diffuse knapweed requires nitrogen, we suspect that a trade-off between allocation of nitrogen for root exudates and allocation of nitrogen to seed production occurs in this species. Our data suggest that knapweed in grasslands containing sufficient competitors becomes seed limited once the herbivore *L. minutus* becomes abundant. Thus, allocation to allelopathic materials in the face of significant top-down controls is not going to contribute to the success of the species. We note that, in the context of either the enemy release hypothesis or the evolution of increased competitive ability hypothesis (see Inderjit et al., this volume), escape from herbivory and root pathogens may have allowed *Centaurea* species to produce sufficient root exudates to generate allelopathic chemicals that is described by the novel weapons hypothesis. Hence, the existence of novel weapons, should it be proven to be a fairly common trait of invaders could be a consequence of the absence of biological controls in the invaded communities and, if this is the case, should be regarded as a consequence of factors identified in the enemy release hypothesis.

Missing from our knowledge is the extent to which *Centaurea diffusa* and soil biota of the Colorado Front Range are similar to other communities of *C. diffusa* in other regions of North America. Certain populations of *C. diffusa* may differ in their abundances of alleopathic agents, and certain populations may have more soil pathogens and fewer soil symbionts in other regions (e.g., [22, 33]). If so, then our results on top-down controls in these areas might not have generality. We strongly believe, however, that we have described the general case. Top-down controls have been reported in Montana and British Columbia [25, 26], areas with different climates, different soils, and, presumably, very different soil biota. Second, *C. diffusa* was able to invade and dominate in our region regardless of its specific chemistry or the specific composition of soil biota. Thus, for now at least, top-down controls in some and perhaps most regions appear to negate whatever combination of invasive traits *C. diffusa* has mustered. Not all of our study areas have responded as quickly as the site shown in Figure 1, but sites that appear slower to increase in seed head weevil abundance and decrease seed production have all started with much larger densities and seed sources of knapweed.

Will the top-down effects we observed for *C. diffusa* be repeated for other species of invasive *Centaurea* in North America? The demise of a dominant species requires greatly reducing propagule pressure, plant survivorship, or significant reductions in both of these variables. We suspect that short-lived species that by necessity rely heavily on seeds as a mechanism for success will likely be most susceptible to the top-down controls observed here. Longer-lived, iteroparous plants such as *C. maculosa* may be less vulnerable to insects like the seed head weevil for several reasons. First, annual seed production per plant appears relatively low, implying that maximum seed head weevil numbers, which are limited by the number of seed heads produced, will also be relatively low. Densities of adult weevils on a per-plant basis therefore may never match those numbers occurring on *C. diffusa*. This would diminish tissue dam-

age caused by the adult weevils. Second, perennial plants may be able to persist over multiple years by producing few or even no flowers. Seed head weevils could not persist in such areas and therefore the densities of weevils required to control perennial *Centaurea* species may never be obtained. Finally, the allelopathic agent identified for spotted knapweed is a carbon-based compound. Hence, nitrogen allocation conflicts are not likely to be as important. This does not preclude the possibility of other insect species with different life history strategies to function as potential biological control agents. For example, there exists some hope that the root-feeding weevil, *Cyphocleonus achates,* may eventually function in this fashion at least in some regions for *C. maculosa* [34].

A subset of exotic plants exhibit a combination of traits such as enhanced rates of alleopathic chemical production and beneficial plant-microbial interactions formed when exotic plants enter new communities. These 'bottom-up' effects appear to give this group the properties of 'super invaders'. Exotic control agents, some which may also exhibit more effective control characteristics due to release from their own predators and pathogens, can greatly diminish the dominance of these invaders. While high competitive ability can confer high survivorship of mature plants, seeds, seedlings and juvenile plants appear more vulnerable to top-down controls and also appear more susceptible to competition-mediated resource limitations. The net outcome between the relative strengths of 'bottom-up' and 'top-down' benefits and constraints produces the patterns we observe for invasiveness and dominance. While *Centaurea diffusa* appears to no longer be an unmanageable invasive threat, we do not know if the control mechanisms that reduce the dominance of diffuse knapweed will work for other invasive *Centaurea* species.

Summary

The relative importance of mechanisms explaining the invasiveness and dominance of alien plant species remains a subject of active debate. Diffuse knapweed has been identified as a strong competitor capable of using allelopathic chemicals to achieve dominance in plant communities that have not co-evolved with this species. Positive feedbacks with soil biota may further enhance the competitive abilities of *Centaurea* species. The failure of classical biological control after 30 years of effort was seen as negative evidence for the enemy escape hypothesis as a mechanism explaining dominance. However, control of this invasive species by insect herbivory now appears to have been achieved in widely separated ecosystems in North America. While we do not know if these same insects exerted this regulatory function in the native habitat of diffuse knapweed, we do see top-down controls operating effectively in the invaded ecosystems. Traits conferring strong competition such as enhanced rates of allelopathic chemical production or those produced by new plant–microbial interactions formed when exotic plants enter new communities can be negated by biological control mechanisms.

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Defining a regional approach for invasive plant research and management

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Introduction

Invasive plants are now recognized as a serious threat to most extensive management systems, such as forests, meadows, deserts, and riparian areas [1–3]. Vitousek et al. [3] described exotic plant invasion as a significant element of global environmental change because exotic plants can alter primary productivity, decomposition, hydrology, nutrient cycling, and natural disturbance regimes. Non-native plants also impact landscapes by changing the structure, composition, and successional pathways of native communities [3–8].

In North America, preventing, reducing or eliminating undesirable impacts of non-native invasive plants is a difficult challenge facing public and private land managers. Non-native plants account for about 65% (over 1,350 species) of the total number of invasive species in the United States and impacts to the US economy are believed to exceed $13 billion per year [9]. In the Pacific Northwest Region (PNW, Fig. 1), non-native plant invasions began in the mid-1800 s with the arrival of European settlers. Non-native invasive plants initially spread through contaminated crop seeds, a rapidly developing railroad system, and often-intense livestock grazing [10]. More recently, road building, road use, logging, grazing, forage seeding, certain erosion control practices, fire rehabilitation measures, and irrigation ditching facilitate the spread of non-native invasive plants [11–13]. Harrod [8] reviewed the effects of invasive plants on land management in eastern Oregon and Washington, and found that 65 plant species in the Blue Mountains (Fig. 1) were listed as "noxious weeds" by federal and state agencies. The Invaders Database [14] lists 53 non-native plant species characterized as noxious that are found in eastern Oregon. An additional 16 non-native species to those found in eastern Oregon were characterized as noxious in Idaho and Washington (Tab. 1).

Because of the serious invasive plant problem in the PNW, there is a need to develop research programs than span biological and spatial scales while at the same time facilitate relationships between scientists and land managers. This is not easily accomplished and requires considerable coordination and communication. In this paper, we present a framework for research that can be
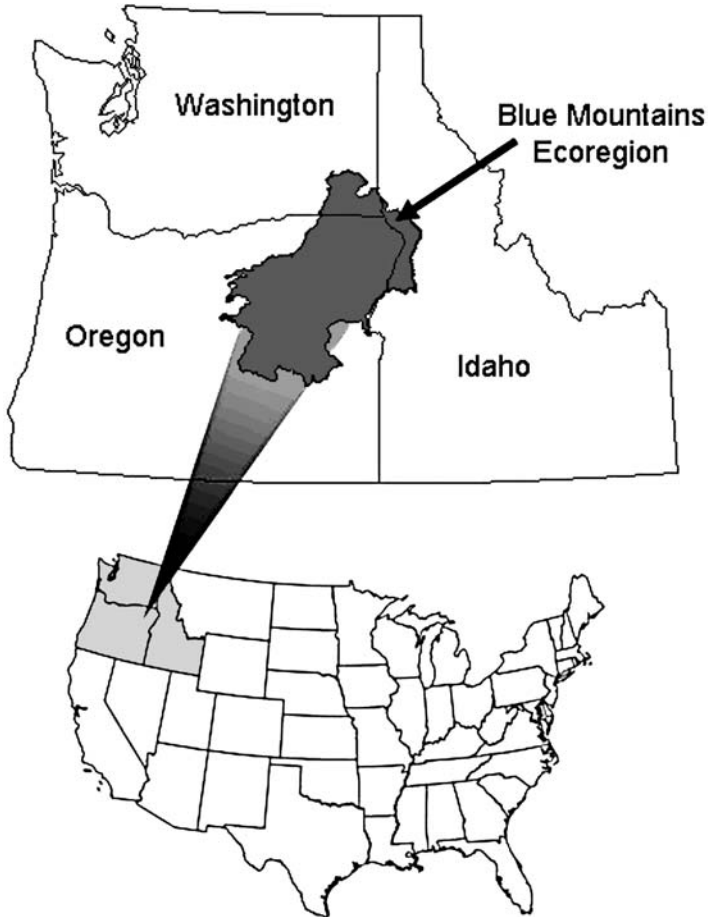
Figure 1. The Blue Mountains Ecoregion is represented in the three states that form the Pacific Northwest Region of the United States – Oregon, Washington, and Idaho.

valuable for directing and conducting regional invasive plant management. The proposed approach strengthens partnerships between researchers and land managers and can result in effective, responsive invasive plant management and habitat restoration programs.

Components of a regional research framework for invasive plant management

Empirical studies and observations of non-native exotic plant invasions can greatly assist development of management programs for prevention, containment or eradication of particular invasive plant species. Such management pro-

Table 1. Noxious exotic plant species occurring in Idaho, Oregon and Washington east of the Cascade Range [101]. Noxious weeds are species specified by law as being especially undesirable, troublesome, or difficult to control; precise definitions vary according to state laws and legal interpretations.

Latin name	ID	OR	WA	Latin name	ID	OR	WA
Abutilon theophrasti		•	•	*Hyoscyamus niger*	•		•
Aegilops cylindrica	•	•	•	*Hypericum perforatum*		•	•
Agropyron repens		•		*Hypochaeris radicata*			•
Anchusa officinalis	•	•		*Iris pseudacorus*			•
Anthriscus sylvestris		•		*Isatis tinctoria*	•	•	•
Artemisia absinthium		•		*Kochia scoparia*		•	•
Cardaria draba	•	•	•	*Lepidium latifolium*	•	•	•
Cardaria pubescens	•	•	•	*Linaria dalmatica*	•	•	•
Carduus acanthoides		•	•	*Linaria vulgaris*	•	•	•
Carduus nutans	•	•	•	*Lythrum salicaria*	•	•	•
Carduus pycnocephalus		•	•	*Matricaria maritima*			•
Centaurea diffusa	•	•	•	*Myriophyllum spicatum*	•	•	•
Centaurea jacea		•		*Nardus stricta*	•	•	
Centaurea biebersteinii	•	•	•	*Onopordum acanthium*	•	•	•
Centaurea pratensis	•	•	•	*Panicum miliaceum*		•	
Centaurea repens	•	•	•	*Peganum harmala*		•	
Centaurea solstitialis	•	•	•	*Phalaris arundinacea*			•
Centaurea triumfettii		•		*Polygonum cuspidatum*		•	•
Chondrilla juncea	•	•	•	*Polygonum sachalinense*		•	•
Chrysanthemum leucanthemum		•		*Potentilla recta*	•		•
Cirsium arvense	•	•	•	*Rorippa sylvestris*		•	
Cirsium vulgare		•	•	*Rubus discolor*		•	
Conium maculatum	•	•	•	*Salvia aethiopis*	•	•	
Convolvulus arvensis	•	•	•	*Salvia sclarea*			•
Crupina vulgaris	•	•	•	*Secale cereale*			•
Cynoglossum officinale		•	•	*Senecio jacobaea*	•	•	•
Cyperus esculentus		•	•	*Sonchus arvensis*	•		•
Cytisus scoparius	•	•	•	*Sorghum halepense*	•	•	•
Daucus carota		•		*Sphaerophysa salsula*	•		•
Euphorbia esula	•	•	•	*Taeniatherum caput-medusae*	•		
Euphorbia myrsinites		•		*Tamarix spp.*	•		•
Gypsophila paniculata		•		*Tanacetum vulgare*			•
Halogeton glomeratus		•		*Tribulus terrestris*	•	•	•
Hieracium aurantiacum	•	•	•	*Xanthium spinosum*	•		•
Hieracium pratense	•	•	•				

grams can, in turn, be helpful to further identify research needs. Research to inform regional management of invasive plant species requires explicit consideration of scale, while empirical study may be concentrated on species biology, population demography and/or habitat level risk assessment (Fig. 2). This paper discusses the three components necessary to develop a regional approach for invasive plant research and management: 1) an understanding of the steps for plant invasions to occur, 2) consideration of relevant biological and geographic scales, and 3) interaction with natural resource managers. We then present an example research framework to inform scientists and managers about the potential of this regional research approach using the invasive plant *Potentilla recta*.
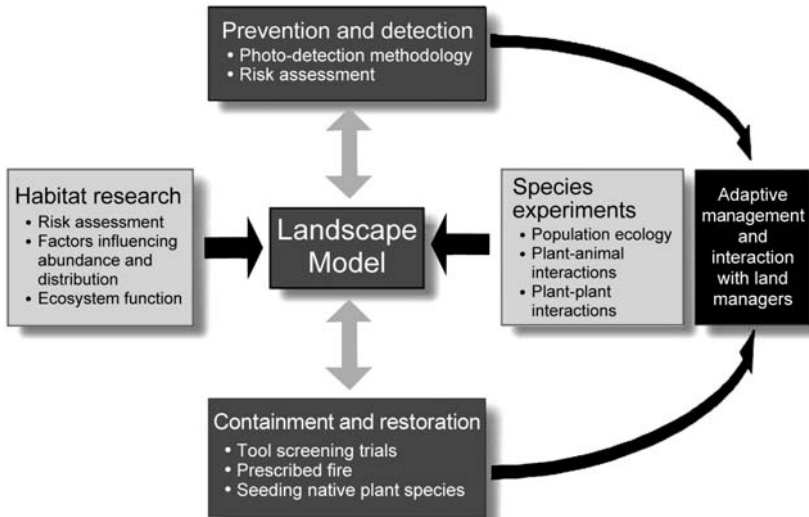
Figure 2. Regional approach for *Potentilla recta* research and management in the Blue Mountains Ecoregion of the Pacific Northwest, USA. The research approach was developed for management of a single species, *Potentilla recta*, and may become more complex as additional species are added to the framework.

Steps of the invasion process

Cousens and Mortimer [15] indicate that the process of plant invasion consists of three phases – introduction, colonization, and naturalization – while Richardson et al. [16] restructure the invasion process into introduction, naturalization and invasion. Richardson et al. [16] reserve invaders as a special plant category whereby exotic plant species occupy and expand into areas without further assistance from humans. Disturbance is generally accepted to be a fundamental factor for successful introductions and colonization/naturalization phases in both classifications [5, 17, 18].

Humans to some degree have modified most of the world's ecosystems, and this has a direct effect on invasibility. Some ecosystems are altered by the presence of exotic plants themselves [19], through an increase in fire frequency, nitrogen depletion or allelopathic chemicals. Other species are adapted to conditions following land use changes, whereas native species are not, e.g., resilience to grazing pressure in the Great Basin of the western United States [20]. An explanation for semi-arid and grassland vulnerability to invasion by exotic plant species is that these areas have spatially open niches, microsites that are devoid of vascular plants for some or most of the year [21]. Plants that have life forms dissimilar to the native vegetation also have invaded some ecosystems. For example, the conversion to annual grasslands from tussock grasslands in California, and the invasion of *Opuntia stricta* into Australia (a cactus where no members of Cactaceae existed previously) are examples where

biological characteristics play an important role in the invasion process as well as site factors and disturbance.

Species invasions can generally be depicted by a logistic growth curve [22]. Population growth curves may then be generated for plant species given their initial population size, intrinsic growth rate, and time. Small populations are often undetected during the early introduction phase of invasion because individual plants may remain unnoticed for long periods of time. Dispersed seed must compete with the established flora that is well adapted to the site in the absence of disturbance; thus few introductions proceed to the next phase of invasion. For example, Williamson [23, 24] estimates that only about one percent of all introduced species into the British flora become established and are invasive enough to be considered as pests [25].

Colonization/naturalization [15, 16] is characterized by exponential population growth of the introduced species. During this explosive growth phase, the species often becomes apparent to land managers and control efforts begin. This phase of invasion is closely related to the intrinsic rate of increase for the plant species. Hence, predictions of colonization/naturalization rates and management options should focus on the intrinsic biology of the species. For example, Maxwell et al. [26] divided the life history of *Euphorbia esula* L. into five stages: seed, buds, seedlings, vegetative shoots and flowering shoots. By identifying these stages, the process of population development was determined using a stage-based matrix model. In this way the process of population development and expansion was determined.

Theoretically, at some carrying capacity, *K*, the species' population approaches a quasi-threshold density where its population growth stabilizes or does not expand quickly. At this point colonization/naturalization is complete. The *K* density occurs when niche occupancy and available resources limit the rate of species spread, which is controlled by environmental or habitat-level factors like competition or herbivory. Thus predictions of risk for species approaching *K* also should focus on habitats or the disturbance of them. Table 2 delineates disturbance types important for habitat susceptibility to non-native invasive plants in one of our study areas in northeast Oregon.

Descriptions of biological and environmental characteristics for most invasive species are often lacking or only general in nature. Thus, it is difficult to determine which plant species are most likely to be invasive [1, 10, 27]. Formation of a landscape-level model augmented by empirical study of habitat (environmental) and species (biological) factors can inform the overall program for non-native invasive plant management in extensive production systems (Fig. 2).

Relevant scales and disturbances

Sauer [28] and Forman [29] indicate that ecological processes that determine the function and stability of plant communities during plant invasions are

Table 2. Primary disturbance types that may modify carrying capacity, *K*, of habitats comprised primarily of native species in the Starkey Experimental Forest and Range, Oregon

Disturbance	Affected plant communities
Fire (prescribed and wild)	Grand fir, Douglas-fir, mixed conifer, ponderosa pine, lodgepole pine, bunchgrass, Sandberg's bluegrass, Idaho fescue, wet meadow, low sagebrush, and juniper communities
Livestock grazing	Plant communities within current grazing allotments, including grand fir, Douglas-fir, mixed conifer, ponderosa pine, lodgepole pine, bunchgrass, Sandberg's bluegrass, and Idaho fescue communities
Timber harvest, fuels reduction, or canopy thinning activities	Grand fir, Douglas-fir, mixed conifer, ponderosa pine, and lodgepole pine stands
Roads	All plant communities

scale-dependent and range from individual species to landscapes. Land managers need research that incorporates both specific biological and habitat-level inputs over a broad landscape. Scales too large to detect local-level invasions or too small to find and monitor invasive plants effectively are, therefore, of limited use. Management policies for invasive plants are developed best for broad regional scales, while managers require tools that directly aid detection, monitoring, and containment of invasive plants at scales small enough for eradication or control (Fig. 2).

Species

A regional research program to implement prevention tactics or control and restoration after exotic plant introduction must necessarily focus on the biology of the invading species and steps of the invasion process (above). However, the species is also likely to affect the composition of plant communities (habitats), and thereby the functions and patterns of those ecosystems and landscapes that are invaded.

Habitat

Habitat characteristics and their modification often have a direct bearing on the success or failure of particular invasions [30]. The environmental factors most responsible for floristic growth and persistence of invasive plant species are soil, climate, and land use.

Many studies show that plant growth and invasive plant prevalence occur within certain ranges of habitats [31], and usually species are most productive within certain soil types. Although soil classification can be used to study and develop predictive landscape-level models of plant invasions, soil mapping units of extensive land management systems are generally too coarse to be of use for that purpose. In addition, other microsite factors such as small mounds or ephemeral pools may play a role in the overall invasive process. However,

such fine-grain factors are also difficult to quantify for landscape-level models or habitat-level risk assessments [32]. Climate also drives abiotic and biotic thresholds for plant growth in particular ecosystems. For example, the retreat of forests to mountainous areas over the last 10,000 years is a direct result of changing climate [33]. Climate can also change habitat suitability over short timescales through drought, seasonal frost, and flooding [34]. Invasive plant species tend to adapt well to a variety of habitats but usually invade regions with similar climates to their native range first, then adapt to other climates later [35]. Edaphic characteristics such as topography and elevation modify climate, and therefore influence the plant species that can grow at a given location. Land use and the resulting condition of the environment is a third driving component of habitat suitability and invasion. Changes in land use are thought to be the single most important factor in species extinction [15] and to have strong influences on invasible sites [36].

Landscapes

Across a region, a species may be detected in the late colonization/naturalization or early naturalization/invasive phase [15, 16] and thus be considered a stable population. However, this stable source population contributes to many subsequent local infestations through seed dispersal. These small satellite populations are sinks from the source and can become additional source populations themselves, which expand markedly from the original infestation area [37]. Rates of increase for satellite populations can be extremely high because satellite introductions have a much higher probability of success than initial introductions as a result of the constant seed flow that arises from source areas [38, 39].

Landscape features and connectivity relationships become important for predicting spread from source populations to new and as yet unoccupied locations for exotic plant species. Regions are composed of a mosaic of extensive natural resource areas (forests, rangelands, wetlands, etc.), intensively managed locations (farms, paddocks, holding areas for livestock, etc.), urban areas of various sizes (intensities), and the corridors (roads, rivers, etc.) that connect them all [32]. Invasive plants can be present in each landscape feature. The spread of *Bromus tectorum* across most of the western United States since 1900 [40], and the replacement of native hardwood forests in Australia and other regions of the world by *Pinus radiata* [41] are important examples of landscape change by exotic plant species. Transportation corridors can markedly influence the risk associated with species spread as satellite populations [42].

Interaction with land managers

Scientifically rigorous research is fundamental to a regional research program, but the gap between scientific knowledge and existing management practices

must be narrowed for invasive plant management to be most effective. There is a need for biological, ecological and social knowledge to inform decisions (Fig. 2). The use of science adds credibility to management decisions, providing conceptual approaches for complex problems and contributes to new techniques for accomplishing management objectives. However, efforts to inform managers about scientifically derived knowledge and conceptual approaches are often applied *ad hoc*, with most scientific information provided in the form of publications and presentations. Interaction among scientists and managers, working together to ensure that research is pertinent and effectively applied, is most likely to result in success (Fig. 3).

Adaptive management (Fig. 3), whereby management practices are continuously reassessed and modified as new information becomes available, is an appropriate approach to manage invasive plant species [43]. Research can be advanced by partnerships between scientists and land managers, where managers identify concerns and provide information about day-to-day management activities. Direct scientific feedback from researchers also hastens the progress of adaptive management [44–46]. In addition, designing and conducting research in collaboration with local land managers can result in increased applicability of the research [47].

Awareness of regional invasive plant species allows land managers to recognize invasions at early stages. Studies show that invasive species have a lag time, often taking several decades to expand during which they grow in small, isolated populations and do not spread [48, 49]. Non-native species that are not
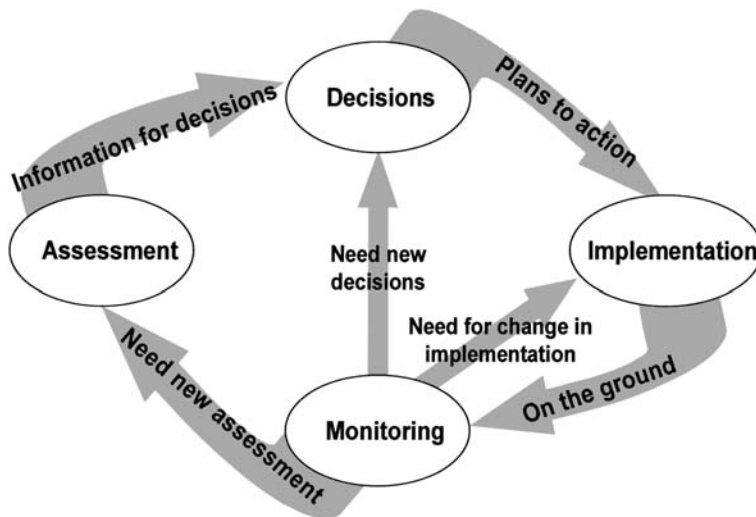
Figure 3. Adaptive management approach for a regional research program that depends on land manager feedback. Modified from [102] for invasive plant management.

currently considered invasive can eventually affect ecosystem function. Thus, it is important to consider the potential impacts of all introduced plants, not just those already discovered or deemed invasive. Including scientists, conservation managers, and local botanists in defining research and management priorities improves detection of a broad range of introduced plants.

Example research framework: *Potentilla recta* in the Blue Mountains Ecoregion of North America

There are many noxious exotic plants presently occurring east of the Cascade Mountains in the Pacific Northwest (Tab. 1). However, only some of these species are considered invasive over large areas, while others are more restricted in distribution. Managers and policy makers want to know the likelihood of new plant species becoming prevalent over large areas, but ecologists are only able to provide after-the-fact explanations for invasions. Predicting which species will be invasive and which habitats and ecosystems are invasible remains difficult [24]. *Potentilla recta* (Tab. 1) is a relatively recent introduction to the PNW with many new infestations reaching environmentally severe sizes and densities [50]. Despite widespread concern about *P. recta,* we were unaware of any ongoing studies, and only sparse information was available in the literature to inform managers about the species.

   Potentilla recta (Rosaceae, common name is sulfur cinquefoil) is a herbaceous perennial forb native of Eurasia. It was introduced to North America prior to 1900 [51], and has since spread across the continent. It has been reported in all states of the USA, except Arizona, Utah and New Mexico. The ten Canadian provinces also have documented the presence of *P. recta*. The plant reproduces only by seed, has a single taproot, and may have several shallow, spreading branch roots, but no rhizomes. *Potentilla recta* has four general life history stages [52]; viable seed in the soil, seedlings, non-reproductive rosettes, and reproductive stemmed individuals [53]. Werner and Soule [54] provide information on the biology of the species from early observations made in eastern North America where *P. recta* is a minor agricultural weed. More recently, *P. recta* is recognized as increasing in the drier climates of northwestern North America and is considered a threat to native plant communities where it forms dense populations [50, 55, 56].

   Dense and continuous *P. recta* populations most commonly occur on areas of soil disturbance (e.g., old fields), but increasingly, populations have been observed in rangelands and in the understory of open-canopied ponderosa pine forests. *Potentilla recta* is unnoticed in many parts of its range because it is similar in appearance to native co-occurring congeners, particularly *Potentilla gracilis* [50]. There are no available biological control agents for *P. recta*. Due to the plant's close genetic relationship to native *Potentilla* species and to cultivated strawberry, finding a host-specific biocontrol agent for *P. recta* is therefore difficult. *Potentilla recta* was first reported in northeast Oregon in 1969.

The research described here is being conducted in the Blue Mountains Ecoregion of the interior PNW (Fig. 1). It consists of interrelated studies to assess habitat risk, project species population spread, and determine the life cycle, dispersal, competition, and containment strategies of the species. Figure 2 depicts the interrelationships of these studies within our regional invasive species research framework. We now briefly describe our ongoing research and how these studies are used to develop a landscape-level projection of range expansion (Fig. 2) and management of *P. recta*.

Habitat-level research

Information on the underlying factors that influence *P. recta* abundance [53, 54, 57] indicates the species has broad ecological amplitude, yet no quantitative assessment of which factors most strongly influence *P. recta* abundance had been conducted. A study was implemented using a geographic information system (GIS) to examine possible relationships between *P. recta* occurrence and environmental, historical and landscape variables. These variables included habitat type, vegetative canopy cover, slope, elevation, aspect, general soil type, land use history (disturbance), and proximity to roads. Information from this study provided insights on the relative contribution of the various factors to *P. recta* occurrence and relative abundance, and is now integrated into the risk assessment and landscape projections of species expansion described below.

Risk assessment

Anticipating species that may become invasive in particular landscapes and knowing where to look for them is a particularly important aspect of invasive plant management. Byers et al. [44] identify four stages of invasive plant risk assessment for biological invasions of non-indigenous species to occur: 1) arrival (risk associated with entry pathways), 2) establishment (risk of forming viable, reproducing populations), 3) spread (risk of expanding its extent), and 4) impact (risk of having a measurable effect on existing species or communities).

At the Starkey Experimental Forest and Range (SEFR) a risk assessment (Figs 2 and 4) was conducted to determine what habitats are at risk to *P. recta* invasion. SEFR encompasses 7,762 ha with elevations ranging from 1,122–1,500 m in northeastern Oregon. Major plant associations (habitats) include *Abies gradis*, *Pseudotsuga menzeiseii*, *Pinus ponderosa*, *Pseudoroegneria spicata*, *Festuca idahoensis*, and *Poa sandbergii* communities. Habitats at risk to *P. recta* invasion were found by integrating three components of habitat vulnerability using GIS technology. The three components are: 1) *Susceptibility* – vulnerability of each habitat to *P. recta* establishment. Susceptibility was determined for each habitat found in SEFR using reports of *P. recta* occurrence in other areas of the Blue Mountains; 2) *Disturbance his-*

tory – includes livestock grazing allotments, sites of prescribed or natural fires, timber harvest, fuels reduction or thinning activities, roads, and other activities that physically disturb the soil or vegetation (Tab. 2); and 3) *Proximity of current infestations* – location of known populations of *P. recta* mapped using global positioning systems (GPS) tools.

The three GIS data layers were then integrated to determine the areas at risk to *P. recta* invasion within SEFR (Fig. 4).

Risk assessment (e.g., Fig. 4) is a valuable tool for land managers to prioritize prevention, containment or control activities. For example, a land manager may choose to contain exotic plant populations that are within high-risk
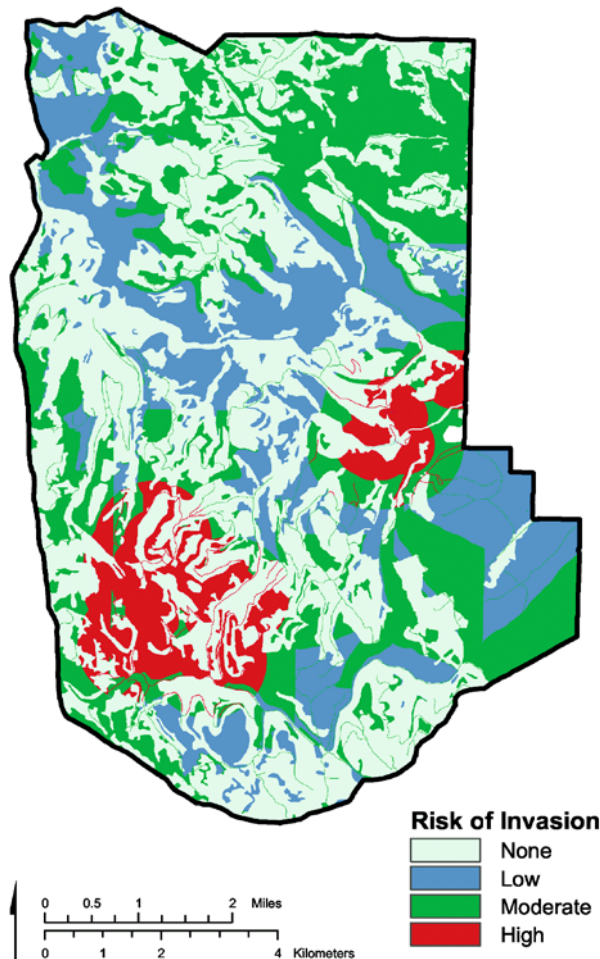
Figure 4. Areas at varying risk to invasion by *Potentilla recta* in Starkey Experimental Forest and Range. Risk depends on the integration of habitat susceptibility, disturbance, and proximity to current infestations.

habitats as opposed to treating multiple infestations that have little potential to spread to adjacent low-risk areas (Fig. 4). Prevention activities are also enhanced by such assessments because managers can direct their inventory and monitoring activities to high-risk areas for early detection and rapid eradication of small exotic plant populations.

Such analyses are also useful for directing the research effort. As our assessment progressed, it became evident that seed dispersal was critical for expansion of *P. recta*. As a result, studies to identify mechanisms of short- and long-distance seed dispersal of the species were initiated and are now being used to make future risk and expansion assessments.

Species-level experiments

In the interior PNW, invasive species such as *C. biebersteinii*, *C. solstitialis*, and *E. esula* have received considerable attention from ecologists and land managers [58, 59]. Relatively little is known, however, about other invasive plants listed in Table 1. Without an understanding of the biology of the species, it is difficult to assess the ecological implications of introductions, determine population expansion rates, or develop appropriate approaches for eradication, containment, or restoration.

Age structure

Age provides the timeline needed to determine population dynamics and patterns of species persistence. It is also frequently related to reproductive potential and size of the species, and defines longevity. Perkins et al. [60] determined the age structure of *P. recta* populations in northeastern Oregon by counting root annual-growth-rings to estimate the age structure of the populations, relate plant size and flower production to plant age, and examine the relation of population age structure to environmental variables and disturbance history. Results from this study indicate that in the Blue Mountains *P. recta* adults average 3.5 years old and range in age from 1 to 10 years. Age was not related to number of flowers, plant size, or site disturbance type, but was positively correlated with site elevation [50, 60].

Life history, demography, and population dynamics

The life history of a plant characterizes its stages of development through germination, growth, reproduction and death. Such demographic attributes influence the population spread, range expansion and subsequent management of invasive species. The population dynamics of *P. recta* were studied by monitoring tagged individuals for 2 years. During this time, plant size, growth, survivorship, and seedling recruitment were tracked, providing information to estimate population growth rates using a population matrix model (Tab. 3).

To construct a population matrix model (Tab. 3), three parameters were determined for each life history stage: 1) the probability that an individual will

Table 3. Example transition matrix for *P. recta* in northeastern Oregon, yielding a population growth rate (λ) of λ = 1.2144. The population is increasing by about 21% annually.

Year 2		Year 1			
	Seed	Seedling	Rosette	Small adult	Large adult
Seed	0	0	0	1211	3528
Seedling	0.001	0	0	0	0
Rosette	0.001	0.05	0.55	0.16	0.02
Small adult	0.0001	0.01	0.21	0.43	0.35
Large adult	0	0	0.01	0.11	0.46

survive and remain within that size class for a year, 2) the probability that an individual will survive and grow into another stage and 3) reproductive output or fecundity [61]. The model (Tab. 3) describes a variety of population parameters including the population growth rate (λ). Initial analyses indicate that *P. recta* populations in old fields expand at about 21% per year.

Relative growth rate and competitive ability
Growth analysis is a methodology to determine plant carbon allocation patterns over time, which may influence competitive ability with other plants in a community. Relative growth rate (RGR) is a measure of dry matter accumulation in relation to size of the individual over time; it is the efficiency of plant growth through time [62, 63]. Tuitele-Lewis [64] determined RGR for *P. recta* over a range of disturbed and undisturbed conditions on three old-field sites in the Blue Mountains Ecoregion. He found that *P. recta* ranged from 0.52–1.01 g g^{-1} week^{-1} for the three sites in 2002, and 0.13–0.2 g g^{-1} week^{-1} in 2003. These values were not unusual when compared to those of other common plant species in the area that were obtained from the literature (Tab. 4). It appears that RGR, as a measure of individual plant resource acquisition, is not

Table 4. R_{max} for certain plant species found in the Blue Mountains of northeast Oregon [64]

Species	R_{max}	Author
Bromus tectorum	0.51 g g^{-1} d^{-1}	Arredondo et al. [98]
Taeniatherumcaput-medusae	0.43 g g^{-1} d^{-1}	Arredondo et al. [98]
Pseudoroegneria spicata	0.36 g g^{-1} d^{-1}	Arredondo et al. [98]
Elymus elymoides	0.41 g g^{-1} d^{-1}	Arredondo et al. [98]
Phleum pratense	0.23 g g^{-1} d^{-1}	Poorter and Remkes [99]
Achillea millenifolia	1.96 g g^{-1} week^{-1}	Grime and Hunt [100]
Festuca rubra	1.18 g g^{-1} week^{-1}	Grime and Hunt [100]
Potentilla recta	0.83 g g^{-1} week^{-1}	Grime and Hunt [100]

an important factor accounting for the ability of *P. recta* to dominate certain forest and meadow sites in northeastern Oregon.

Seed dispersal

Dwire et al. [65] quantified seed production and measured seed dispersal of *P. recta* in different habitats in northeast Oregon. Seed dispersal was measured by using sticky traps that surrounded individual source plants. Seed production, distance of seed dispersal, and timing and duration of seed dispersal were measured. Results indicated that the 83% of the seeds that were produced dispersed within 60 cm from the mother plant. This is an insufficient distance to adequately explain the rapid spread of *P. recta* across the region and dispersal over longer distances than 60 cm appears to be critical for *P. recta* spread. Newbert and Caswell [66] and Caswell et al. [67] indicate that dispersal of relatively few seeds at the edge of an expansion 'wave' can account for the rapid spread of many invasive organisms (Fig. 5). Therefore we are initiating other studies to identify mechanisms of longer-distance dispersal of this and other plant species.
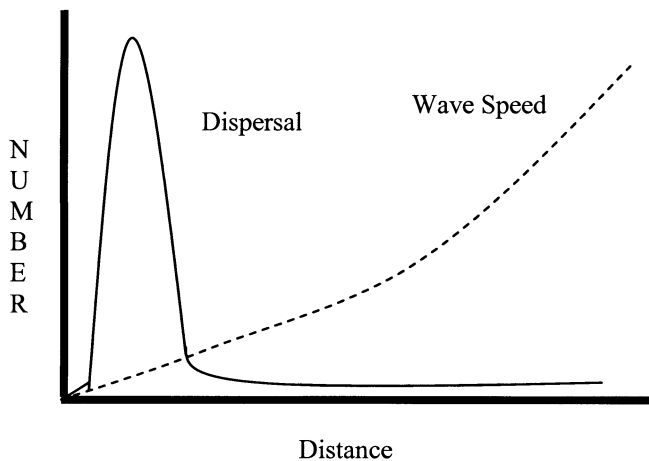
Figure 5. Hypothetical relationship of dispersal distance to dispersal wave speed.

Dispersal and herbivory

Domestic and wild mammal and avian herbivores may contribute to plant invasions by seed transport of invasive plants into previously uninhabited sites through endozoochory [68]. This phenomenon occurs when animals consume seeds in one area and later regurgitate or defecate them in another. Invasive species with thick seed coats dispersed by endozoochory, in addition to benefiting from transport, may have enhanced germination as a result of scarifica-

tion in the gut [69]. Invasive plant seeds, including those of *E. esula, Crupina vulgaris*, *C. biebersteinii*, and *Lonicera maackii* have been recovered from feces and found viable in numerous studies [70–73]. Observations at our study sites suggest that ungulates may be the primary dispersers, as they browse *P. recta* seed heads in the fall [74]. To verify these observations, studies are underway to determine whether herbivores (cattle, elk, deer, quail, wild turkey) consume and transport viable *P. recta* seeds.

Beyond abilities to disperse seeds, ungulates have profound impact on the structure and composition of plant communities [75, 76]. However, the role of ungulates as contributors to the establishment and spread of non-native invasive plants is not well known. Little information is available on use of *P. recta* by ungulates, although it is reportedly avoided by most grazing animals [50]. Despite reports suggesting that *P. recta* is minimally grazed, substantial ungulate herbivory of the species in infested areas of northeastern Oregon have been observed. A study is in progress to determine whether grazing by cattle or native ungulates directly or indirectly affects the density and demography of *P. recta*. This study employs three grazing treatments – extant grazing (cattle, elk, and deer herbivory), deer and elk herbivory only, and total exclusion.

Pollination

The spread of an invasive plant species, especially those that reproduce only by seed, may depend on how successful plants are at competing for the service of resident pollinators. Basic information on the pollination biology and ecology of most invasive plant species is lacking. This information is necessary especially for those species that require out-crossing to produce viable seed. The sparse literature available on pollination biology of *P. recta* indicates that *P. recta* can set seeds without pollinators and that fewer but larger seeds are produced on pollinator-excluded plants [54]. McIver et al. [77] are defining the insect pollinator community for *P. recta*. This research evaluates the dependency of *P. recta* on insect pollinators for seed production compared to co-occurring native *Potentilla* species. Pollinator-excluded plants are evaluated for seed set, seed size, and germination rate. Flower quality comparisons rate the ability of *P. recta* and native *Potentilla* species to attract pollinators via pollen and nectar production. The degree of fidelity of pollen transfer within and among *Potentilla* species is being determined. Results thus far have found that *P. recta* produces flowers with nectar richer in sugar and seed heads twice the mass as compared to native *Potentilla* species. Final results from this study will help clarify *P. recta* reproductive ecology and the ecological relationship of *P. recta* with other species within the community it invades.

Interference/competition

Plant mortality, growth, and fecundity, are key biological mechanisms that can provide insight into the way invasive species affect the habitats into which they are introduced [78–80]. This is especially true if the mechanisms are density dependent [81]. If density dependence is a factor in the overall ecological suc-

cess of a species, whether a plant is density dependent to its own or another species can determine the manner in which the new plant community evolves. The impact of the invasive plants on ecosystem function might then be examined by the degree of niche overlap among the co-existing species as determined by their responses to separate and combined densities. *Potentilla recta* is a highly successful plant species that effectively displaces native vegetation in certain habitats of northeastern Oregon. However, little empirical evidence exists about the mechanism by which such displacements occur.

To clarify the competitive relationship of *P. recta* and other plant species over a range of habitats two experiments were established. In the first experiment the competitive relationship of *P. recta*, *P. gracillis* (a native *Potentilla*), and *Pseudoroegneria spicata* (a native grass) is being examined in an addition series experiment [82, 83]. Various densities of each species are planted alone and in mixtures and by analyzing the effects of the resulting species ratios on mortality, biomass accumulation and reproduction, the interaction among the species can be determined. The second ongoing study is a diallel experiment [82, 83], where intra- and inter-specific combinations of the three species are planted in a variety of habitats (e.g., wet meadow, dry meadow, and open-canopy forest) and elevations. Data from both experiments will be used to determine yield ratios and competitive ability among the species, and should illuminate plant-plant interactions for disturbed and undisturbed areas and site conditions.

Landscape model

Modeling weed infestations has been attempted in numerous studies during the last decade with varying success [38]. Predictive models thus far have generally used analytical diffusion equations in an attempt to apply any weed species to any area [84, 85]. However, both biological (species) and environmental (habitat) factors form the baseline to determine the invasion risk and subsequent spread of non-native plant introductions. Modeling to assess the risk and spread of plant invasions should be at this interface of a species' biology and the speed at which it can occupy habitats as modified by environment, land uses and disturbances [38, 66]. Development of a prototype cellular automata-type model to project geographic spread of *P. recta* and other invasive plant species in the PNW (Fig. 2) is underway following the theoretical papers of Caswell and associates [66, 67, 86]. This landscape model couples a population matrix that describes population growth (e.g., Tab. 3) with an integrodifference equation [66] to account for species seed dispersal wave speed (Fig. 5) at which an exotic plant population, such as *P. recta*, might expand.

Requirements for the model are life stage parameters to calculate the dominant eigenvalue for population growth of the exotic species (Tab. 3) and a determination of propagule dispersal distance or wave speed over the life cycle of the plant [65]. When these calculations are combined with a GIS risk assess-

ment (e.g., Fig. 4) it should be possible to project areal expansion of the species over time. Such determinations for exotic invasive species are invaluable to land managers because the consequences of management or no action can be determined and policies justified.

Management-level studies

Land managers are responsible for a wide range of actions in response to plant invasions including invasive plant mapping, monitoring, and habitat treatment and restoration. However, the tools available for managers to effectively address plant invasions are limited and invasive plant research programs can play a valuable role in the development, application and evaluation of tools, methods and approaches that land managers might use to manage plant invasions. Traditionally, the development of tools for land managers has not been the focus of invasive plant research projects. Moreover, many invasive plant research efforts have been unresponsive to land manager needs and biased toward small-scale, short-term results in sometimes artificial environments, which thereby limits their applicability [47]. The applicability of many invasive plant research projects have also been limited because they often fail to incorporate interacting, complex processes that operate at large scales (e.g., fire, herbivory, succession, land use change, disturbance corridors such as roads and riparian zones) that land managers must explicitly consider in their management programs. Within our research program, we attempt to overcome these obstacles by initiating research projects designed to develop tools and approaches for invasive plant prevention, detection, control and restoration.

Prevention and detection

A critical question central to invasive plant management is "How can managers accurately and cost-effectively inventory and monitor non-native invasive plants across large landscapes?" This question is particularly important since many non-native invasive plants are easiest to control when populations are small. Owing to limited finances and personnel to sample, inventory, and monitor large areas, the development of methods such as remote sensing to detect invasive plant species is needed.

A wide range of remote sensing techniques have been utilized to detect invasive species, from coarse-scale satellite imagery to fine-scale aerial photography taken from fixed-wing aircraft. Processing and analysis varies from photo-interpretation techniques used to identify invasive species infestations by color, pattern, shape, or photo-texture, to analyses of spectral signatures using image-processing software. Despite the advocacy of remote sensing as a key to early detection of plant invasions, the results have generally been mixed [87–91], and may be of best use over large landscapes with limited access such as wilderness and roadless areas.

To detect *P. recta* infestations in open forest and grassland plant communities in the Blue Mountains Ecoregion, Naylor et al. [92] evaluated natural color aerial photography at three spatial scales. Natural color aerial photography is one of the least expensive remote sensing approaches and color photographs are widely available. For example the Oregon Department of Forestry regularly collects color photographs for a wide range of resource applications. The objectives of this study are to 1) evaluate aerial photography effectiveness in detecting and estimating percent cover of *P. recta*, 2) determine the minimum percent cover of *P. recta* detected at each flight scale and 3) assess this detection method as a tool for resource managers. Naylor et al. [92] indicated that natural color aerial photography can be used to identify *P. recta* populations, even at low densities and is most effective in grassland communities or open forests with little canopy cover to inhibit detection. Future research may employ this technology to analyze more remote areas for *P. recta* invasion.

Containment and restoration
Containment and restoration experiments are critical when promoting regional invasive plant management research programs. There are, however, significant conceptual and logistical challenges to implementing scientifically sound restoration research. Michener [93] reviews these constraints and discusses appropriate research approaches and analytical tools for ecological restoration research.

In areas where invasive species are already well established, tools for effective containment and restoration activities are needed. In the past, weed control strategies that focused solely on the eradication of undesirable species by herbicide or fire often failed, as other weeds quickly colonized the area [58]. For decades, herbicides have been an integral part of invasive species management. For example in 1997, 25% of the 988 million acres of rangeland in the United States, were treated with herbicides [94]. The application of herbicide alone, however, is rarely successful in controlling invasive species. In the short term (1–5 years), herbicides may reduce invasive species abundance, although in the absence of a source of native seeds the treated area is often recolonized by the same species or by other invasive plants. For example, areas treated with herbicide for *Centaurea* spp and *E. esula* control often become dominated by *B. tectorum*, thus further stressing the plant community [94]. As a result, management approaches that integrate invasive species control with habitat restoration through the evaluation of integrated containment/restoration activities are of most value.

Little information exists to indicate whether herbicides are effective in reducing *P. recta* abundance and vigor, or whether subsequent sowing of native seeds facilitates the establishment of native species on treated areas. Consequently, a study was established to address which herbicides, rates, and timing of application are most effective to control *P. recta*, while minimizing impacts on native plant species. A further objective is to determine if post-herbicide reseeding facilitates native plant establishment. This study involves

screening six herbicides at two rates of application over three application periods on sites with extensive *P. recta* infestations (densities often > 100 stems/m^2). Following herbicide applications, half of each plot was sown with a native grass seed mix. A range of response variables, including *P. recta* control, and native and non-native species abundance and richness, were recorded [95]. Plots are being monitored for several years to understand longer-term implications of various herbicide and seeding treatments.

To complement the herbicide screening study, an experiment was established to examine the importance of prescribed fire, herbicide application, and native grass seeding on grassland restoration. In the PNW few studies have been conducted on the response of invasive plant species to fire, and only one limited study has explored the effects of fire on *P. recta* [96]. This information is helpful to land managers because it remains unclear if fire, an increasingly popular management tool, facilitates, inhibits or has no effect on the spread of *P. recta*. Basic information on plant species and community responses to fire are necessary for resource managers to assess ecological conditions and trends following treatments, and for the development of post-fire management strategies that enhance plant community restoration, wildlife habitat or other components of biological diversity. In this study [97], three prescribed fire treatments (spring, fall, and no burn) were used in combination with sowing a mix of six native grass species and the application of the best performing herbicide (over 1 year) from the previously described herbicide screening experiment. Reductions of *P. recta* abundance and change in overall community structure and composition, including native plants, are being evaluated.

Integrated tool experiments that combine invasive plant control with restoration activities are likely to be more successful in creating sustainable plant communities in the long-term. This study of fire, herbicide, and restoration seeding, supports information on the ecology of *P. recta*, and provides data on the species' response to fire, herbicide, and native seeding. Results from this study provide land managers, especially those interested in promoting native plant communities, guidance to integrate herbicides, fire, and native plant seeding into an overall invasive plant control program.

Adaptive management and interaction with land managers

Conducting scientifically rigorous research is fundamental to our regional research framework on invasive plant species. Scientific expertise from various sources is being coordinated with land managers to produce information about areas that are at-risk, human uses, and the land values associated with those areas.

Land managers involved in our program represent the United States Forest Service, United States Bureau of Land Management, Oregon Department of Fish and Wildlife, Oregon Department of Forestry, The Nature Conservancy, local weed management districts and private companies and landowners.

These managers provide on-the-ground concerns and information about day-to-day management activities while direct feedback from researchers hastens the process of adaptive management (Fig. 3). Designing and conducting research in collaboration with local land managers also is resulting in increased applicability of the research. Each study was conceived and implemented with land managers. During the course of data collection field tours to view experiments and field training sessions are conducted as an integral part of the regional research program.

Research results are often difficult to apply directly to large landscapes because managers do not always incorporate scale and the nested interaction of complex processes such as fire, herbivory, succession, land use change, or disturbance corridors into their activities. Researchers, on the other hand, do not usually integrate the routine operations of land managers, who are the end-users of invasive plant experiments, into their studies. The studies we present in our research framework were designed from the onset to incorporate the invasion process, scale, and land manager input. By using the adaptive management in our research framework (Fig. 2), we place research activities within a management context, and thereby avoid ineffectual approaches and overcome manager criticisms.

Conclusions

There are many plant species present east of the Cascade Mountains in the Pacific Northwest, as indicated in Table 1. Each of these species can be of concern to local land managers in the Blue Mountains Ecoregion. Hobbs and Humphries [30] suggest an approach to set priorities for management of invasive plants based on land value and the degree of disturbance or risk of invasion (Fig. 6). However, most extensive land management areas represent locations where determining management priorities is much more difficult than the process indicated by Hobbs and Humphries [30]. Scientists can provide insight into the management priority setting process by providing information on the biology of invasive species, invasibility of habitats, and effectiveness of management tactics. We believe that a regional network of scientists and natural resource managers working together is most effective in determining what species to study and to diminish the impacts of invasive plants on extensive land management systems. Scientific and other forms of expertise from various sources can be coordinated to produce state-of-the-art knowledge about natural resource areas that are at-risk and the human uses and values associated with those areas.

Experiments, risk assessments of invasive species, and projections of species spread across susceptible landscapes after introduction help managers evaluate the consequences of management activities, including doing nothing. Combining information about multiple species also should result in a powerful database for land managers to decide what areas and species should receive par-
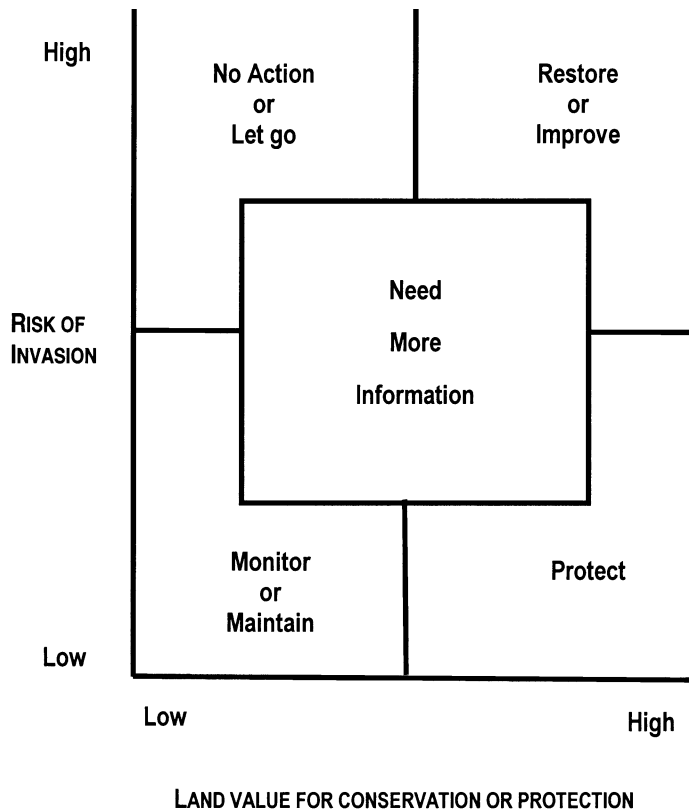
Figure 6. Assessment of management priorities for a region based on relative values of different sites for conservation and/or production, and their relative degree of risk to invasion. Modified from [25, 30].

ticular attention. Thus, scientifically rigorous and timely research is fundamental to a regional research framework (Fig. 2) for invasive plant management. Adaptive management (Fig. 3), where research results are continually brought forward and management practices are reassessed as new information becomes available, is a workable approach to integrate management and science to manage invasive plant species in extensive resource areas across a region [43].

Research can be advanced best with partnerships between scientists and land managers, where managers indicate crucial concerns and provide information about day-to-day management activities. Designing and conducting experiments in collaboration with local land managers can result in increased applicability of the research. A regional approach that places scientific study within a management context (Figs 2 and 6) can result in increased implementation of research results, continual adaptation of management plans and greater overall success in managing invasive plants.

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Allelopathy as a mechanism for resisting invasion: the case of *Polygonella myriophylla*

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Overview

Studies of the mechanisms by which grasses and herbs are excluded from the Florida scrub provide evidence that allelopathy by perennial shrubs in this community plays a primary role in preventing invasion of neighboring species. The Florida scrub serves as a compelling counter-example to recent papers linking the success of certain invasive plants to allelopathy, and suggests that the role of allelopathy as a mechanism in plant invasions is more complex than has been appreciated. This perspective deserves special emphasis given the current dominance of the viewpoint that invasive species are superior allelochemical species.

Polygonella myriophylla and resistance to invasion

Characteristics of the scrub community

The Florida sand pine scrub occurs on well-drained sandy soils along Florida's central Lake Wales ridge and coastal dunes. This community contains a number of perennial shrubs (e.g., *Polygonella myriophylla* (Small) Horton, *Conradina canescens* (Torr. & Gray) A. Gray, *Ceratiola ericoides* Michx., *Chrysoma pauciflosculosa* (Michx.) Greene, and *Calamintha ashei* (Weatherby) Shinners) for which there is evidence of allelopathic interference toward invasive grasses of the adjacent sandhill community. Scrub vegetation is vulnerable to fire, and sandhill grasses such as wiregrass (*Aristida stricta* Michx. *var. beyrichiana* (Trin. & Rupr.) D.B. Ward) and little bluestem (*Schizachyrium scoparium* (Michx.) Nash) would provide fuel for fires if they became established. Richardson and Williamson [1] proposed that allelopathic interference by the fire-sensitive scrub species deters invasion by fire-prone grasses, herbs, and pines of the neighboring fire-adapted sandhill community. The work on allelopathy in the Florida scrub has been the subject of a number of reviews [2–5]. Key points will be highlighted here.

Older literature reports sharp ecotones between scrub and sandhill communities, marked by a persistent bare zone 1–2 m in extent [6–8]. Due to extensive disruption of Florida's natural landscape, few of these boundaries remain. However, pronounced ecotones marked by a 1–2 m bare zone are observed where scrub sites border roadsides and fields, and sandhill species are absent. The success of *Polygonella myriophylla* and other scrub vegetation in preventing invasion by perennial, rhizomatous grasses like bahiagrass, *Paspalum notatum* Fluegga, along roadsides and fields (Fig. 1) is striking, and raises questions about the hypothesis that allelopathy is more likely to be important as a mechanism for opportunistic exotic invaders.

Figure 1. Patches of *Polygonella myriophylla* (left) dominate the edge of a scrub near Sun Ray, FL. This scrub borders an abandoned citrus field that has been invaded by bahiagrass, *Paspalum notatum*, and other ruderal species. The bare zone is approximately 1 m wide. (Original figure appeared in Weidenhamer and Romeo [9]; used with permission of Plenum Publishing Corp.)

Field investigations and bioassays

At a field site where a native scrub community had been disturbed by construction some time before, and ruderal species including bahiagrass had been able to invade and become established in a portion of the original scrub, a large patch of *P. myriophylla* was found that was more than 4 × 9 m in extent. It bordered an area of bahiagrass, and dead or dormant rhizomes of bahiagrass littered the bare zone (0.6–1 m wide) and were also found beneath the plant. Thus, it appeared that this was a case where, over time, *P. myriophylla* had invaded space previously occupied by bahiagrass. Soil properties across the ecotone were fairly uniform [9]. Soil cores for estimation of root mass were taken within the large patch of *P. myriophylla*, at the edge of the patch, in the

bare zone, and within the bahiagrass stand. Root mass of *P. myriophylla* at the edge of the patch was only 37% compared to *P. myriophylla* root mass in the center of the patch, and only 3% in the bare zone (Fig. 2). Given the low growth habit of *P. myriophylla,* which precludes significant shading, these results suggest a noncompetitive interaction between the two species [9]. Animal activity, which has been shown to contribute to the development of bare zones around shrubs in the California chaparral [10], has been ruled out as a cause of bare zones in the scrub [9].

Bioassays were conducted of soils collected biweekly for one year from beneath *P. myriophylla*, the bare zone, and adjacent grassed areas. Effects on both germination and growth of bahiagrass were pronounced. Relative to adjacent grassed area soil controls, average germination of bahiagrass was reduced 29% in *P. myriophylla* soil, and 19% in bare zone soil. Shoot dry weights were reduced 52% in *P. myriophylla* soil, and 19% in bare zone soil (Fig. 3). Nutrient analyses showed that bare zone soil was only slightly lower in P, K, Mg, organic matter, and total N than the *P. myriophylla soil.* The reduced growth in *P. myriophylla* soil relative to the bare zone is, thus, attributed to the presence of higher concentrations of allelochemicals. The reduced growth in *P. myriophylla* soil relative to grassed area controls was attributed to the combined effect of phytotoxins and slightly lower levels of P, K, and N in the *P. myriophylla* soil [9].

Figure 2. The distribution of root mass around a mature shrub shows that *P. myriophylla* root mass is concentrated beneath the shrub and does not extend into the bare zone, making resource competition an unlikely explanation for the bare zones around the plant. Data originally appeared in tabular form in [9].

Bahiagrass bioassay
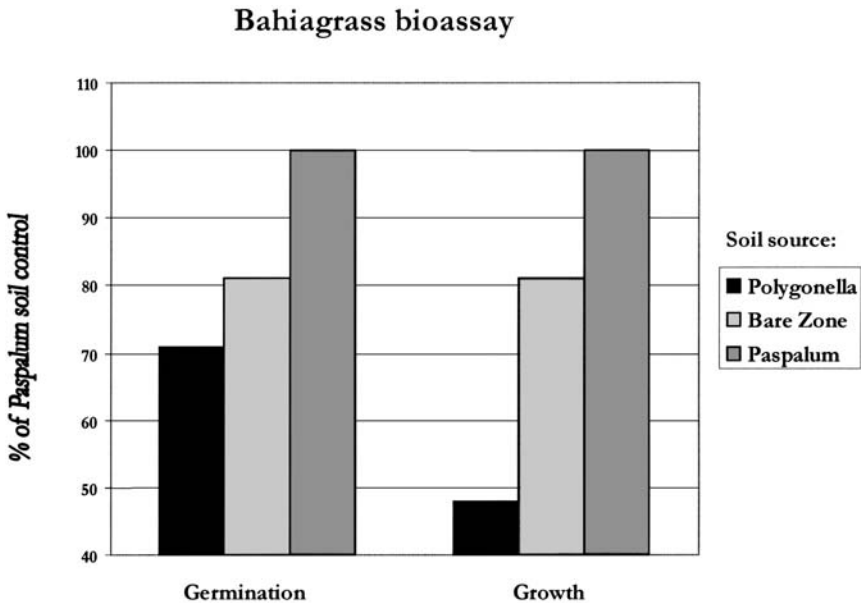
Figure 3. Summary results of bioassays with bahiagrass (*Paspalum notatum*) conducted on soils collected biweekly for one year from beneath *Polygonella myriophylla*, the surrounding bare zones, and adjacent grassed areas (predominantly *P. notatum*). The data presented here are averages for the entire year. Soils were assayed in 6-month sets, and differences in both germination and growth were significant between the three soil types. The original data and statistical analyses are presented in [9].

Environmental activation of plant allelochemicals

Glycosides of hydroquinone and gallic acid are the major allelochemicals of *P. myriophylla*, and occur in high concentrations in the foliage. Microorganisms readily degrade these compounds in soil. Arbutin is rapidly converted to hydroquinone, and hydroquinone is rapidly converted to benzoquinone (Fig. 4) [11]. Whole plant bioassays with soil treated with hydroquinone and gallic acid show increasing toxicity to bahiagrass long after these compounds disappear, suggesting the importance of microbial and non-microbial oxidation products in the allelopathic activity of this plant [12].

Environmental activation processes appear to be important for other scrub species as well. Aqueous leaf washes of *Ceratiola ericoides* contain the inactive dihydrochalcone ceratiolin. On exposure to light, ceratiolin degrades to the much more phytotoxic hydrocinnamic acid [4, 13]. Microorganisms rapidly degrade hydrocinnamic acid to acetophenone, which also has activity as a germination and growth inhibitor [14].

The importance of environmental and microbial processes in activating relatively non-toxic allelochemicals in Florida scrub plants implies that the use of bioassay-guided fractionation of crude plant extracts may be misleading when environmental transformation of plant allelochemicals is significant. The

Arbutin
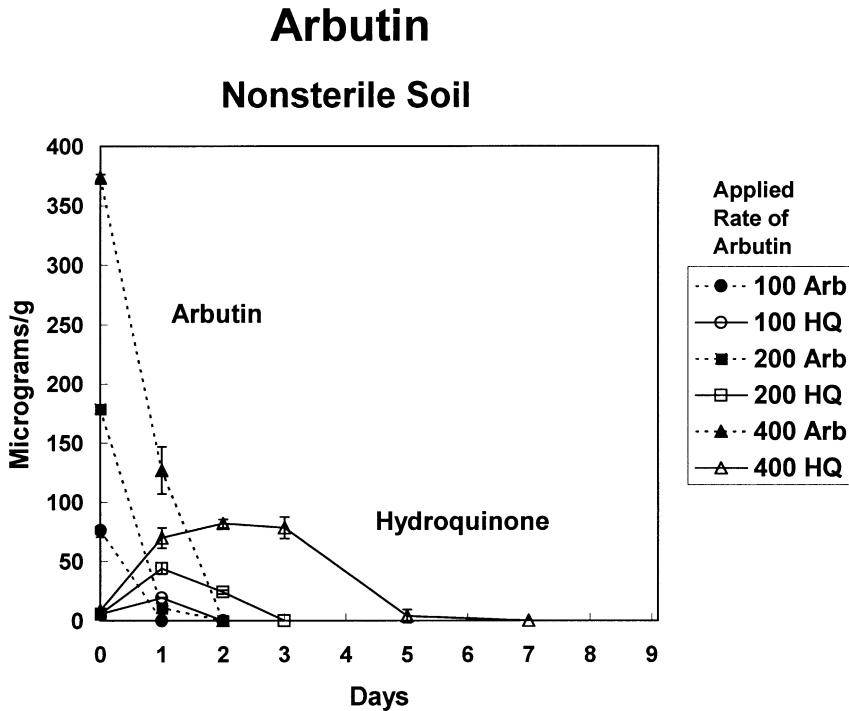
Nonsterile Soil

Figure 4. Degradation of exogenously applied arbutin (Arb) in nonsterile soil from beneath *Polygonella myriophylla*. Dashed lines show the disappearance of arbutin, while solid lines show the appearance and disappearance of hydroquinone (HQ), which was formed by microbial degradation of its glycoside arbutin. In sterile soil, arbutin was stable over the time period of the experiment. Bars indicate standard error. If not shown, standard errors are too small to depict visually. (Original figure appeared in Weidenhamer and Romeo [11]; used with permission of Plenum Publishing Corp.)

active compound(s) in allelopathic interactions may not be in the same chemical form found in the plant [11].

Role of environmental factors

The scrub environment is harsh. Soils are almost 100% sand, and available nutrients are low. Soil surface temperatures can reach 50 °C on sunny days, and there can be periodic drought during breaks between summer rains [9, 15].

The low organic matter and clay content of scrub soils likely increases the activity of any allelochemicals present in the soil, even though some water-soluble compounds would be expected to leach away during the frequent summer rains. Environmental stress factors such as high temperatures and nutrient limitation are known to increase the toxicity of allelochemicals, and nutrient limitation also increases allelochemical concentrations in some species [16–17].

There is evidence that environmental factors are important in mediating the activity of scrub allelochemicals. The toxicity of hydrocinnamic acid, the breakdown product of ceratiolin, to the sandhill grass little bluestem (*Schizachyrium scoparium*) was greater in low-N and low-K treatments during a greenhouse bioassay lasting over four months [18].

Noting the data that support increased allelopathic effects in resource-poor environments, Hierro and Callaway [19] predicted that "the invasibility of plant communities should increase as resource availability decreases." This prediction contrasts with models which hold that invasive species should be more successful in communities with fluctuating levels of resources [20]. In the Florida scrub, however, it appears that environmental factors that intensify allelopathic effects, such as low nutrients and high temperatures, play a role in the *defense* of this community against invasion. The general point is that allelopathy may also be a more common mechanism in structuring natural plant communities in resource-poor environments. While limited resources may increase the success of some invasive species with allelopathic potential, data from the Florida scrub suggest that limited resources may also work against invasive species in a community already defended by allelopathic mechanisms.

Role of plant density

Weidenhamer et al. [12] showed that allelopathic effects are increased at low plant densities. Bahiagrass (*Paspalum notatum*) was grown in soil treated with hydroquinone and gallic acid, the putative inhibitors from *P. myriophylla*. At eight weeks, shoot biomass of bahiagrass grown in soil treated with 400 µg/g of each compound was 63% of the corresponding control at a density of two seedlings per pot, but there was no inhibition in plants with 16 seedlings per pot. Stimulation of bahiagrass growth was observed at lower concentrations, and was also density-dependent. In communities like the Florida scrub, where plant densities are constrained by limited resources and harsh environmental conditions, it is likely that low plant densities contribute to the increased effectiveness of phytotoxins, and hence that there has been selective pressure for their production [12].

The role of allelopathy in plant invasions

The demonstration that allelopathy appears to play a primary role in preventing colonization by invasive grasses and herbs in the Florida scrub suggests that the hypothesis that allelopathy is a mechanism of primary importance in exotic plant invasions may not hold up in every community. A number of explanations have been posed to explain the success of weedy invasive species. The predominant one has been the "natural enemies hypothesis", which holds

that invading plants succeed because they have escaped natural enemies and pathogens that would otherwise suppress their growth [21–23]. Recent work with *Centaurea maculosa* Lam. provides some support for this hypothesis. Callaway et al. [24] found that soil microorganisms from the native European range of *C. maculosa* were strongly inhibitory to its growth, while soil microorganisms associated with *C. maculosa* in North America, where it is an invader, were much less inhibitory. Biomass of *C. maculosa* increased by 166% with sterilization of European soils, but only 24% with sterilization of North American soils.

There are, however, questions about whether escape from natural enemies is the major or only mechanism for the success of invasive plants. In a recent review, Hierro and Callaway [19] note that the release of biological control species, generally herbivorous insects, represents a test of the natural enemies hypothesis, and that most of these controls have not been effective for invasive plants [25]. They discuss evidence for the allelopathic effects of several invaders, and propose that allelopathy will be an important mechanism for exotic invasions because native vegetation may not have an evolved tolerance to chemical compounds produced by an invading plant. This model predicts that in native communities, where plants have had time to adapt to chemical compounds released into the environment, a reduced role for allelopathy would be expected [19].

Evidence for allelopathic interference by invasive species

Hierro and Callaway [19] noted that there are many invasive species for which allelopathy has been alleged, although the evidence is in many cases of dubious quality. However, there are a number of carefully conducted studies that provide evidence of allelopathic effects for important invasive species. Three examples are noteworthy and are reviewed below.

Crowberry

A series of investigations by Nilsson, Zackrisson, and co-workers ([26–30], reviewed in [31–32]) demonstrated that allelopathic effects of crowberry (*Empetrum hermaphroditum* Hagerup) contribute to conifer regeneration failure in Scandinavian forests. Crowberry is a fire-sensitive shrub that spreads primarily by vegetative propagation. It is not an exotic species, but has become more dominant as the frequency of fires in these forests has been reduced. Nilsson [30] designed experiments to separate allelopathic effects of crowberry from belowground competition. Root competition was reduced by the use of PVC pipes. Allelopathy was reduced by the application of activated carbon, which is an effective adsorbent for many organic compounds. The greatest inhibition of pine growth occurred when pines experienced both allelopathy

and resource competition [30]. The allelopathic inhibition has been traced to compounds in glandular trichomes on the leaf surface, and one compound (5-methoxy-3,3'-dihydroxystilbene, batatasin III) has been found to account for 28% of the observed activity [28].

Diffuse knapweed

Centaurea diffusa Lam. is a Eurasian species that has become invasive following its introduction to North America. Callaway and Aschehoug [33] grew *C. diffusa* in competition with grass species from its native Eurasia and closely related species from North America. Experiments were conducted with and without activated carbon to reduce the effects of allelochemicals including 8-hydroxyquinoline released by *C. diffusa*. *C. diffusa* had much stronger inhibitory effects on the growth of the North American grass species, and these effects were greatly reduced by the incorporation of activated carbon, again strongly supporting an allelopathic mechanism.

Spotted knapweed

Since its introduction into North America from Eurasia, *Centaurea maculosa* Lam., spotted knapweed, has invaded millions of hectares in the Pacific Northwest. Ridenour and Callaway [34] found that root exudates of *Centaurea* were inhibitory to *Festuca idahoensis* Elmer, and that this effect could be reduced by the addition of activated carbon. In further studies [35–36], it was found that *C. maculosa* roots exude a mixture of (±)-catechin. The (+)-catechin enantiomer shows activity against microbial root pathogens, while (–)-catechin is phytotoxic. Racemic catechin was isolated from field soil [35, 37] at concentrations shown to be inhibitory in bioassays. Using *Arabidopsis thaliana* (L.) Heynh., a susceptible species, it was shown that exposure to (–)-catechin triggers intracellular generation of reactive oxygen species, sequentially followed by a Ca^{2+} signaling cascade that results in extensive changes in gene expression and finally cell death [37]. Tests of (–)-catechin against native species displaced by *C. maculosa* have not yet been reported.

Recent studies suggest a more complex situation in the field. Carey et al. [38] report greenhouse experiments showing that *Centaurea maculosa* can parasitize carbon from neighboring *Festuca idahoensis*, a native bunchgrass, via soil arbuscular mycorrhizal (AM) fungi. They estimated that as much as 15% of the aboveground carbon in *C. maculosa* plants is obtained through carbon parasitism. Callaway et al. [39] explored interactions of *C. maculosa* with six North American native species in a field study with and without the application of the fungicide benomyl to reduce AM colonization of roots. Effects were complex, and *C. maculosa* growth was either stimulated or inhibited depending on the specific combination of fungicide and competitor. Finally, as

noted above, the recent finding [24] that Eurasian soil microbes have a strong inhibitory effect on *C. maculosa* growth, while North American microorganisms are much less inhibitory suggests that the success of *C. maculosa* may involve both the escape from certain enemies and pathogens as well as allelopathy.

Conclusions

Past research on allelopathy has been plagued by methodological criticisms [2, 5, 40], and one lingering result of this has been that allelopathy has often been viewed as the "hypothesis of last resort". However, a body of recent work provides a new basis for supporting allelopathic mechanisms for some striking phenomena – the noteworthy examples include the obvious, devastating success of some invasive species (described above), as well as the equally impressive resistance to invasion by a natural community seen in the Florida scrub. Furthermore, the success of scrub vegetation in deterring invasion raises questions about the hypothesis that allelopathy will be most likely to occur as a mechanism that enables exotic invasions. The argument that allelopathy is likely to be of limited significance in natural communities is based on the assertion that over time, plants will likely have evolved tolerance to chemical defenses of their neighbors [19, 40]. However, the evolution of tolerance to chemical defenses should be no more significant among neighboring plants in terrestrial plant communities than it is for herbivores or pathogens of these plants. There are many examples of evolution of tolerance to toxins by specialist herbivores and pathogens, but for unadapted organisms in natural communities these defenses usually remain effective.

Bioassays with *Centaurea diffusa* imply an important role for allelopathy in *natural* community structure, a point which has been overlooked [33]. While activated carbon increased the growth of North American grasses at the expense of *C. diffusa* (supporting the hypothesis of allelopathic effects by *C. diffusa* in this exotic environment), the growth of Eurasian grasses from its native habitat was reduced by activated carbon, and *C. diffusa* biomass increased. These results are consistent with allelopathic inhibition of *C. diffusa* by grasses in its native habitat, and contrary to the hypothesis that allelopathic interactions will be most important for exotic species invading new habitats. Considered together with work on the Florida scrub and on non-exotic invaders such as crowberry (*Empetrum hermaphroditum*), these results require the admission that while allelopathy may be of importance to the success of certain exotic invaders, it may be an important factor, along with competition, herbivory, and abiotic factors, in structuring natural plant communities.

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Section 2: Agricultural aspects

Ecology and management of an exotic weed *Phalaris minor*

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Introduction

Phalaris minor Retz. (littleseed canarygrass), belonging to the family Poaceae, is an annual non-native cropland weed of India (Fig. 1a). It is found predominantly in fields cultivated for wheat (*Triticum aestivum* L.) in the states of Haryana and Punjab in northwestern India (Fig. 2). *P. minor* is indigenous to

Figure 1. (a) A field of cultivated wheat infested with *P. minor;* (b) a few *P. minor* plants growing on a roadside in the state of Punjab; (c) labour carrying *P. minor* after manual weeding; and (d) a field showing that *P. minor* grows taller than wheat

Figure 2. Worldwide distribution of *P. minor* (above); its infestation in the Indian States in 1987 (gray scale); and areas of isoproturon resistance in 1997 (black scale). Source: [1]. Reproduced with permission from Elsevier.

the Mediterranean region and was introduced to Australia, Africa, Hawaii, India, Pakistan and since then to many countries of the world [1] (Fig. 2). It is a major weed of Latin America [2]. It supposedly was introduced in India through import of Mexican wheat [1]. *P. minor* adversely affects the growth

and yield of wheat, particularly in the wheat–rice (*Oryza sativa* L.) cropping system in India and Pakistan [1, 3, 4].

Wheat yield reductions are positively correlated with *P. minor* densities [5]. A density of 50 and 250 *Phalaris minor* plants m^{-2} reduced wheat yield by 8% and 44%, respectively [6]. Continuous and excessive use of isoproturon (*N,N*-dimethyl-*N*'-[4-(1-methylethyl)phenyl]urea) has selected for resistant biotypes of *P. minor* in Haryana and Punjab [1]. Isoproturon-resistant *P. minor* has caused yield reductions of 30–80% and thus massive income losses. New herbicides, such as clodinafop ((*R*)-2-[4-[(5-chloro-3-fluoro-2-pyridinyl)oxy]phenoxy]propanoic acid), fenoxaprop ((±)-2-[4-[(6-chloro-2-benzoxazolyl)oxy]phenoxy]propanoic acid), sulfosulfuron (1-(2-ethylsulfonylimidazol[1,2-*a*]pyridin-3-ylsulfonyl)-3-(4,6-dimethoxypyridimidin-2-yl)urea) and tralkoxydim (2-[1-(ethoxyimino)propyl]-3-hydroxy-5-(2,4,6-trimethyl phenyl)cyclohex-2-enone), resulted in four-fold increases in herbicide cost from INR 450 per ha (approximately US$ 10 per ha) to INR 1,500–1,800 per ha (approx. US$ 33–40 per ha) [7].

Poor farmers, due to inadequate finances, continue to use isoproturon, which further magnifies the problem of *P. minor* resistance to isoproturon. Inadequate management of *P. minor* results in low wheat yield; consequently low income and lack of capital in the subsequent year, which is a self-perpetuating mechanism [8].

Most research on *P. minor* has focused on its management; questions regarding its ecology largely remain neglected. These include: 1) why is *P. minor* the predominant weed in wheat fields, particularly in a wheat–rice cropping system; 2) why is it largely restricted to cultivated fields and not escaping its field boundaries; and 3) what makes a favorable habitat for *P. minor* establishment and growth? Answers to these questions may help in designing an effective management strategy to control *P. minor*.

The aim of this article is to discuss: 1) *P. minor* as an invasive weed; 2) favorable habitats for *P. minor*; 3) agricultural practices that affect herbicide efficacy on *P. minor*; iv) correlation between *P. minor* biotypes, herbicide resistance, and substratum ecology; and v) an integrated management approach for *P. minor*.

Is *Phalaris minor* an invasive weed?

There are diverse views concerning invasive weed terminology [9–12]. Colautti [13] reviewed invasion terminology and argued in support of stage-based terminology for invasive plants. Pyšek et al. [14] suggested definitions for native, exotic, naturalized, and invasive plants (Tab. 1). However, these authors cautioned that their definitions might not fit universally because various stages of invasion represent a continuum. *P. minor* is not native to India, and therefore is an exotic plant. Two questions arise: 1) whether *P. minor* can be identified as a naturalized plant and 2) is it an invasive plant?

Table 1. Terminology for alien plants

Terminology, synonyms (in parenthesis), definition, and interpretation

Native plants (indigenous plant)

Taxa that have originated in a given area without intentional or unintentional involvement of humans. *P. minor* is not a native plant of India, because it was introduced from Mexico.

Alien plant (exotic plant, introduced plant, non-indigenous plant/species (NIS), non-native plant)

Taxa that are not native to the area and whose presence in the area is due to intentional or unintentional human involvement. *P. minor* is an exotic or alien plant of India because it is not native and is present in cultivated fields, particularly wheat.

Naturalized plant (established plant)

Alien plant that sustain self-replacing populations for at least ten years without direct intervention of humans by recruitment from seed or ramets capable of independent growth. *P. minor* is not a naturalized species, because it is successful in cultivated fields but rarely observed in abandoned fields. Long-term studies are needed to determine the survival rate and growth of *P. minor* in wheat fields abandoned for at least ten years.

Invasive plant (invader)

Invasive plants are a subset of naturalized plants that reproduce in large number at considerable distance from the parent plant, and thus have the potential to spread over a large area. Currently we do not have evidence that *P. minor* is an invader, because *P. minor* has restricted itself to cultivated fields and its presence in northwestern India is due to wheat seed contamination.

Terminology for *P. minor*

Based on field observations and empirical evidence of the ecology, *P. minor* can be best identified as an alien (exotic or non-indigenous) weed in India, because: i) it is a non-native plant; ii) it is not escaping its boundaries and is largely restricted to cultivated fields; and iii) it is growing where it is not desired, causing considerable crop damage (particularly wheat), and therefore has significant economic and environmental (due to extensive herbicide use to control *P. minor*) impact.

Modified after [14]. Reproduced with permission from Editors, Taxon

We are not aware of any study showing the potential of *P. minor* to persist in cultivated fields abandoned for several (>10) years. *P. minor* maintains self-replacing populations through seeds in cultivated fields with human involvement. During wheat harvest, *P. minor* seeds are incorporated into the soil, which serves as a seed bank for subsequent years. Agricultural practices, such as tillage, irrigation and fertilization, seem necessary for *P. minor* to establish and grow successively each year. Therefore, *P. minor* is not a naturalized species in India.

At present we do not have sufficient empirical evidence to identify *P. minor* as an invasive weed. *P. minor* has the following characteristics: i) new to the region, i.e., non-native, ii) not desirable in cultivated fields, iii) causes significant economic losses in wheat production, and iv) herbicide use for its control causes environmental concerns. Based on the above characteristics, *P. minor* is recognized as an exotic weed and should not be identified as a naturalized plant (Tab. 1).

To identify *P. minor* as an invasive weed, it should escape its boundaries and must reproduce at a considerable distance from the parent plant. During our field visits, *P. minor* was mainly restricted to cultivated fields and rarely observed in abandoned fields or on roadsides (Fig. 1b). However, we are not sure whether the weed has escaped its boundaries; perhaps growers have dropped seeds of *P. minor* on the ground while transporting the weed after manual removal from the field (Fig. 1c). Therefore, the question of identifying *P. minor* as an invasive weed still needs further investigations.

What makes a favorable habitat for *P. minor*?

The resource fluctuation hypothesis explains habitat susceptibility to invasion [15, 16]. An increase in unused resources makes a community susceptible to invasion [16]. An increase in resources occurs when resource use declines or when there is an increase in resource supply [16, 17]. Disturbance, such as tillage or herbicides, releases resources and therefore is a key determinant in invasion [18–21].

P. minor thrives under moist, nutrient-rich conditions [22]. For example, the dry weight of *P. minor* increased by 42% when nitrogen was increased from 30 to 120 kg ha^{-1} while wheat biomass increased by only 9% [23]. Cultivated fields therefore have unused resources that *P. minor* uses to establish and thrive. Disturbance such as tillage further aids in its establishment; for example, plowing brings seeds of *P. minor* up to the soil surface.

Mustard (*Brassica campestris, B. napus* or *B. juncea*) and wheat are the preferred winter crops in northern India. The reduced success of *P. minor* in mustard fields compared to wheat is likely due to mustard's vigorous growth and lower requirement for irrigation compared to either *P. minor* or wheat.

Farmers in the wheat–rice belt prefer to cultivate dwarf wheat varieties due to their high potential yield. *P. minor*, however, grows taller than dwarf wheat (Fig. 1d) and thus is highly competitive for light. Paul and Gill [24] showed that height, dry matter, yield and number of nodes on primary shoot of *P. minor* are considerably reduced when grown with tall wheat varieties compared to semi-dwarf and dwarf varieties. These authors suggested that semi-dwarf wheat varieties should be cultivated, because they combine weed smothering potential and reasonable grain yield.

In summary, the habitat created by wheat cultivation is more suitable to *P. minor* establishment and survival than the habitat in mustard crops. Resources, particularly nutrients and light, are important factors for *P. minor* establishment and growth. Allelopathy has been suggested as a mechanism for its interference to weed species [25–27], but we do not have any empirical evidence to support the hypothesis that mustard could interfere with *P. minor* growth and establishment through release of allelochemicals. This aspect needs further experimentation.

P. minor is a bigger problem in wheat–rice cropping systems compared to where rice is not sown after wheat. Wheat–rice cropping systems are prevalent in Punjab and Haryana where *P. minor* has been selected for herbicide resistance [1, 22]. Anaerobic conditions due to cultivation of lowland rice may contribute to maintaining the viability of *P. minor* seeds. Parashar and Singh [28] found that *P. minor* seeds enter into secondary dormancy under anaerobic conditions. It is hypothesized that *P. minor* seeds have potential to tolerate oxygen stress due to synthesis of secondary metabolites that change membrane permeability.

Management

Herbicide-resistant weed species are a serious threat to agriculture, and their management is receiving considerable attention from researchers and industry [29]. Although manual removal of *P. minor* still occurs (Fig. 1c), farmers rely heavily on chemical control (Tab. 2). Isoproturon has been used to control *P.*

Table 2. Herbicides recommended for *P. minor* control

Herbicide	Mode of action	Chemical class	Time of application
Metsulfuron (Escort/Ally)	ALS inhibitor	Sulfonylurea	Pre- & Post-emergence
Sulfosulfuron (Leader)	ALS inhibitor	Sulfonylurea	Pre- & Post-emergence
Tribenuron (Express)	ALS inhibitor	Sulfonylurea	Post-emergence
Isoproturon (Techical)	PS II inhibitor	Phenylurea	Pre- & Post-emergence
Chlorotoluron	PS II inhibitor	Phenyl urea	Pre- & early post-emergence
Metribuzin (Sencor)	PS II inhibitor	Triazine	Pre- & Post-emergence
Atrazine (AAtrex)	PS II inhibitor	Triazine	Post-emergence
Terbutryn (Prebane)	PS II inhibitor	Triazine	Pre- & Post-emergence
Metaxuron (Dosanex)	PS II inhibitor	Subsituted urea	Pre- & Post-emergence
Methabenthiazuron (Tribunil)	PS II inhibitor	Subsituted urea	Post-emergence
Clodinafop (Topik)	ACCase inhibitor	Aryloxyphenoxy propionate	Post-emergence
Diclofop (Hoegrass)	ACCase inhibitor	Aryloxyphenoxy propionate	Post-emergence
Fenoxaprop-P (Cheetah super, Whip)	ACCase inhibitor	Aryloxyphenoxy propionate	Post-emergence
Tralkoxydim (Grasp)	ACCase inhibitor	Cyclohexanedinone	Post-emergence
Pendimethalin (Stomp)	Microtubule-assembly inhibitor	Dinitroaniline	Pre-emergence
Nitrofen	PPO inhibitor	Diphenylether	Pre-emergence or pre-plant incorporated

ALS, acetolactate synthase; PS, photosystem; ACCase, acetyl-CoA carboxylase; PPO, protoporphyrinogen oxidase

minor in wheat for the last 30 years [30]. Continuous and excessive use of iso-proturon has resulted in selection for resistant biotypes of *P. minor* [1]. Sharma et al. [31] found that isoproturon at $0.5–1.5$ kg ha^{-1} applied pre-emergence significantly inhibited seedling emergence of a Delhi biotype but not a Haryana biotype of *P. minor*. Delhi biotypes were completely killed by isoproturon at 1.5 kg ha^{-1} applied pre-emergence and at all post-emergence doses. However, the Haryana biotype was only killed at the highest post-emergence dose of 1.5 kg ha^{-1}. Resistant *P. minor* biotypes in Punjab were not controlled by doubling the recommended dose of isoproturon to 1.9 kg ha^{-1}, which was phyto-toxic to wheat [32].

P. minor biotypes in the Middle East developed resistance to fenoxaprop-P [33]. Resistance of *P. minor* to isoproturon in India was reported in 1990. Since then, several alternative herbicides are recommended for *P. minor* control, such as clodinafop, fenoxaprop-P, sulfosulfuron, trifluralin (2,6-dinitro-*N,N*-dipropyl-4-(trifluoromethyl)benzenamine), diclofop (2-[4-(2,4-dichlorophe-noxy)phenoxy]propanoic acid), 2,4-D ((2,4-dichlorophenoxy)acetic acid), metribuzin (4-amino-6-(1,1-diethylethyl)-3-(methylthio)-1,2,4-triazin-5(4*H*)-one), and tralkoxydim (Tab. 2).

Following the reports of isoproturon-resistant biotypes of *P. minor* in 1990s, the list of alternate herbicides recommended for its control included fenoxaprop-P. Later, Heap [33] reported detection of fenoxaprop-P resistance in *P. minor*. Thill and Lemerle [34] discussed world wheat and herbicide resistance development. They state that while trifluralin may injure wheat, chlorotoluron (*N'*-(3-chloro-4-methylphenyl)-*N,N*-dimethylurea) and tralkoxy-dim may be useful for *P. minor* management in wheat.

Kaur et al. [35] conducted glasshouse experiments to explore the potential of isoxaflutole (5-cyclopropyl-4-isoxazolyl)[2-(methylsulfonyl)-4-(tri-fluromethyl)phenyl]methanone) to control *P. minor* and reported that a concentration of 0.5 mg L^{-1} reduced *P. minor* shoot height without affecting wheat. Also, isoxaflutole did not alter pH, organic matter, and macro or micro inorganic ions. However, this response may be restricted to soil type and dose of herbicide used in the study. Isoxaflutole and metsulfuron (2-[[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]carbonyl]amino]sulfonyl]benzoic acid) may be better herbicides than atrazine (6-chloro-*N*-ethyl-*N'*-(1-methylethyl)-1,3,5-triazine-2,4-diamine) for *P. minor* control (Fig. 3), field trials are needed to substantiate the glasshouse results.

Resistance of *P. minor* to isoproturon is governed by an increased activity of cytochrome (Cyt) P450 monooxygenase enzyme. Singh et al. [36] studied the effect of the monooxygenase enzyme inhibitor, ABT (1,aminobenzotria-zole), on the activity and rate of degradation of isoproturon in resistant and susceptible biotypes of *P. minor*. The resistant biotypes had higher activity of enzymes responsible for isoproturon degradation.

Questions that need to be addressed are: i) why does continuous herbicide use, e.g., isoproturon, lead to high activity of Cyt P450 monooxygenase, and ii) how many monooxygenase enzymes are involved in isoproturon degrada-
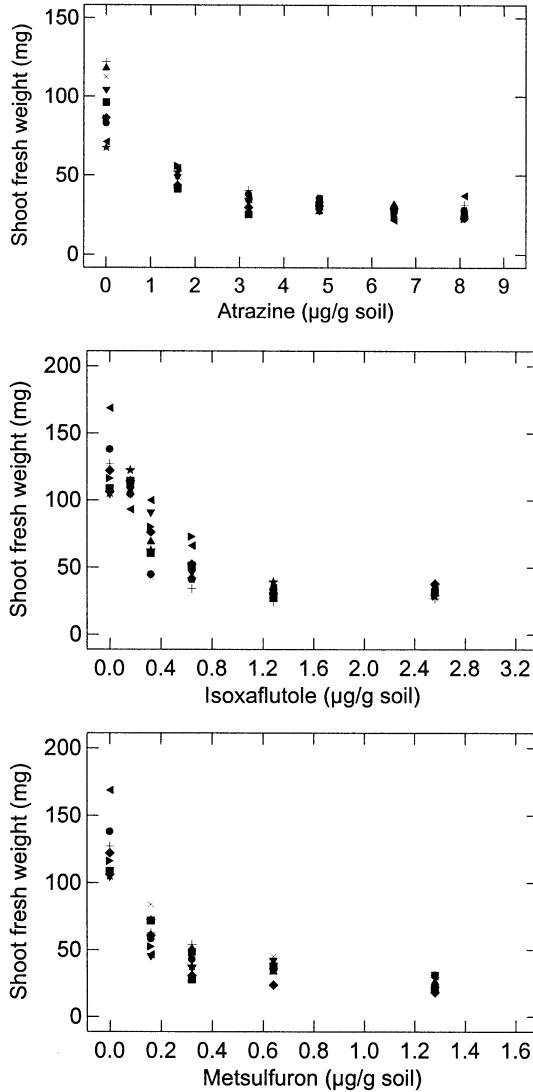
Figure 3. Effect of atrazine, isoxaflutole, and metsulfuron on shoot fresh weight of *P. minor*. Values for 10 replicates are shown by different symbols.

tion? P450s are known to metabolize phenylurea herbicides. Plant Cyt P450 CYP76B1 purportedly is the major phenylurea-metabolizing P450 enzyme and likely plays an important role in detoxification of PS II inhibitors [37]. Robineau et al. [37] reported that CYP76B1 is strongly induced by xenobiotics, e.g., phenylurea herbicides. We hypothesize that in resistant biotypes of *P. minor*, CYP76B1 is induced and involved in isoproturon metabolism.

However, CYP76B1 was not induced in susceptible *P. minor* biotypes and iso-proturon was degraded more slowly. The validity of this hypothesis needs experimental confirmation.

Agricultural practices and herbicide efficacy

Agricultural practices specific to the region may influence herbicide activity. After harvesting wheat or rice, unharvested straw is left in the field, and some-times is burned to reduce the amount of straw (Fig. 4). Farmers in northwest-ern India incorporate unharvested straw (unburned or burned) into soil [38]. Kaushik and Inderjit [39] studied the effect of rice straw (unburned and burned) incorporation on phytotoxicity of isoxaflutole to *P. minor*. The soil amended with rice straw, especially burned rice straw, reduced the level of *P. minor* control attained with isoxaflutole.

Chhokar and Malik [22] suggested that rotation of crops and herbicides are two effective ways to minimize herbicide resistance in *P. minor*. Heavy infesta-tions of *P. minor* are found mainly with a wheat–rice cropping system, which provides favorable conditions for emergence, growth, and development of *P. minor* seedlings [40, 41]. Malik and Singh [41] surveyed wheat fields at 10 km intervals and interviewed 100 growers. They concluded that evolution of resist-ant *P. minor* biotypes was higher (67%) in the areas with rotations of continu-ous wheat–rice compared to rice–berseem (*Trifolium hybridum*)–sunflower (*Helianthus annuus*)–wheat (8%), cotton (*Gossypium hirsutum*)–pigeon pea (*Cajanus cajan*)–wheat (16%) or sugarcane (*Saccharum officinarum*)/vegeta-bles–wheat (9%). The rotation of wheat with non-cereal crops, such as sun-flower or sugarcane, likely stimulates seed germination of *P. minor*, which then

Figure 4. A cultivated field showing unharvested rice straw, both unburned and burned.

may be controlled through tillage or herbicides, thereby reducing the *P. minor* seed bank [29, 34]. However, this aspect needs further experimental evidence.

Herbicide efficacy and soil factors

Soil has many features that influence the behavior, persistence, and bioavailability of soil-applied herbicides. Soil organic matter, clay content, pH, and moisture generally vary from field to field, and thus influence bioactivity of soil-applied herbicides [42]. Selected soil properties – organic matter and clay content, pH, and cation exchange capacity – influence the fate and behavior of herbicides in soil [42, 43]. Hydrolysis of sulfonylurea herbicides, for example, is temperature- and pH-dependent [44, 45]. Triasulfuron (2-(2-chloroethoxy)-*N*-[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]carbonyl]benzenesulfon-amide) [46] and amidosulfuron (*N*-[[[[(4,6-dimethoxy-2-pyrimidinyl)amino] carbonyl]amino]sulfonyl]-*N*-methylmethanesulfonamide) [47] become inactive at low pH, because they rapidly degrade under those conditions. The amount, distribution, and physical and chemical properties of various organic and inorganic soil constituents along with the type of herbicide used, dose applied, and prevailing climatic conditions influence herbicide movement in soil, which affects herbicide uptake by target plants [48, 49].

Sprague et al. [50] reported that isoxaflutole degradation was pH-dependent. Degradation was much faster at pH = 10 (86%) compared with pH = 4 (16%) or pH = 7 (20%). Isoxaflutole rapidly converts to diketonitrile in plants and soil, which is an active component of isoxaflutole that inhibits HPPD (4-hydroxyphenylpyruvate dioxygenase) enzyme [51–53]. Diketonitrile further is converted into an inactive benzoic acid derivative and finally forms carbon dioxide [53]. The term 'active herbicide' refers to the sum of the phytotoxicity of isoxaflutole (parent compound) and its biologically active degraded metabolite, diketonitrile.

Fields in northern India are irrigated with tube-well water and ground water that is saline at some locations. When fields are irrigated with saline ground water, soil pH and the concentration of soluble salts often are affected, which can influence the fate of soil-applied herbicides. Additionally, several fields in Haryana and Uttar Pradesh are infested with the perennial weed *Pluchea lanceolata* [54]. Inderjit [55] reported that *P. lanceolata* has potential to alter soil chemistry, particularly the concentration of soluble salts, chloride ions and phenolics. *P. lanceolata* may affect the efficacy of soil-applied herbicides for *P. minor* control, but this has yet to be documented.

Residual effects of herbicides employed to control P. minor

Herbicide persistence is an important consideration when choosing a herbicide for *P. minor* control. Mung bean (*Phaseolus aureus*) is often grown after wheat

harvest during the fallow period. In addition to being used for *P. minor* control, herbicides such as metsulfuron and atrazine are also used to control weeds in a wheat–rice cropping system, including weeds of the fallow crop. Kaushik and Inderjit [56] found that isoxaflutole reduced shoot growth of mung bean, while isoxaflutole and metsulfuron reduced chlorophyll concentration. Therefore, before recommending a herbicide for *P. minor* management, it is important to assess its potential effect on succeeding crops.

Conclusion

P. minor is an alien weed with serious environmental and economic consequences. Although there is appreciable progress in the area of *P. minor* management through herbicides, its ecology still needs to be explored. Vilà et al. [57] suggested that there is a need to assess and quantify the impact of alien species at several levels of ecological complexity in order to gain influence in their management and control. Several herbicides are available for *P. minor* control (Tab. 2); however, the joint action of herbicides with different molecular targets to *P. minor* management has not been well investigated.

There is a need to utilize an integrated approach that combines ecological and agronomic aspects to design better *P. minor* management. Possible avenues of future research are: 1) use of novel selective herbicides, 2) mixtures of herbicides with different molecular targets, 3) crop rotation, zero tillage, narrow row spacing, early sowing, and improved straw management, and iv) allelopathic wheat cultivars. Questions addressing the ecology of *P. minor* include: 1) what makes a habitat favorable for *P. minor*; 2) what characteristics of *P. minor* make it successful in wheat fields; and 3) why it is not escaping its field boundaries?

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Reducing agroecosystem vulnerability to weed invasion

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Invasion opportunities

Invasions, whether human, animal or plant, are most successful when weaknesses and opportunities in communities are successfully exploited. Invading species and the habitats they invade can both influence invasion outcomes [1, 2]. In plant communities, the niches that allow avenues of introduction for invading plants can be reduced by careful agronomic management.

Although strict definitions of plant invasions usually involve species expansion in an area not normally occupied by that species [3], we consider the annual proliferation of weeds in crop canopies to be an invasion of the space intended for crop species. Whether it is appropriate to label repeated weedy incursions in agricultural land as establishment or invasion processes is debatable. The subject of this chapter is restricted to the repeated invasions of long-established common weeds in annual cropping systems, as opposed to invasions by exotic or alien plant species. Nevertheless, management techniques that reduce agroecosystem vulnerability to long-established weeds will also restrict invasive opportunities for exotic species.

Herbicide application has traditionally been an effective and relatively economical means of managing weeds in crops, and can be important in ensuring that new weed introductions do not proliferate in cropland and adjacent areas. However, over-dependence on herbicides can lead to shifts in weed community composition. Anecdotal evidence indicates that the widespread use of growth regulator herbicides in western Canada in the 1950s and 1960s resulted in an eventual increase in the incidence of herbicide tolerant dicot weeds such as hempnettle (*Galeopsis tetrahit* L.) and smartweed (*Polygonum* spp) and monocot weeds such as wild oat (*Avena fatua* L.) and green foxtail (*Setaria viridis* (L.) Beauv.) The incidence of herbicide resistant biotypes has also increased dramatically over the last twenty years [4]. In addition to varying in their response to herbicides, resistant and susceptible weed biotypes can differ in several other respects including competitiveness [5] and seed dormancy characteristics [6]. Thus a more holistic approach to weed management

is necessary since relying on herbicides as the sole strategy can simply shift the balance in favour of invasions from alternative weed species or biotypes with variable genetic and phenotypic traits. Here we discuss management techniques that may be used to reduce agroecosystem habitat vulnerability to the invasion and establishment of weeds in cultivated crops.

Healthy crops limit weed invasion

Most agricultural weeds have rapid growth rates [7–9] and a high relative susceptibility to the negative effects of shade [10, 11]. They have adapted over long periods of time to the repeated cultivation of annual crops [12]. Cropping systems impose major disruptions on natural ecosystems [13], and maintain plant communities at very early stages of succession [14]. Crop monocultures are commonly grown over hundreds or thousands of hectares under resource-rich cultural conditions [15]. Indeed, annual monoculture cropping favours all three habitat characteristics that encourage plant invasions: disturbances, low species richness and high resource availability [1]. In addition, environments with low climatic and herbivore resistance to specific weeds also favour the proliferation of those species [16].

Viable weed propagules can invade and establish themselves when they occupy a "safe site" [17]. In annual monoculture cropping, tillage and/or herbicides are commonly employed to "clear" the ground in order to successfully establish the desired crop. This major disturbance before seeding helps provide the safe site that weeds require to establish and thrive in agroecosystems [9, 11, 18]. After soil disturbance, given their superior colonizing abilities, weeds can rapidly preempt growing space [16, 19] and avail themselves of resources intended for crop growth. Therefore, when, how, and to what degree cropping areas are disturbed can determine whether crop or weed establishment is favoured.

The health status of a crop influences its susceptibility to weed invasion. Crop health implies that crop roots and shoots are robust and will compete with weed species to the full extent of their genetic potential. In situations where crop health is compromised due to environmental limitations such as temperature extremes (frost and heat stress), restricted growing-degree days, limited available water and light [20], weed safe sites will increase. Given the diverse community of weeds present in most agricultural soil seed banks, there is probably at least one weed species that will be favoured by a particular environmental "limitation" more than the crop. Plant diseases and insect pests may also reduce crop health and limit a crops ability to deter weed invasion. It may also be detrimental to crop health, as well as biologically inefficient, to manage fields for yield goals significantly higher or lower than the attainable yield in a given agroecosystem [21]; in such fields, lower crop health and vigour exposes niches for weeds to exploit. Lastly, crop health is dependent upon soil

health. Therefore, practices such as zero tillage that retain crop residues and increase soil biodiversity will sustain crop health [22].

Field borders may be particularly susceptible to weed invasion. The edge of the field is the first point of contact for equipment that may be carrying weed propagules. In addition, field borders are usually more intensively disturbed and degraded than other areas of the field, and may require more careful management to ensure crop health.

Crop vulnerability to weed invasions can be limited if light, nutrient, and water resources are rapidly captured by the crop. It is imperative that crop managers facilitate rapid crop emergence and early crop growth to counter the invasive characteristics of weeds. Competitive cultivar selection, careful seed placement, optimum seeding rates, strategic fertilizer placement, and diverse crop rotations, which favour optimal crop health, will minimize the probability of successful weed invasions. Combining some of these factors at optimal levels will reduce the need for herbicidal intervention and improve efficacy when herbicides are necessary.

Competitive cultivar selection

Some crop species compete with weeds better than others [23, 24]. For example, in central Alberta, barley (*Hordeum vulgare* L.) is generally more competitive than canola (*Brassica napus* L.), which is generally more competitive than field peas (*Pisum sativum* L.) [25]. In addition, crop species exhibit considerable intraspecific variation in their competitive ability with weeds. Differences in competitive ability among cultivars of the same crop species has been demonstrated in narrow-row crops such as barley [26, 27], canola [28–30], wheat (*Triticum aestivum* L.) [31–35], peas [36–38], and rice (*Oryza sativa* L.) [39–44]. Mohler [45] provides a comprehensive summary of literature documenting genotypic variation in competitive ability among crop species.

Intraspecific competitive differences with weeds among row crop cultivars such as corn (*Zea mays* L.) and sorghum (*Sorghum bicolour* (L.) Moench.) have also been documented [46–48]. However, weed invasions appear to be more ably limited in wide-row crops by simply using narrower row spacings as opposed to using competitive cultivars. For example, in soybeans (*Glycine max* L. Merr.), weed populations were significantly reduced by combining decreased row spacing with increasing plant populations [49, 50]. Narrowing row spacing has also increased the competitive ability of grain sorghum with weeds [51] and dry bean (*Phaseolus vulgaris*) with hairy nightshade (*Solanum sarrachoides*) [52]. Cultivar height, leaf architecture and leaf area all contribute to the competitive ability of specific cultivars, but it is probably just as important to select cultivars that are well-adapted to specific soil zones and ecoregions as it is to concentrate on competitive plant archetypes.

Careful seed placement

For crop seedlings to occupy space early and successfully compete with weeds [45], careful placement of seed in the soil is essential. Careful seed placement is a management technique that requires little or no additional costs. Nevertheless, it makes little sense to purchase seed and other physical inputs such as fertilizer and fail to give crop seed the best possible chance of defending itself against weeds.

Careful placement of seed in the soil may involve several compromises. Seeding depth must be sufficient to place the seed near soil water, but shallow enough to facilitate rapid crop emergence. Packing should be substantial enough to favour adequate seed–soil contact but not cause "hard-pan" or crusting. Packing should also be over the crop row and not extend too far into the inter-row space so as not to favour weed emergence. Crops should be seeded as soon as possible after weeds are removed with pre-seed tillage or herbicides to get a competitive edge on and avoid yield losses from early-emerging weeds [53–55], but care should be taken to avoid leaving excessive spaces between drill passes since this can provide safe sites for weeds to proliferate and compete with the crop (Fig. 1). It is also important to ensure that sufficient physical separation exists between crop seed and fertilizer salts, since close prox-

Figure 1. Mature barley with extra space between seeding drill passes. The space (niche) is filled with spiny sowthistle [*Sonchus asper* (L.) Hill]. The picture was taken in 2000 near Lacombe, Alberta, Canada

imity of fertilizer to seed can impair crop health and thus exacerbate competition from weeds (see Strategic Fertilizer Placement below).

Optimizing crop seeding rate and plant density

The most important weed management input is crop seed. Enhancing crop competitiveness with relatively high seeding rates and plant densities is an effective form of biological weed control (although crop seed is not commonly considered to be a biological weed control agent). In our opinion, the majority of crop producers would do well to increase seeding rates in all crops from 25% to 100%.

Numerous studies document the weed management advantages of higher than recommended crop density. Mohler [45] found that of 91 cases in the literature in 29 different crops, only 6 failed to show decreasing weediness with increasing crop density. Additional studies with similar results were also reported in barley [56], canola [57] and soybeans [58]. On the other hand, management practices that compromise seedling emergence, such as the low plant densities associated with dormant fall-seeded canola, will require a higher level of weed management [59, 60]. Higher plant densities have also been reported to reduce weed biomass and increase seed yield in perennial stands of alfalfa (*Medicago sativa* L.) [61]. For wide-row crops, increasing crop densities may be a somewhat less efficient way of rapidly occupying space and preempting resources from weeds as opposed to simply planting in narrower rows.

Despite overwhelming evidence, most crop producers seem reluctant to choose higher seeding rates over simply applying more herbicides; they have yet to be convinced that high crop density is a viable weed management strategy. Studies that report the economic viability and risk-benefits of higher seeding rates over the long-term would help growers make more informed crop seeding rate decisions.

There are situations where high seeding rates will not be a beneficial management strategy. If crop seed is of poor quality and littered with weed seed, then seeding at high rates may benefit weeds more than the crop. Cleaning seed and/or sowing certified seed reduces such problems [9]. Increasing seed rates in crops with relatively high seed costs may not be economically viable in some cases [62, 63]. Malt barley quality traits (high test weight, high kernel weight and low protein content) may also be compromised at higher than normal barley densities [64]. Nevertheless, in many cropping situations, increasing crop density is one of the most effective weed management strategies.

Strategic fertilizer placement

High resource availability is a habitat characteristic that encourages plant invasions [1]. Fertilizer is an obvious resource that weeds use to their advantage if

it is not carefully managed [56, 57]. Without strategic fertilizer placement, weeds may use fertilizers such as nitrogen more effectively than the crop [65–70]. Banding fertilizer near the crop row [71–75] or banding fertilizer deeply to reduce access to it by shallow-rooted weed seedlings [76] favours crop growth over weed growth.

In limited quantities fertilizer can be placed directly with crop seed. However, too much fertilizer placed with crop seed can injure the crop and compromise weed management. When 90 kg ha^{-1} of nitrogen was placed in the seed row compared to banding near the seed row, barley canopy cover in mid June decreased from 78% to 22%, and wild oat biomass before barley harvest in the fall increased from 192 to 967 kg ha^{-1} (dry weight) [unpublished observations]. The combination of the relatively open plant canopy and the excess fertilizer underutilized by the damaged crop allowed the exploitation of light, space, and fertilizer resources by the wild oat plants. Thus while strategic placement of fertilizer can often benefit the crop over weeds, fertilizer placed too close to the seed can have the opposite effect resulting in crop injury and enhanced competition from weeds.

Diverse crop rotations

For centuries, crop producers have employed crop rotations to improve productivity and to manage agricultural pests. Diverse rotations employ crops with different planting and harvest dates, growth habits, residue characteristics, tillage and weed management practices [77]. Derksen et al. [78] found that weed densities were minimized when diverse cropping systems were used to constantly change the selection pressure on weed communities. Diverse rotations have weed management benefits because different crop species and their associated management practices present different challenges for weeds; this diversity prevents unrestricted growth and reproduction for any given weed species. Nevertheless, spatial and temporal plant species diversity in current agricultural ecosystems has dropped precipitously in recent years [77]. Most of this reduction in diversity relates to economies of scale, specialization and the replacement of purchased inputs for labour and management time.

Diverse seeding dates may be the most important rotational factor influencing weed population composition [13, 79–81]. In addition, crop producers can use operational diversity by seeding crops at unconventional dates. For example, studies conducted in western Canada have shown that spring canola can be dormant-seeded in the fall prior to soil freezing [81, 82], or seeded much earlier than normal in the spring [60]. This seeding date variability as well as earlier than normal harvest date adds diversity that can have beneficial impacts on weeds in terms of their restricted success in emergence, crop competition and seed rain. Diverse crop rotations impose resource and management practice diversity that is difficult to completely document, but that restricts the invasive ability of weeds.

Combining optimal factors

Arable land is repeatedly disturbed [16] and maintained at very early stages of succession [14]. In the past, researchers have been successful at isolating important factors that benefit weed management specifically and crop production generally. Factors such as competitive cultivar selection, careful seed placement, high seeding rates, strategic fertilizer placement and diverse crop rotations can all lead to significant weed management improvements. For example, in canola, competitive cultivars [57], timely weed removal [83, 84] and higher than normal plant densities [57, 85] are individual factors that have been reported to improve weed management. However, even simple plant communities are far too intricate to expect that single manipulated factors will yield consistent positive returns [86]. As Tilman [87] indicated: "…we know all too little about how ecosystems work".

Restricting weed populations may be more successful if several factors are combined at optimal levels for a multi-pronged restraint of weed invasions. There are few reported cases of such studies in the literature. The following examples from recently conducted research illustrate how the combination of several optimal agronomic factors can provide effective weed management.

A study involving relatively competitive (InVigor 2153) and non-competitive (Exceed) canola cultivars, three stages of herbicide application (2-, 4-, and 6-leaf canola) and three canola seeding rates (100, 150, and 200 seeds m^{-2}) was conducted over three years at two Alberta locations [28]. The best factor combination (InVigor 2153, 2-leaf herbicide application, 200 seeds m^{-2}) yielded 41% higher than the worst combination (Exceed, 6-leaf herbicide application, 100 seeds m^{-2}). More importantly, the best yield combination also provided greater weed management and lower weed biomass variability. In another recent study involving a barley–pea–barley–pea rotation in a direct seeded production system, combining early seeding, higher crop seed rates, and spring-applied fertilizer provided the most competitive cropping system over the four years of the study [88]. In-crop herbicides applied at 50% *versus* 100% recommended rates sometimes resulted in greater weed biomass and lower crop yields with recommended crop seed rates but few differences between herbicides rates were noted at relatively high crop seed rates. In addition, after 4 years, the amount of weed seed in the soil seed bank was similar at 50% compared to 100% herbicide rates when high crop seed rates were utilized.

In an ongoing study (unpublished observations) we are investigating cultivar, seeding rate, herbicide rate and crop rotation effects on barley productivity and weed management. Individually, these factors had considerable effects on wild oat, but when combined, the effects were dramatic (Tab. 1). For example, the higher seeding rate decreased wild oat biomass and seed numbers approximately four-fold while the tall barley cultivar decreased wild oat biomass and seed numbers approximately ten-fold compared to the short cultivar. Combining higher seeding rates with the taller barley cultivar decreased wild

Table 1. Crop rotation, barley cultivar height, and barley seeding rate effects on wild oat biomass and seed production in year three of a long-term rotation at Lacombe, Alberta, Canada. Herbicides were applied at 25% of recommended rates (unpublished observations)[a].

Crop rotation[b]	Barley cultivar height	Barley seeding rate (# m^{-2})	Wild oat biomass (kg ha^{-1})	Wild oat seeds (# m^{-2})
Barley	Short	200	2019 (811)	4318 (1756)
Barley	Short	400	521 (330)	1079 (754)
Barley	Tall	200	199 (90)	346 (160)
Barley	Tall	400	50 (21)	92 (39)
B–C–B–P	Short	200	660 (104)	1304 (240)
B–C–B–P	Short	400	259 (62)	485 (117)
B–C–B–P	Tall	200	40 (22)	82 (40)
B–C–B–P	Tall	400	21 (10)	32 (16)

[a] Values in parentheses represent standard error of the mean
[b] B–C–B–P = barley–canola–barley–pea

oat biomass and seed numbers approximately 40-fold. Growing barley in rotation with canola and pea rather than continuously, and combining the rotation effect with higher seeding rates and the taller barley cultivar decreased wild oat biomass and seed numbers approximately 100-fold. The impact that crop rotation provided is not well understood. In addition to reduced leaf and root diseases, there may also be more subtle rotational responses that favour crop health and enhanced crop competition with weeds. However, this study clearly demonstrates that optimal factor combinations can have very significant influences on weed management outcomes. Indeed, combining these factors at optimal levels may be a more consistent and sustainable weed management option than the repeated use of herbicides.

Summary

There are many agronomic variables and management strategies other than herbicides that can be manipulated to discourage weed invasion. Combining several management strategies rather than relying on one will increase the likelihood of successful weed management. Encouraging optimal crop canopy health can guide decision-making and render agricultural land less susceptible to weed invasion. Then, when necessary, herbicides can be judiciously used to supplement cultural weed management techniques.

In this review we have attempted to address two of the three major habitat characteristics that influence weed invasions – disturbances and, to a lesser extent, high resource ability. The remaining habitat characteristic, low species diversity, is difficult to address in modern agriculture, but can be an avenue of defence against invading species [89]. However, even intercropping, which is

an effective ecological weed management technique [90], does not approach species diversity levels in natural ecosystems. A compromise to high species diversity in space is to maximize species diversity in time; this is best accomplished by ensuring that a given field is subjected to diverse rotational crops. Diverse crop rotations are probably the most effective management tool in maintaining crop health and limiting weed invasion opportunities.

In the future, very clean (near weed-free) fields may not be considered acceptable [91]. We might do well to alter our view of what is desirable: from an "ultra-clean" crop with no weeds visible to a more species-rich field with sub-threshold communities of weeds. This approach could be termed "ecological weed management" [92]. Pest management in disciplines other than weed science may benefit from a few weeds [93, 94]. For example, root maggot (*Delia* spp) egg deposition and larval damage were reduced in plots where weeds were left in canola longer than the period recommended for optimal yields [95]. Combining and applying the techniques discussed above, reducing herbicide use, and tolerating low infestations of weeds may be the most sustainable form of weed management over the long-term. Ignoring ecological weed management techniques and maintaining current herbicide application practices will ensure a higher frequency of weed invasions of the resistant type [96, 97].

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Tillage intensity affects weed communities in agroecosystems

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Introduction

Farmers must continuously deal with weed infestations in agroecosystems and their importance is reflected in the amount of manual labour, herbicides and other measures used for their control. Pimentel et al. [1] estimated costs of invasive plants on agricultural land in the USA at over $34 billion annually. Herbicides typically comprise 20–30% of crop input costs in North America [2]. In Canada, over 80% of total pesticide sales are herbicides and they account for over $1 billion in annual sales [3].

Changing tillage practices on the Canadian prairies

The Canadian Prairies is a large area of 35 million ha of crop land that has been subdivided into eight ecoregions with soils commonly being Aridic and Typic Haplustolls [4, 5]. Historically, this region has been dominated by spring cereal production with fallow being a common part of the rotation. The primary limiting factors for crop production are low annual precipitation and a short growing season. Annual precipitation ranges from 350–550 mm and the frost-free growing season ranges from 90–130 days depending on latitude [6, 7].

Tillage intensity in Canadian Prairie crop production systems has markedly decreased during the last two decades as a means of reducing soil erosion, as well as increasing soil moisture availability, crop yield and economic return [8–10]. In this region, conventional tillage typically consists of both a fall and spring operation with either a sweep-plow or tandem-disk prior to seeding spring crops, and tillage is used to control weeds in fallow. Minimum-tillage consists of only one tillage operation performed shortly before seeding, with a combination of herbicides and tillage being utilized to control weeds in fallow. In zero-tillage systems, crops are planted directly into the previous crop's stubble with a minimum amount of soil disturbance (<30%) and herbicides are exclusively used for fallow weed control. A recent survey indicated that 31%

of the cropped land on the Canadian Prairies is seeded with minimum-tillage and 31% with zero-tillage practices [11].

Despite the successful adoption of zero tillage on the Canadian Prairies, concerns have been expressed regarding potential shifts in weed species or increased weed densities with adoption of reduced tillage practices [2]. An increase in annual grass and perennial weed species with reduced tillage has been documented in several studies around the world [12–14], and this has led to the overall prediction that these species will become the predominant weeds in reduced tillage cropping systems. However, Pollard et al. [15] reported an increased density of four annual species, a decreased density of six annual species, and no change in density of seven other annual species with zero tillage. Additionally, reduced tillage has resulted in an increase in volunteer crops in some studies [16] but not others [17]. Indeed, several studies found that generalizations regarding reduced tillage effects on weed community dynamics were far from robust [12, 18]. Thus, further efforts aimed at gaining a better understanding of weed community responses to changing tillage practices are warranted.

Invasive weeds and weed communities

Plant invasion refers to the geographical expansion of a species into an area not previously occupied by that species [19]. Successful invasion requires that a species arrive, establish, spread and integrate with other members of a community. Plant invasions occur at many scales from introduction of a non-native plant into a continent to the establishment of a new weed in an agricultural field. Three habitat characteristics that are generally thought to encourage invasions are disturbance (tillage), low species richness, and resource availability. Agricultural ecosystems possess all of these characteristics.

The main interest of farmers, and many weed scientists, is how best to control a newly invasive weed species on agricultural lands. However, farmers should also be concerned with stopping the invasion process as early as possible (i.e., preventing weed establishment). Most research has concentrated on the control of individual weed species once they become established in cropping systems. A greater understanding is needed as to why weeds occur where they do and how they respond to the external stimuli around them.

The study of weed communities, rather than just problem weed species, may have merit in understanding and managing weeds in agroecosystems [20, 21]. Individuals do not act independently; they are embedded in community fabric. A community is most commonly defined as an assemblage of species that occur in the same space and time [22]. Communities are dynamic; continually changing in response to external and internal forces. As a community develops, it follows a trajectory through time. A trajectory is a series of community states. As a community progresses along its trajectory, a series of changing constraints and processes control its pathway. Belyea and Lancaster

[23] state that there are three principal determinants of community assembly: 1) dispersal constraints, 2) environmental constraints, and 3) internal dynamics. Weed responses to these constraints is complex, as weeds can be affected at numerous stages in their life cycle.

Potential tillage effects on weed community development

Numerous constraints (filters) affecting weeds exist in agricultural systems. Timing and intensity of tillage is potentially one of the more important 'filters' affecting assembly trajectory of weed communities [20]. Tillage affects weed growth and productivity in several ways. Tillage uproots, dismembers and buries growing weeds and dormant perennating organs; thereby killing many plants [24]. However, infrequent tillage can increase the productivity of some perennials, such as quackgrass [*Elytrigia repens* (L.) Nevski], by fragmenting rhizomes and thus releasing rhizome buds from apical dominance. Additionally, tillage implements can spread vegetative fragments and seeds throughout a field, or from field to field, and thus contribute to weed dispersal.

Tillage also moves weed seeds vertically and horizontally and changes the soil environment in ways that can promote germination and establishment. In the absence of tillage, seeds infiltrate into soil via cracks, frost action and soil fauna activity. However, this type of infiltration is limited and slow. Thus, most weed seeds remain at or near the soil surface in zero tillage systems [25, 26]. Seeds on the soil surface, compared to buried seeds, are more susceptible to environmental extremes such as desiccation and freeze–thaw cycles [27] and predation by rodents, soil fauna, and pathogens [28–30].

Tillage promotes germination of many agricultural weeds, provided that soil disturbance comes at a time of year when seeds are not innately dormant [24, 31, 32]. Agricultural weeds are thought to have adapted to respond to cues associated with soil disturbance because their small seedlings make them poor competitors early in life. Recently-tilled land is often warmer, has greater diurnal temperature fluctuations, higher nitrate concentration, and increased aeration [33]. Emergence of some weeds may be greater in loose (tilled) soil than in compacted (untilled) soil [34]. Additionally, tillage exposes buried seeds to light that facilitates germination of many species [35].

Crop residues on the soil surface increase with zero tillage. Crop residues can suppress weed establishment by altering environmental conditions related to germination, physically impeding seedling growth, and through allelopathic interactions [36, 37]. Zero tillage also tends to increase the number and/or diversity of soil microbes [38], soil fauna [39], earthworms [40] and mycorrhizal associations of crops and weeds [41, 42]. These organisms can directly or indirectly affect weed seed survival and germination as well as weed growth and productivity.

Plant traits and functional groups

Plant communities do not conform strictly to any given set of constraints because the 'filters' are not perfect and because species are not homogeneous [19]. Thus, predictions on weed species response to changing agricultural practices (including tillage intensity) have been difficult and prone to error.

Some researchers have suggested using plant traits, instead of species, as the unit to examine constraints on community assembly [20, 43]. Traits are the physical and physiological characteristics that determine the ecological function of a species. Dispersal and environmental filters plus internal mechanisms remove species from an overall species pool that lack specific traits and thus traits, rather than species, are filtered. Traits associated with both plant growth and reproduction should be considered [44]. Booth et al. [19] suggest numerous potential traits (e.g., plant morphology, growth rate, reproductive potential, seed dormancy, life cycle) for consideration in trait-based analysis.

The trait-based approach may be further simplified by grouping a similar set of traits into functional groups [20]. A functional group contains species with a similar set of traits. They have similar ecological functions in a community and therefore respond similarly to changing constraints. If sufficient information exists, functional groups can be created by selecting important traits based on ecological knowledge and experience, or by applying clustering techniques to data sets with the goal of detecting correlations among traits across species. The use of plant traits and functional groups may increase our understanding of weed community development and allow better prediction of how weed communities respond to changing agronomic practices (such as tillage) over time.

Approaches to studying tillage effects on agricultural weed communities

The following discussion presents examples from the Canadian Prairies on how weed communities respond to tillage and attempts to determine what traits respond to tillage and whether species can be grouped into functional groups. It is recognized that these results are specific to the cropping systems and environmental conditions of this region. Nevertheless, it is reasonable to expect that some of the generalized results would be relevant to other agricultural regions of the world.

Case 1 – A long-term study at one site

An 11-year field study was conducted at Lethbridge, Alberta, Canada, to determine the effect of various winter wheat (*Triticum aestivum* L.) rotations and tillage treatments on crop yield, soil quality and weed infestations [45, 46]. The crop rotation treatments were: 1) winter wheat–oilseed rape (*Brassica rapa* L.), 2) winter wheat–lentil (*Lens culinaris* L.)/linseed (*Linum usitatissi-*

mum L.), where linseed replaced lentil in the latter five years, 3) winter wheat–fallow and 4) continuous winter wheat. The tillage treatments were conventional, minimum, and zero tillage. Tillage treatments were organized as randomized subplots within the main rotation plots. Weeds were counted by species in twelve randomly placed 0.25 m^2 quadrats per subplot in early May, in mid-June (prior to applying post-emergence in-crop herbicides) in the spring-planted crops, and in October in winter wheat each year.

Multivariate analyses of weed community composition were conducted using principal components analysis (PCA) and canonical discriminant analysis (CDA) in statistical analysis system (SAS) [47]. Data were log transformed, and species occurring in less than 10% of the plots were removed, before input into PCA. Significance testing for weed community compositional differences was accomplished using a data reduction step [48], where significant axes from PCA were used as variables for input into CDA. CDA represents multi-dimensional data structures in one or two dimensions, while maximally preserving the trends in variation that are present in the data [49]. Ordination axes are extracted in order, with each axis summarizing the maximum amount of information not yet accounted for by previous axes. Thus, the first axis is always the most important, followed by the second, the third, etc. Biplots of weed species and tillage system, crop rotation and time are formed and species associations can be ascertained by the direction of vectors. Vector length indicates the relative strength of the association; the longer the vector the stronger the association.

The 22 weed species in this Lethbridge study consisted of summer and winter annuals, perennials, and volunteer crops. Over all rotations, zero tillage had greater weed densities than either minimum or conventional tillage (Tab. 1). Previous studies have similarly reported greater weed densities with zero than with conventional tillage [50], but other studies have found that total weed numbers were largely unaffected by tillage regime [51].

Table 1. Mean weed densities in winter wheat in May averaged over years as affected by tillage intensity

Rotation	Zero tillage	Minimum tillage	Conventional tillage
		plants m^2	
Winter wheat–oilseed rape	15 (5)	5 (1)	5 (1)
Winter wheat–linseed	5 (1)	11 (3)	7 (2)
Winter wheat–fallow	6 (2)	13 (4)	8 (1)
Continuous winter wheat	98 (32)	18 (4)	31 (12)
Tillage mean[b]	31 (9) A	12 (2) B	13 (3) B

[a] Values in parentheses represent standard error of the mean
[b] Tillage means followed by the same letter are not significantly different according to the LSD test at the 5% level
Adapted from Blackshaw et al. [46]

Over all years and rotation treatments, CDA analysis of weed data in May indicated that downy brome (*Bromus tectorum* L.), dandelion (*Taraxacum officinale* Weber in Wiggers), and to a lesser extent Russian thistle (*Salsola iberica* Sennen & Pau) and kochia (*Kochia scoparia* L.) were associated with zero tillage (Fig. 1A). Other species, as indicated by their short vector length, were not associated with any specific tillage systems at this sampling date.

June weed data indicated that kochia, downy brome, redroot pigweed (*Amaranthus retroflexus* L.), prostrate pigweed (*Amaranthus blitoides* S. Wats.), dandelion and perennial sowthistle (*Sonchus arvensis* L.) were associated with zero tillage (Fig. 1B). Common lambsquarters (*Chenopodium album* L.) and wild mustard (*Sinapis arvensis* L.) were associated with minimum tillage. Field pennycress (*Thlaspi arvense* L.) and volunteer winter wheat were associated with conventional tillage.

Weed data in October indicated that downy brome and dandelion were associated with zero tillage (Fig. 1C). Flixweed [*Descurainia sophia* (L.) Webb. Ex Prantl] and Canada thistle [*Cirsium arvense* (L.) Scop.] were associated with minimum and conventional tillage.

Canonical discriminant analysis *P*-values for each of the May, June, and October weed data sets indicated that the weed community was different in zero tillage compared to either minimum or conventional tillage and that there was no significant difference between minimum and conventional tillage.

Case 2 – A multi-site study

The goal of this study was to combine weed data from several sites to gain knowledge of weed community responses to changing agricultural tillage practices. Specific objectives were to determine weed species response to various tillage systems and to group species into plant functional types according to the similarity of their response to tillage systems.

11 field experiments ranging in duration of 4–12 years were included in this multi-site study. A zero tillage cropping system was present in all studies and it was compared with either one or both of minimum and conventional tillage systems. Species level comparisons of responses to the three tillage systems were conducted using indicator species analysis [52]. This method combines information on the abundance of a species in a particular group (tillage system) and the exclusiveness of occurrence of a species to a particular group [53]. An indicator value for a species can range from zero (no indication of a relationship with a specific tillage system) to 100 (exclusive association with a specific tillage system). Indicator values were calculated for each species on nontransformed density data using PC-ORD [54]. A table of indicator values for each site-year and tillage system was created and used to determine species association with tillage system.

Of the 71 weed species enumerated, 56% were associated with minimum and/or zero tillage and 27% were associated with conventional tillage (Tab. 2).
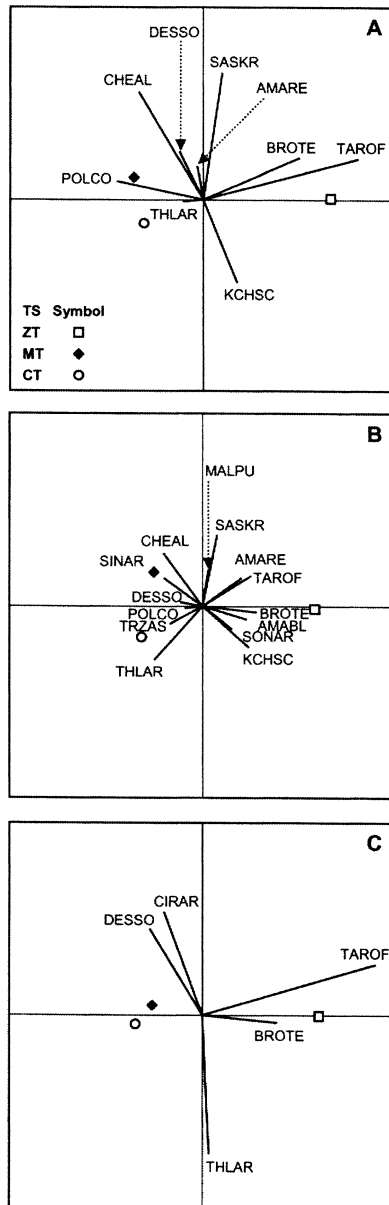
Figure 1. Canonical discriminant analysis ordination biplot of tillage treatment centroids and weed species present in A) May, B) June, and C) October from weed density data. ZT represents zero tillage; MT represents minimum tillage; and CT represents conventional tillage. AMABL = prostrate pigweed; AMARE = redroot pigweed; BROTE = downy brome; CHEAL = common lambsquarters; CIRAR = Canada thistle; DESSO = flixweed; KCHSC = kochia; MALPU = round-leaved mallow; POLCO = wild buckwheat; SASKR = Russian thistle; SETVI = green foxtail; SINAR = wild mustard; SONAR = perennial sowthistle; TAROF = dandelion; THLAR = field pennycress; and TRZAS = volunteer winter wheat

Table 2. Species association with tillage system as determined from 56 site-years of data from the Canadian prairies

Common name	Scientific name
Minimum-zero tillage	
Annuals	
Annual sowthistle	*Sonchus oleraceus* L.
Common groundsel	*Senecio vulgaris* L.
Kochia	*Kochia scoparia* (L.) Schrad.
Pineapple-weed	*Matricaria matricariodes* (Less.) C.L. Porter
Prickly lettuce	*Lactuca serriola* L.
Russian thistle	*Salsola iberica* Sennen & Pau
Winter annuals	
European sticktight	*Lappula echinata* Gilib.
Catchweed bedstraw	*Galium aparine* L.
Downy brome	*Bromus tectorum* L.
Greenflower pepperweed	*Lepidium densiflorum* Schrad.
Horseweed	*Conyza canadensis* (L.) Cronq.
Narrowleaf hawksbeard	*Crepis tectorum* L.
Pigmyflower	*Androsace septentrionalis* L.
Redstem filaree	*Erodium cicutarium* (L.) L'Her. ex Ait.
Scentless chamomile	*Matricaria perforata* Merat
Shepherd's-purse	*Capsella bursa-pastoris* (L.) Medicus
Wood whitlowgrass	*Draba nemorosa* L.
Biennials	
Biennial wormwood	*Artemisia biennis* Willd.
Yellow sweetclover	*Melilotus officinalis* (L.) Lam.
Western salsify	*Tragopogon dubius* Scop.
Perennials	
Absinth wormwood	*Artemisia absinthium* L.
Canada goldenrod	*Solidago canadensis* L.
Canada thistle	*Cirsium arvense* (L.) Scop.
Dandelion	*Taraxacum officinale* Weber in Wiggers
Field horsetail	*Equisetum arvense* L.
Foxtail barley	*Hordeum jubatum* L.
Perennial sowthistle	*Sonchus arvensis* L.
Rose	*Rosa* spp
Quackgrass	*Elytriga repens* (L.) Nevski
Smooth brome	*Bromus inermis* Leyss
Conventional tillage	
Annuals	
Ball mustard	*Neslia paniculata* (L.) Desv.
Common lambsquarters	*Chenopodium album* L.
Cutleaf nightshade	*Solanum triflorum* Nutt.
Dog mustard	*Erucastrum gallicum* (Willd.) O.E. Schulz
Green foxtail	*Setaria viridis* (L.) Beauv.
Green smartweed	*Polygonum scabrum* Moench
Oakleaf goosefoot	*Chenopodium glaucum* L.
Prostrate pigweed	*Amaranthus blitoides* S. Wats.
Redroot pigweed	*Amaranthus retroflexus* L.
Thyme-leaved spurge	*Euphorbia serpyllifolia* Pers.
Wild buckwheat	*Polygonum convolvulus* L.
Wild mustard	*Brassica kaber* (DC.) L.C. Wheeler

Table 2. (Continued)

Common name	Scientific name
Conventional tillage	
Winter annuals	
Field pennycress	*Thlaspi arvense* L.
Volunteer crops	
Barley	*Hordeum vulgare* L.
Lentil	*Lens culinaris* L
Pea	*Pisum sativum* L.
Sunflower	*Helianthus annuus* L.
Rye	*Secale cereale* L.
Ubiquitous across tillage systems	
Annuals	
Barnyardgrass	*Echinochloa crus-galli* (L.) Beauv.
Common chickweed	*Stellaria media* (L.) Vill.
Cowcockle	*Vaccaria pyramidata* Medicus
Nightflowering catchfly	*Silene noctiflora* L.
Prostrate knotweed	*Polygonum aviculare* L.
Round-leaved mallow	*Malva pusilla* Sm.
Wild oat	*Avena fatua* L.
Winter annual	
Flixweed	*Descurainia sophia* (L.) Webb. ex Prantl
Volunteer crops	
Oilseed rape	*Brassica napus* L.
Linseed	*Linum usitatissimum* L.
Mustard	*Brassica juncea* L.
Wheat	*Triticum aestivum* L.

Species ubiquitous across tillage systems represented the remaining 17%. Despite more than one-half of all weeds being associated with minimum-zero tillage, most of these weeds were not new weeds to these agricultural systems but they increased in density and distribution with the adoption of reduced tillage cropping practices.

All perennial species were more strongly associated with minimum-zero tillage than with conventional tillage (Tab. 2). Canada thistle, perennial sowthistle and quackgrass were present in all tillage systems but their densities often increased with zero tillage. Others, such as dandelion and foxtail barley (*Hordeum jubatum* L.), exhibited large increases in density with zero tillage. Native species, such as Canada goldenrod (*Solidago canadensis* L.) and rose (*Rosa* spp), rarely occurred with conventional tillage but became increasingly prevalent with time in zero tillage systems.

Biennial weeds have been predicted to increase with reduced tillage and this occurred in our study. Biennial wormwood (*Artemisia biennis* Willd.), yellow sweetclover [*Melilotus officinalis* (L.) Lam.] and western salsify (*Tragopogon*

dubius Scop.) were associated with minimum-zero tillage and rarely occurred with conventional tillage (Tab. 2).

The association of annual weed species with tillage system was more complex than that noted with biennial or perennial weeds. Of the 39 annual weed species in these studies, 44% were associated with minimum-zero tillage, 33% with conventional tillage and 23% were ubiquitous across tillage systems (Tab. 2). Many of the annual species associated with minimum-zero tillage have wind-disseminated seed capable of germinating on the soil surface; examples being annual sowthistle (*Sonchus oleraceus* L.), common groundsel (*Senecio vulgaris* L.), prickly lettuce (*Lactuca serriola* L.) and narrowleaf hawksbeard (*Crepis tectorum* L.). Many of the hard-seeded annuals, such as mustards, pigweeds, wild buckwheat (*Polygonum convolvulus* L.) and common lambsquarters, were associated with conventional tillage. 11 of 13 winter annual species were associated with minimum-zero tillage. The prediction that annual grass species will proliferate with conservation tillage was not supported in these studies. While downy brome was associated with minimum-zero tillage, green foxtail (*Setaria viridis* (L.) Beauv.) was associated with conventional tillage and barnyardgrass (*Echinochloa crus-galli* (L.) Beauv.) and wild oat were ubiquitous across tillage systems.

Volunteer crops were not necessarily associated with minimum-zero tillage (Tab. 2). The large-seeded crops such as lentil, pea and sunflower (*Helianthus annuus* L.) exhibited a strong association with conventional tillage, indicating the need for greater soil–seed contact for germination of these species. Barley (*Hordeum vulgare* L.) and rye (*Secale cereale* L.) also were associated with conventional tillage but oilseed rape, linseed, mustard (*Brassica juncea* L.), and wheat were present at similar levels across tillage systems.

Identification of plant functional groups based on response to tillage system was difficult. A classification based on life cycle alone was not feasible as exceptions were always found. The predicted association of annual weeds with conventional tillage [13, 50] often did not occur. The placement of the annual grass weeds in different response groups and the fact that not all volunteer crops were placed in the zero tillage response group are more examples of exceptions to simple classifications and predicted responses to tillage regime. New classifications were attempted using characteristics such as seed dormancy, seed bank persistence, recruitment depth, dispersal mechanism, and herbicide tolerance. However, inadequate knowledge of species biology and ecology relevant to our regional conditions limited development of any meaningful weed functional groups from this study.

Summary

Cropping studies on the Canadian Prairies indicate that tillage intensity is a strong 'filter' affecting weed communities in agroecosystems. Most biennial and perennial weeds were associated with minimum- and zero-tillage. In con-

trast, the effect of tillage on annual weeds was complex. Winter annual weeds that emerge in fall and survive cold Canadian winters often became more prevalent with reduced tillage, perhaps due to the combined effect of less fall tillage and the insulating effect of increased snow cover facilitated by standing crop stubble. Summer annual weeds with wind-disseminated seed capable of germinating on or near the soil surface also were associated with reduced tillage. However, many other annual weeds were more strongly associated with conventional than with minimum- or zero-tillage and yet others were ubiquitous across tillage systems.

The concept of weed functional groups based on responses to tillage system may have merit as an approach to gain a better understanding of the underlying selection processes, but identification of such weed groups was not achieved in this study. Greater knowledge of weed biology and ecophysiology combined with additional data from other studies in different regions of the world may add to our understanding of tillage effects on weed communities in agroecosystems.

It should be noted that selection pressures exerted by tillage intensity on weed populations can at least be partially offset by other cropping practices. Farmers employing cropping systems that include diverse crop rotations, competitive crop cultivars, green manure and cover crops, altered seed dates, and timely herbicide use (i.e., sound integrated weed management programs) may mitigate some of the weed community changes associated with zero tillage [55, 56]. Indeed, Wicks et al. [57] found at the conclusion of an 18-year study that the overall weed density was lower with zero tillage than with conventional tillage. Farmers should not be deterred from adopting zero tillage production practices because of concerns of increased weed control problems but rather be aware of potential changes in weed communities and how they may be effectively managed.

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Distribution and biological control of *Chromolaena odorata*

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Origin and spread

Chromolena odorata (L.) RM King and H Robinson (Asteraceae) commonly known as chromolaena, Siam weed and by several other names in different countries, is of neotropical origin. Muniappan [1] mentioned the possible introduction of chromolaena to Asia more than once from the neotropics; however, Gautier [2] takes the view that the invasion was initiated from a single site. Voigt [3] in 1845 reported that it was introduced to Calcutta Botanical Gardens in India as an ornamental plant. Clarke [4] in 1876 mentioned it had become wild in parts of India and Java. Hooker [5] in 1882 noted that it was sparingly cultivated in the Calcutta area. Rao [6] reported that in 1918 it was widespread in Assam, West Bengal and Burma. Sipayung et al. [7] were of the opinion that it was introduced to Deli in the east coast of North Sumatra in Indonesia with the start of the commercial cultivation of tobacco at the turn of the twentieth century. According to Grierson [8] it was introduced as an ornamental plant to Peradeniya, Sri Lanka, in 1884 but subsequently died out. However, between 1937 and 1947, it became naturalized. Biswas [9] mentioned that this weed was accidentally introduced around 1934 from West Indies to Singapore through the ballast of ships. Whether the invasion in Asia originated from a single source or multiple introductions, the form of chromolaena seems to be relatively similar.

According to Gautier [2], chromolaena has invaded West Africa from more than one source of introduction but all have originated from Asia. Ivens [10] reported that it was introduced to Nigeria in 1937 through the contaminated seeds of the forest tree, *Gmelina arborea* Roxb. (Verbenaceae) imported from Sri Lanka. Also, it was thought that in 1936–37, pepper and coffee planters from Southeast Asia who settled in Cameroon and Central African Republic, brought the species with them [11]. It is also speculated that chromolaena was introduced either by accident or deliberately to the Ivory Coast after World War II [2, 12]. From these introductions, it has spread to most of the humid

tropical regions of West and Central Africa. In the Indian Ocean island of Mauritius it was introduced around 1949 [2].

Unlike in West Africa, the introduction of chromolaena to South Africa took place directly from the neotropics. It was first recorded growing in Cape Town Botanical Gardens in 1858 but then not recorded until 1947 in Natal [13, 14]. It became naturalized around Durban in the late 1940s [15]. This supports the view that the biotype of South African chromolaena is different from the one that invaded other parts of the world [16, 17].

Waterhouse [18] reported the establishment of chromolaena in the area spanning hundreds of square kilometers near Tully and Bingil Bay in northern Queensland in 1994 and more recently an area near Townsville, Queensland in Australia (Rachel McFadyen, personal communication).

The herbarium specimens collected in Guam indicate that the introduction of chromolaena to Micronesia took place in the early 1960s [19]. Since then, it has spread to the rest of the Micronesian Islands mostly through the movement of the contaminated equipment for road construction and other activities.

Currently chromolaena has spread to most of the humid tropical regions of West and Central Africa, Southern Africa, Asia, Micronesia and a few places in northern Queensland, Australia (Fig. 1).
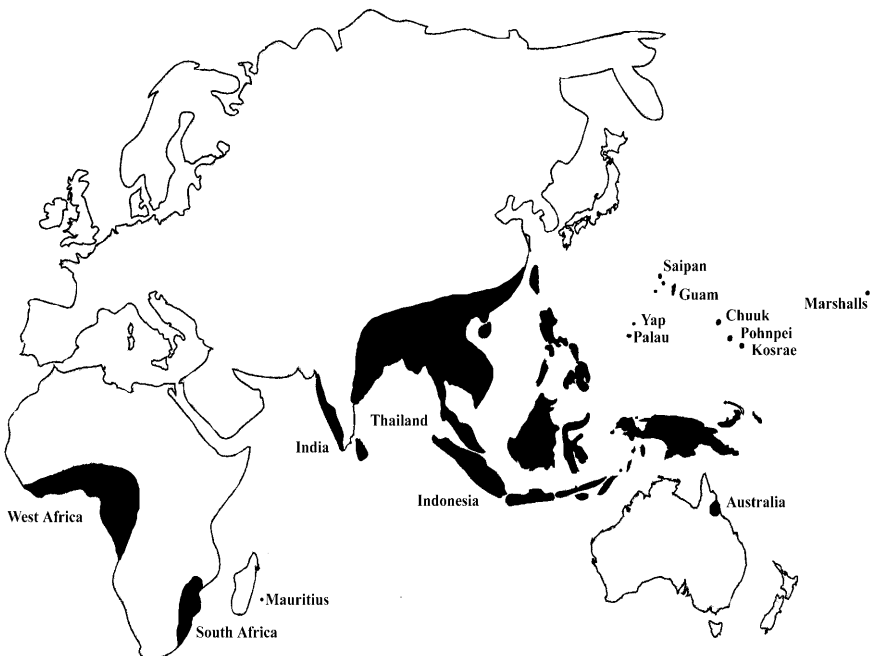
Figure 1. Distribution of *Chromolaena odorata* as a weed

Ecology

Chromolaena odorata was previously known as *Eupatorium odoratum* before the genus *Eupatorium* was split by King and Robinson [20]. Genus *Eupatorium*, before it was split up, contained 1,200 species and the genus *Chromolaena* contains 129 species, all from South and Central America and the West Indies [21]. Chromolaena is distributed from Cuba to northern Argentina. Cruttwell McFadyen [21] has given a detailed account of its ecology in the neotropics. In its native habitat, it poses no threat as a weed as it is kept under check by the native vegetation and natural enemies [21].

Chromolaena is a perennial plant, forming scrambling thickets and grows to a height of 3 m. In areas near the equator, it grows up to an elevation of 1,000 m and thrives well where the average rainfall is about 2,000 mm per year. It flowers during November–December in the northern hemisphere and June–July in the southern hemisphere. Seeds are produced prolifically on achenes and dispersed by wind. Because of its allelopathic properties, it suppresses neighboring vegetation [22]. In addition, during the dry season, the aerial stems dry up and readily burn, but the stubbles remain alive and grow rapidly to cover the area in the succeeding rainy season. This aggressive invader reduces biodiversity and it is known to replace some of the other invasive species such as *Lantana camara* L. (Verbanaceae) and *Imperata cylindrica* (L.) Beauv. (Poaceae).

In the invaded areas of the world, it has become a serious weed in plantation crops such as oil palm, coconut, citrus, cashew, teak and rubber, disturbed forests, pastures and natural reserves. Chromolaena is not a problem in annual crops as frequent ploughing and other cultural operations keep this weed under control. In the disturbed forests, quick establishment of chromolaena prevents self-seeding of forest trees. The thickets also interfere in the free movement of wildlife. Growth of chromolaena along the riverbanks in South Africa threatens Nile crocodile breeding [23].

Physical and chemical control

A slash and burn method of control is practiced in subsistence agricultural regions in Asia and Africa. Mechanical control is widely used in plantation crops but it is labor intensive and requires repeated operations. Tools used vary depending upon the size of the operation. In small-scale operations, hand tools such as picks, hand hoes, shovels and mattocks are used; while in large-scale clearing situations, motorized brush cutters and tractor drawn mowers are being used [24]. Fire has been proven effective in controlling early establishment of the South African biotype of chromolaena but the biotype in other parts of the world is resistant to fire.

Herbicides such as trichlopyr, glyphosate, 2,4-D amine, 2, 4-D/ioxynil and picloram/2, 4-D have proven effective in controlling chromolaena [24].

However, both mechanical and chemical control methods are expensive and require frequent applications. Since classical biological control offers a long-lasting, effective and economical solution to this problem, it has been explored and implemented in several countries.

Biological control

In 1966, the Nigerian Oil Palm Research Institute, recognizing the seriousness of chromolaena, requested Commonwealth Institute of Biological Control (CIBC) (now CABI Bioscience) to initiate a biological control program by conducting exploration for natural enemies in the neotropics. In this project, 207 insect and 2 mite species that attack chromolaena in neotropics were identified [25], of which about a quarter were host-specific [26].

Pareuchaetes pseudoinsulata *Rego Barros (Lepidoptera: Arctiidae)*

This was one of the first natural enemies identified in the CIBC project. It was host specificity tested in Trinidad and India and initial field releases were made in Sabah, Malaysia, from 1970–74, India in 1973 and 1978, Sri Lanka in 1973, Ghana in 1970–74, and Nigeria in 1973–78 [26–30]. Of these releases, only in Sri Lanka was the establishment of the moth confirmed [28]. About a decade after the release in Sabah the establishment was confirmed [31]. The recovery of *P. pseudoinsulata* in the Palawan Island of the Philippines in 1985 [32] could possibly have been a fortuitous introduction from Sabah, Malaysia. Releases of *P. pseudoinsulata* from 1984 onwards in India resulted in establishment [29, 33].

Pareuchaetes pseudoinsulata, introduced to Guam from India and Trinidad, became established in 1985. Subsequently it was introduced to the neighboring islands in the Commonwealth of the Northern Marianas (Rota, Tinian and Saipan) in 1986–87 [34–36]. Introduction to Yap in 1989–91, Pohnpei in 1988–92, Kosrae in 1992, and Chuuk in 2004 resulted in its establishment [37–39] in Micronesia. It was imported into Palau in 2004 and is currently being field released (Muniappan, personal observation). Release of *P. pseudoinsulata* from Guam to Ghana from 1991–93, Indonesia in 1991 and 1993 and Papua New Guinea in 1999 resulted in establishment [40–42], however, releases in Thailand in 1987, South Africa in 1988 and the Ivory Coast in 1991–93 did not establish. Experience from the introductions of *P. pseudoinsulata* in the above-mentioned countries indicates that release of several thousand caterpillars on constant intervals for a long period in one area is necessary to overcome the predatory pressure and to allow establishment. The failure of establishment of *P. pseudoinsulata* in South Africa was due to the incompatibility of the biotype of chromolaena that grows there [16, 17, 43].

Apion brunneonigrum *Beguin-Bellecoq (Coleoptera: Brenthidae)*

This weevil lays eggs on developing flower heads; the larvae feed on flowers and reduce seed production. Pupation occurs in the flower heads and emerged adults remain feeding on tender leaves until next year for oviposition on flowers [44]. Small releases were made in Sabah, Malaysia in 1970, Nigeria in 1970–79, India in 1972–73, Sri Lanka in 1974–76, Ghana in 1975 and Guam in 1984 but it did not establish in these countries [1].

Acalitus adoratus *Keifer (Acari: Eriophyidae)*

This erineum forming mite feeds on the lower surface of the leaves. The abnormal growth of the epidermal hairs, due to feeding of the mites, forms the erineum. McFadyen [45] suggested the possibility that it was accidentally introduced to Sabah, Malaysia, when the field collected weevils of *A. brunneonigrum* from Trinidad were released in 1970. Since then, this mite has fortuitously spread throughout Asia, and Micronesia [26, 45].

Mescinia parvula *Zeller (Lepidoptera: Pyralidae)*

This moth lays eggs individually on tender leaves of chromolaena. The larvae bore into the terminal or axillary buds. They bore down the stem and cause death of the shoots. Pupation takes place outside on the stem or in the debris [46]. Attempts to breed these in laboratory captivity were unsuccessful in Trinidad, Guam and India. A small number of moths were released in 1984 and 1986 in Guam but it did not establish. Two shipments of this insect were received in India but they were not released in the field [26, 35, 47].

Melanagromyza eupatoriella *Spencer (Diptera: Agromyzidae)*

The adult fly lays eggs individually on terminal or axillary shoot tips. Maggots bore in to the stem. Pupation takes place in the bore hole. It was imported to Thailand in 1978 but no field releases were made [48]. Similarly a shipment was received in Guam in 1987 but most of the pupae were parasitized and no release was made [49].

Cecidochares connexa *Macquart (Diptera: Tephritidae)*

This fly lays eggs on terminal or axillary buds. Eggs are laid in packed masses of 2–16 per tip. The larvae tunnel into the stem and form galls. It takes about 45–75 days to complete the life cycle [50]. A culture of this gall fly was

established in Marihat, North Sumatra, Indonesia from the galls received from Colombia. After host specificity testing, the flies were released and established in North Sumatra in 1995 [51]. Since then it has been released throughout Indonesia [52]. A shipment of this gall fly was received in Guam in 1998 from Indonesia and field released in 2002. However, a serious typhoon in July 2002 disrupted its establishment. Again a culture was imported from Palau (which was originally sent from Guam) and field established in 2003. From Guam shipments of this fly were sent to Palau in 1999 [53], Saipan and Rota in 2003, and Pohnpei in 2003 (Muniappan, personal observation) and established in the field. A shipment of this fly was also sent to Chuuk from Pohnpei (K Englberger, personal communication).

   Cecidochares connexa was imported to the Philippines from Indonesia in 1999 [54] and then to Papua New Guinea from the Philippines in 2001. It has been established in Papua New Guinea [55] but it is still in quarantine in the Philippines. It was imported to India in 2002 from Indonesia and is currently being host specificity tested. It was also sent to Taiwan from Guam in 2004 and it is being cultured in the quarantine facility. It was imported to South Africa from Indonesia in 1996 and 1998 but it did not survive on the South African biotype [56].

Actinote anteas *Doubleday and Hewitson (Lepidoptera: Nymphalidae: Acraeinae)*

This butterfly was imported to Indonesia from Costa Rica in 1996 [51]. The life cycle takes about 73–102 days. Eggs are laid in batches. Caterpillars feed on chromolaena and *Mikania micrantha* Kunth (Asteraceae) leaves. It was released and established in the field Indonesia in 1999 [51].

   Actinote anteas was imported in to South Africa in 1990 but the laboratory culture died out as the South Africa biotype of chromolaena was not suitable for the insect or due to disease [17]. Another species *Actinote thalia pyrrha* Fabricius (Lepidoptera: Nymphalidae: Acraeinae) was imported from Brazil to South Africa in 1995 but it was not released for safety reasons as it fed on *Mikania* species [16]. Both *A. anteas* and *A. thalia pyrrha* were imported to Guangdong Entomological Institute, China, in 2001 for control of chromolaena and *Mikania* [57].

   A list of major natural enemies of chromolaena introduced to different countries and their status is given in Table 1. In general, *P. pseudoinsulata* and *C. connexa* have proven effective among the various natural enemies evaluated.

South Africa

Since the South African biotype of chromolaena is different and the attempts to utilize natural enemies released for control of chromolaena in Asia were not

Table 1. Status of natural enemies introduced for biological control of *Chromolaena odorata*

Country/territory	*Pareuchaetes pseudoinsulata*	*Cecidochares connexa*	*Actinote* spp	*Acalitus adoratus*
Guam	E	E		E
Rota	E	E		E
Saipan	E	E		E
Palau	*	E		E
Pohnpei	E	E		E
Chuuk	E	E		E
Yap	E	–		E
Kosrae	E	–		E
Indonesia	E	E	E	E
PNG	E	E		E
Philippines	E	Q		E
China	–	–	Q	?
Taiwan	Q	Q		E
Malaysia	E	–		E
Thailand	NE	NE		E
India	E	Q		E
Sri Lanka	E	–		?
Ghana	E	–		–
Ivory Coast	NE	–		–
South Africa	NE	NE		–

Q: In quarantine; E: Established; NE: Not established; *Currently released

successful [16, 17, 58]. South Africa has initiated a biocontrol program for its biotype of chromolaena by exploring the natural enemies in the neotropics. Since implementing this program in 1988, several natural enemies have been imported screened and released [16, 56, 58]. Recent research seems to point out that the South African biotype originated from the northern Caribbean region [59].

Eradication

When an infestation of chromolaena was observed in north Queensland, Australia in 1994, an eradication program was initiated. It involved quarantining the area and treating infested areas with herbicides, hand pulling and fire [60]. Recently a new infestation near Townsville, northern Queensland was found (Rachel McFadyen, personal communication).

International workshops

The successful establishment of *P. pseudoinsulata* in the Mariana Islands in the mid 1980s provided the initiative to organize International Workshops on

biological control of *Chromolaena odorata*. The first workshop was held in Bangkok, Thailand, in 1988. Since then five workshops have been held, in 1991 (Bogor, Indonesia), 1994 (Abidjan, Ivory Coast), 1996 (Bangalore, India), 2000 (Durban, S. Africa) and 2003 (Cairns, Australia). The proceedings of these workshops and in addition 15 *Chromolaena odorata* newsletters were published. A Working Group of *Chromolaena* has also been established in the International Organization for Biological Control and a *Chromolaena* Network has been formed. The proceedings of the workshops and newsletters can be retrieved at: http://www.ehs.cdu.edu.au/chromolaena/siamhome.html

Conclusions

Chromolaena odorata is a neotropical plant introduced to humid tropical Asia and Africa in the mid 1800 s. In the mid 1900s it became a weed problem in West, Central and Southern Africa, South and Southeast Asia and Micronesia. It is highly allelopathic and fire prone. It invades disturbed forests, vacant lands, wildlife reserves, riverbanks, pastures and plantation crops. Mechanical and chemical methods of controlling this weed are expensive and require repeated operations. Classical biological control has been implemented in several countries. The natural enemies *Pareuchaetes pseudoinsulata* and *Cecidochares connexa* have been successfully introduced to several countries in Asia and Micronesia with positive results. Another natural enemy, *Acalitus adoratus* has been fortuitously introduced to Asia and Micronesia. The South African biotype of chromolaena is different from the biotype that invaded the rest of the world and the natural enemies which proved effective on the later biotype do not thrive on the former. The origin of the biotype of chromolaena in South Africa has been narrowed down to northern Caribbean region. Natural enemies from this region are being screened in South Africa.

Australia has implemented a program to eradicate chromolaena from a small area of infestation in northern Queensland. The Working Group of Chromolaena and the Chromolaena Network have been conducting International Workshops and publishing newsletters since 1988.

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Biology and anthropology of plant invasions

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Introduction

Invasive plants have a significant effect on the biological and human communities in which they appear. These effects include economic, environmental, aesthetic, and biological harm to biodiversity, ecosystem function, and human welfare. The appearance of invasive plants in terrestrial and aquatic landscapes is associated with perturbations resulting from human population growth and activity that affect the environment. There exists a perception that invasive species are increasing of late due to increased global movement of people, trade, and transport of biological and agricultural commodities and novel plant materials. Pimentel et al. [1] estimate that non-indigenous species in the US cause environmental damage of more than $138 billion per year. They estimate there are 50,000 foreign species in the US, and that 42% of the native species on the US Federal Threatened or Endangered Species lists are at risk because of these foreign invaders. Conversely, non-native species contribute to the useful crop and animal species used for human food consumption, as well as other species used for land restoration, biological pest control, sport, pets and food processing. Other introduced species have caused economic, environmental and aesthetic harm in human managed and native biological communities.

To mitigate or ameliorate the harm caused by invasive species, knowledge of their biology and behavior is needed. This management information is often incomplete, especially that concerning behavior in the newly invaded communities and the life history traits they possess allowing invasion. Also of critical importance is consideration of the roles played by human activity, perception, public policy and social values. Management of plant invasions is a complex task, requiring consideration of the roles played by the biological community and humans, both of which must be considered in any rational management system.

With these challenges to invasive plant management in mind, herein is posed a conjecture that a successful plant invasion is the consequence of the presence of a non-native species possessing life history traits suitable to exploit an opportunity space in a particular locality. An invasive species must successfully survive three processes: dispersal into new locality, followed by colonization and enduring occupation of the habitat. The last part of the con-

jecture is that species succeeding in occupying a locality must be perceived by humans as being problematic. Without the occurrence of all three processes, a plant species is not labeled invasive.

If this is a valid conjecture, then a broad perspective is required of everyone involved in the dialogue of invasive species. Those interested and involved in invasion biology are a very diverse range of humans, including citizens, biological and social scientists, and those with governmental, environmental or public policy roles. The terminology used by those interested in invasion biology is often defined somewhat differently by these respective groups (see Chapter 1). As such, to avoid confusion herein essential terminology is defined to ensure clarity in the presentation of this conjecture. Where differences may occur, alternative forms of those definitions are provided.

The biology of plant invasion

A successful plant invasion may result from the presence of a particular species possessing life history traits suitable to exploit an opportunity space in a particular locality. The presence of that species may be dependent on its ability to disperse into the locality, or disturbance at that locality creating opportunity, or both.

Local opportunity: space and time

Plants will fill any available and habitable growing space; therefore the primary resource limiting plant growth is habitable space. Available and habitable space to an invading plant is opportunity space at a particular time. Opportunity space for plant invasion is a consequence of disturbance, a change in local conditions, and the first selection pressure on invasive populations.

Disturbance

Competitive exclusion by extant individuals within a plant community puts invading species at a disadvantage in establishment. The reasons invasions occur when confronted with existing plant communities is based on an appreciation of the role disturbance plays in creating space for new individuals to grow in.

Disturbance is defined as i) the act of disturbing or the state of being disturbed [2, 3], ii) an interruption or intrusion [2, 3], or iii) destruction of biomass by any natural or human agency [4]. Disturbance herein is defined as interruption or intrusion with direct and indirect spatial, temporal, biological, or abiological effects that alters or destroys a biological individual or community.

Dimensionality of disturbance

Disturbance is more than the direct cause of damage or mortality to a plant. It also includes the indirect effects of the abiotic environment, and the biological

community (neighbors), with which the individual phenotype interacts. Disturbance of plant communities can be human-mediated or not. Disturbance possesses dimensionality. Disturbance can be understood by considering the biological community structure, and the abiotic environment, influencing the community at a locality (the population) and microsite (the individual) (Tab. 1).

Vulnerability to disturbance

The susceptibility and sensitivity of a locality or microsite to invasion varies with the robustness and resistance of a local community. The vulnerability of habitats to invasion is often a function of the extent of direct and indirect disturbance by humans.

Ironically, many agroecosystems have stable weed communities that resist invasion by new species. Weed populations often are stable due to the high, consistent level of disturbance management of these controlled systems. Population shifts are most likely to occur in these agriculture fields when crop management tactics change, e.g., introduction of new herbicides or herbicide resistant crops [5]. Disturbed habitats are often more vulnerable to invasion due to the fact that direct and indirect disturbance can change the ecological balance within these unmanaged biological communities, creating new opportunities (e.g., plant community changes due to the loss of large herbivores with human colonization of North America).

Table 1. Dimensions of disturbance regimes (spatial, temporal, biological community, abiotic environment), disturbance factors within each dimension, and examples of factors

Disturbance dimension	Disturbance factor	Examples
Spatial	• proximity of effect: direct or indirect • localized or widespread • heterogeneity and fragmentation	• direct, localized: lightning strike spot in field • indirect, widespread: highway corridor effects on adjacent forests • variable erosion and drainage effects with landscape elevation
Temporal	• severity: quantity, frequency and duration • regularity and predictability of patterns	• cycles: annual winter soil freezing • crashes: yearly tillage of crop field • catastrophes: removal of tropical rain forests
Biological community	• competitive neighbor interactions • specificity and vulnerability: sensitivity and resistance • change in biodiversity	• competitive exclusion by earliest emerging seedling in field • response to predators, parasites and diseases • increase in prairie fires with loss of large herbivores
Abiotic environment	• resource availability • inhibitors and stress • climate and weather	• drought • herbicides • winter freezing of soil

Phenotypic life history traits

Given an opportunity in a locality, the second condition necessary for plant invasion is the presence of propagules of a particular species possessing life history traits suitable to exploit that space. A life history perspective provides some advantages in understanding how invasion occurs in a community. Plants experience the same general life history processes (birth, dispersal, recruitment, vegetative and seed reproductive growth). This life cycle can be described by the underlying plant morphological structures, developmental processes and whole plant activities that occur during each of these phases (Tab. 2). The time a plant performs these developmental processes and activities, relative to that of its neighbors, determines its success in the invasion process: timing is everything. If a particular invading plant is at the right place, at the right time, it is the traits that it expresses at those times that make it a winner or a loser relative to its neighbor. A plant's life cycle is a Markov Chain process in which the state of the plant at any one time is a direct consequence of its state in the previous time period [6]. Failure at any time in the life history ends the invasion process.

Phenotypes and traits inevitably fill opportunity spaces in disturbed localities. Selection favors individual phenotypes and traits that preferentially take advantage of these opportunities at the expense of their neighbors (Tab. 3). Selected

Table 2. Plant morphological structures, developmental (physiological, morphogenic) processes and whole plant phenotypic activities during the plant life history processes of birth, dispersal, recruitment, vegetative growth and seed reproductive growth

Life history process	Plant morphological structure	Developmental (physiological, morphogenic) process	Whole plant activity-phenotype
Birth	Seed or vegetative bud (parental)	• fertilization • zygote • embryogenesis • bud morphogenesis • dormancy induction	• seed and bud formation
Dispersal	Seed or vegetative bud (independent ramet; parental ortet)	• dormancy maintenance	• spatial dispersal • spatial foraging (ortet) • seed or bud pool formation (dispersal in time)
Recruitment	Seedling or bud shoot (juvenile)	• germination or bud growth • emergence from soil • first leaf greening	• establishment
Vegetative growth	Vegetative plant (adult)	• growth • meristem morphogenesis • senescence of some tissues	• interactions with neighbors
Seed reproductive growth	Flowering plant (adult)	• flower formation • senescence • meristem morphogenesis	• pollen dispersal

Table 3. Plant traits conducive to invasibility, colonization and weediness during the plant life history processes of birth, dispersal, recruitment, vegetative growth and seed reproductive growth

Life history process:	Traits
Birth	**Genetic:** • variability of progeny by genomic rearrangement • local adaptation: 　a] by genotypic and phenotypic variability (biotypes) 　b] by epigenetic/epistatic mechanisms (e.g., chromosomal methylation) • small genome size [7] **Fertilization:** • attractants for pollinating species: chemical, morphological • plastic stigma receptivity timing **Seed development:** • rapid seed maturity • rapid development of germination competence of immature, prematurely harvested, seeds • seed or bud primary dormancy induction: 　a] heterogeneous among seeds of a cohort 　b] inherent and dynamic in response to post-abscission experience (seed memory) • optimized seed size (and seed components) for habitats exploited • high seed quality regardless of seed productivity • Constitutively expressed polymorphic seed production (e.g., sunflower seed dimorphism) **Environmental:** • fertilization and flower/zygote development stress tolerance
Dispersal	**Spatial:** • seed shattering • dispersal structures: 　a] for habitat placement by exploitation of wind, water, and animal vectors 　b] multiple dispersal modes 　c] lack of dispersal structures (gravity) for ensuring local placement • perennial bud dispersal: 　a] independent buds: ramet 　b] parental buds: ortet • attractants for dispersal vectors (e.g., animals): chemical, morphological **Temporal:** • formation of soil seed and bud pools (dispersal in time) • seasonal seed and bud dormancy cycling: after-ripening and secondary dormancy induction • soil predator and disease tolerance (e.g., endophytic fungi colonization of seed for disease tolerance)
Recruitment	**Seed:** • heterogeneous emergence timing from differential dormancy levels among seed of a cohort (including non-dormancy) • germination over wide range of soil and resource conditions

(Continued on next page)

Table 3. (Continued)

Life history process:	Traits
	• bud dormancy • allelopathy: e.g., neighbor seed germination inhibitor production • seedling vigor and high relative seedling growth rates • specialized structures for self-planting in soil (e.g., corkscrewing hydroscopic awns) Soil: • emergence from soil depth • allelopathy: e.g., neighbor seed germination inhibitor production • seedling vigor and high relative seedling growth rates • exploitation of all available germination microsites in a locality • early emergence timing for competitive exclusion of neighbors Environment: • germination over wide range of conditions • stress-tolerant germination and establishment • disturbance-facilitated recruitment

Vegetative growth	Genetic:
	• exploitation of overlapping niches in a locality by a species-group (intra-genus, inter-specific variation) OR association of closely related (intra-genus) species: species-group formation
	
	Plant:
	• rapid and efficient vegetative growth (high relative growth rates)
	• optimum root-shoot partitioning of vegetative growth
	• optimized timing of life history seasonal development forms (somatic polymorphism):
	  a] perennating underground structures
	  b] biennial plant form: overwinter rosette, elongated spring form (bolting)
	• resource acquisition:
	  a] high water use efficiency
	  b] enhanced nutrient uptake; luxury consumption
	  c] root system morphology and architecture for efficient water/nutrient extraction
	  d] leaf size/structure somatic polymorphism
	  e] efficient photosynthesis for locality (e.g., C4, CAM metabolism)
	• whole plant regeneration:
	  a] shoot fragment rooting
	  b] root fragment shoot growth
	• senescence timing
	• accumulation of food reserves in underground perennating tissues
	• vegetative tissue dormancy
	
	Environment:
	• vegetative growth plasticity sized to environment
	• stress tolerance: herbicides; temperature; mowing/cutting; temperature; resource availability
	• shoot flexibility and brittleness to survive tillage
	• internode shortening in response to wind

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Table 3. (Continued)

Life history process:	Traits

Competitive interactions with neighbors:
- offensive abilities against neighbors:
  a] allelopathy
  b] host for crop and neighboring plant species diseases with self disease tolerance
- spatial foraging ability
  a] photomorphogenesis:
    1] internode elongation for light capture in response to shading
    2] canopy architecture
  b] rapid exploitation of the local soil space
  c] perennial plant foraging: shoot/root; ramet/ortet
- defensive abilities against neighbors:
  a] specialized anti-herbivore, anti-grazing structures
  b] chemical repellants and poisons
  c] crop mimicry
  d] competition avoidance: temporal phase shift of development for neighbor avoidance

Seed reproductive growth

Genetic:
- mating system matched to optimizing local condition variability:
  a] Outcrossing:
    1] outcrossing rate optimized for more changeable environments
    2] dioecy for more efficient seed production:
      – lower local male plant pollen production costs
      – lower female plant seed production costs
    3] genetic flexibility from monoecious form of dioecious species
    4] monoecy or outcrossing rate regulation
    5] self-incompatibility mechanisms
  b] Selfing
    1] self pollination and apomixis for more stable, environments
    2] lower seed costs with no pollen production in apomicts
  c] optimized balance of self and outcrossing pollination for local conditions

Plant:
- secondary flowering culms and branches
- prolific seed production under wide range of conditions
- some seed production under stress conditions
- intra-plant resource allocation to seed production
- pollen dispersal (+/–)
- extended, plastic, seed production period maximizes favorable periods; "anticipates" crop harvest timing

Environment:
- stress tolerance:
  a] flowering in intact plants
  b] flowering in injured plants
- reproductive plasticity: flower number sized to environment
- flower timed to photoperiod (+/–)

phenotypes dominate their neighbors because the timing of their life history optimizes their relative fitness and minimizes mortality. The character of these opportunity spaces can be deduced by observing the new phenotypes adapted to these new spaces, and what traits they possess allowing such ready invasion.

The plant invasion process

Given a plant species with certain life history traits and a vulnerable local opportunity space, the invasion process consists of three component process-es: dispersal of the species into that locality, followed by colonization and enduring occupation of the habitat (Tab. 4). The invasion is successful only when all these are accomplished. Most invading species probably fail to com-plete all three steps, and there is little experimental information estimating the failure rate.

Plant invasions are events in the ecology of community assembly and suc-cession, as well as in the evolution of niche differentiation by speciation. There is not a meaningful difference between the invasion process and these process-es except the scale of attention humans bring to their observations. In all these processes disturbance is a prime motivator of change. The scale of habitats in time and space is continuous; and all communities are inter-related.

Dispersal
The first activity in invasion is successfully introducing propagules (seeds, vegetative buds, etc.) into a candidate opportunity space. Dispersal is previ-

Table 4. The invasion matrix: the processes (invasion, colonization, enduring occupation), life histo-ry activities (dispersal, recruitment, establishment including reproduction, and several modes of enduring occupation) and examples

Invasion process	Life history activity	Example
Invasion	Dispersal	propagule (e.g., seed, vegetative bud, spore, pollen) movement from one continent (or locality) to another and fails to reproduce
Colonization	All events must occur: a] recruitment b] establishment c] reproduction	volunteer maize (*Zea mays* L.) lives for only one generation (F_2) in a field, failing to colonize due to lack of dormancy
Enduring occupation	Several modes possible: a] enduring presence for more than one generation b] range expansion c] formation of soil propagule (e.g., seed) pool	successful, long-term, agricultural weeds; e.g., North America: *Amarathus* spp-gp.; *Setaria* spp-gp

ously defined as 1) the act of scattering, spreading, separating in different directions [3], 2) the spread of animals, plants, or seeds to new areas [2], 3) outward spreading of organisms or propagules from their point of origin or release [8], iv) the outward extension of a species' range, typically by a chance event [8]. I defined the dispersal as the search by plant propagules (e.g., seeds, buds) for opportunity space.

Colonization
The process of colonization includes three activities: recruitment, establishment and reproduction at the new locality. Colonization could be defined as 1) (of plants and animals) to become established in (a new environment) [2], 2) the successful invasion of a new habitat by a species [8], 3) the occupation of bare soil by seedlings or sporelings [8].

Recruitment
Recruitment is the 1) seedling and bud shoot emergence, and 2) the influx of new members into a population by reproduction or immigration [8].

Establishment
Establishment   is the process of growing and reproducing successfully in a given area [8].

Enduring occupation of a locality
Several modes of long-term presence at a locality are possible. An invading species can have an enduring presence for more than one generation in the same locality. This long-term presence is often facilitated by plant traits that allow the formation of soil propagule (e.g., seed) pools. A species present in one locality can also expand its range into new localities.

Local selection and adapted phenotypes

Once a species successfully occupies a local site of some time period, the action of selection pressures result in local adaptation in favor of particular genotypes and phenotypes. The selection pressures these populations experience in the invasion and occupation phases derives from biological, abiotic and human selection pressures. This local selection also acts on the variable phenotypes of that invading species and selects adapted biotypes that occupy that space into the future. Some of the consequences of this local evolution and adaptation include increases in locally-adapted phenotypes, range expansion beyond the locality, and population shifts in the local community as a consequence of altered neighbor interactions.

    The biology of the invasion process as presented in this section is rational and experimentally tractable. What is less apparent is the human component of the selection process that creates opportunity spaces into which invasive spe-

cies disperse. The direct effects of human activity are also more discernable than the indirect effects. Of critical importance is the role human perception plays in selection and creation of opportunity space for invasive species.

The perception of plant invasion

A species succeeding in occupying a locality must be perceived by humans as being problematic for it to be labeled invasive. The perception of a plant species as invasive by humans is a complex, often highly subjective process. Despite this, there are several systematic ways to understand how human perception and cultural values create selection pressure and opportunity spaces conducive to plant invasions. They include insights gained from public policy and reflection on human values. These social and perceptual factors are inherently anthropological and anthrocentric in nature, and need to be understood in those contexts for a complete understanding of the forces of selection conducive to invasion.

Anthropology	1. The scientific study of human beings, their origins, distribution, physical attributes and culture [3].
	2. The study of man, his origins, physical characteristics, institutions, religious beliefs, social relationships, etc. [2].
Culture	1. The skills, arts, etc., of a given person in a given period [3].
	2. The entire range of customs, beliefs, social forms, and material traits of a religious, social, or racial group [3].
	3. The total of the inherited ideas, beliefs, values, and knowledge, which constitute the shared bases of social action.
	4. The total range of activities and ideas of a group of people with shared traditions, which are transmitted and reinforced by members of the group [2].
Anthrocentric	Centering in man [3].
Anthropocentric	Regarding man as the most important and central factor in the universe [2].

Public policy

Public policy can provide a starting point to determine human perceptions of invasive species, an expression of human values. Of particular interest is public policy on invasive species promulgated by the US Federal government in Executive Order 13112 of 3 February 1999 [9, 10]. Research, management and

dissemination of information about invasive species in the US are funded by government agencies in compliance with this order. The terminology used in this public policy statement reveals how some perceive invasion biology. Therein [9, 10] they define several terms, below included with definitions from more conventional sources:

Invasive species	1. An alien species whose introduction does, or is likely to, cause economic or environmental harm or harm to human health [9].
	2. A species that is non-native (or alien) to the ecosystem under consideration and whose introduction causes or is likely to cause economic or environmental harm or harm human health [10].
Alien species	1. With respect to a particular ecosystem, any species, including seeds, eggs, spores, or other biological material capable or propagating that species, that is not native to that ecosystem [9].
	2. Non-native; a species occurring in an area to which it is not native [8].
Native species	1. With respect to a particular ecosystem, a species that, other than as a result of an introduction, historically occurred or currently occurs in an ecosystem [9].
Native	1. Relating to the indigenous inhabitants of a country or area, a local Inhabitant, an indigenous plant or animal [3].
	2. Relating or belonging to a person or thing by virtue of conditions existing at the time of birth; born in particular place [2].
	3. Indigenous, living naturally within a given area, used of a plant species that occurs at least partly in natural habitats and is consistently associated with certain other species in these habitats [8].
Nativism	1. The doctrine of innate ideas.
	2. In US, the advocacy of the claim of native as opposed to that of naturalized Americans [3].
	3. *Chiefly US* the policy of favouring the natives of a country over the immigrants [2].
Natural	1. Of or produced by nature [3].
	2. In accordance with human nature [2].
	3. Not affected by man or civilization, uncultivated, wild [2].
Introduction	1. Intentional or unintentional escape, release, dissemination, or placement or a species into an ecosystem as a result of human activity [9].

Several aspects of invasion biology are revealed in these definitions. These include the concept of economic, environmental and human harm; the differentiation between alien and native species; the existence of natural conditions; and the purposeful introduction of a plant species to a locality.

The purpose of this paper is only to highlight the explicit statements of human goals and values that may influence invasion biology. Of specific importance to public policy is the value placed on nativism, natural conditions and the different categories of harm. How public policy is implemented with these guiding, often subjective, concepts is at the heart of how these species are managed. The management elicited by public policy is the selection pressure these invasive species will respond and adapt to in their subsequent evolution.

Human values

The historical expansion of human populations, and their activities, has affected almost every habitat on earth to some extent, either directly or indirectly. Air and water pollution alone have affected much of the surface biology of earth (e.g., CO_2, O_3). Human perception of what is natural and indigenous, what is disturbed and artificial, is therefore compromised to some degree. In one form or another, willingly or not, the earth is the garden of humanity. The equivocal nature of what harm is caused by invasive species is therefore confounded by the heterogeneous array of human viewpoints and aesthetic values of what is desirable in landscapes. This heterogeneity of opinion is not resolvable but remains at the core of invasion biology because values guide activity and management. For better or worse, the actualization of human values creates opportunity space for new species to invade: they are a direct reflection of human activity.

The best expression of human-mediated invasion biology can be found in agriculture. With the advent of agriculture some 10,000 years ago, hunter-gatherer and nomadic peoples were displaced gradually by spatially sedentary agriculturists. The opportunity space for agriculture was vast. Humans imposed disturbance regimes on those spaces (e.g., soil tillage) and favored plant species with desirable phenotypic traits to cultivate and harvest. Evolutionary changes in those cultivated species led to somewhat ironic consequences: the formation of stable, long-lived wild-crop-weed complexes [11, 12]. Wild progenitor species were domesticated. Crop phenotypes escaped cultivation and developed weedy habits ideal for infestation with their crop relative, and both shared space with the original wild relatives. Gene flow was continuous between these closely related forms of the same species-group, an ideal genetic situation for the longevity of the species. Archetypical examples of these wild-crop-weed complexes are found in *Amarathus* (grain amaranth, pigweeds), *Setaria* (foxtail millet, green foxtail [13, 14]), *Brassica* (rapeseed and wild mustards), *Helianthus* (sunflowers), *Avena* (oat), *Oryza* (rice), *sorghum* (crop, johnsongrass), *Solanum* (potatoes, nightshades), and *Hordeum* (barley, foxtail barley).

The most important current agricultural plant invasion is the introduction of transgenic crops, often on a vast scale (e.g., glyphosate-resistant crops). Introduction of any trans-gene into the crop cultivars of these wild-crop-weed complexes increases the chances of introgression into its related non-cultivated weedy and wild phenotypes (e.g., 5). The development of these biotechnologies in wild-crop-weed complexes fulfill the conjecture provided in the introduction: a critical interaction of disturbance, dispersal and plant traits adapted for the resultant opportunity space. The introduction of such biotechnologies as herbicide-resistant crops provides a mixture of environmental and economic benefit and harm which makes implementation of public policy as defined by US Federal policy [9, 15] somewhat problematic and highlights the complex interaction of biology and human values.

Conclusions

"With the present tremendous population explosion the most common habitat has become man-made, and it may not be many centuries before this will be the only habitat available. With the disappearance of stable habitats, truly wild species will be the first to become extinct. Wild colonizers may survive as long as habitats remain that are only sporadically disturbed by man. Eventually these must also disappear and *Homo sapiens*, the ultimate of all weeds, will lord it over the domain he has created for himself, his companion weeds, his crops and domesticated animals." JMJ de Wet, 1966 [11]

The human role in creating opportunity space for plant invasion

Invasion biology is a reflection of the impact human populations have on the earth's ecology. Public policy is currently focused on management and control of specific species, but at the same time ignoring the fundamental and complex sources of these changes in biological communities. Fundamentally the problem is human: human population size and collateral disturbance, human dispersal of invasive species propagules, heterogeneous human values about the nature of harm and beauty, and the priorities of human scientific endeavors. In all this there may be some benefit to humans by exploiting the very traits we despise most for plant improvement.

Human population size

Human population size may be the primary cause of invasion biology and changing community structure. With expanding populations are consequential changes in land use and spatial organization, increasing direct and indirect disturbance, increased resource use and loss, and other changes to habitats.

Global propagule dispersal
Human global traffic has increased significantly in recent history. There exists an increased "transferability" of everything in human global society: trade goods and services, human travel and transportation, and ideas. Swept along with this traffic have been vastly increased opportunities of dispersal of biological propagules into available opportunity spaces. World grain traffic alone has moved immense quantities of plant propagules over historical times, despite our best efforts to control the more noxious forms.

Human disturbance
Landscapes and habitats around the world have been influenced by this byproduct of human activity. Air and water pollution is ubiquitous and affects almost all spaces on the earth's surface. Direct and indirect disturbances by humans have altered most of these spaces and the ecological relationships in biological communities, leaving vast new opportunity spaces open and available to species with traits allowing their exploitation.

Human values and culture
Human perception of these changes, public policy initiatives defining environmental and economic harm and human aesthetic values provide heterogeneous and often conflicting value systems to be compromised in reaching a consensus on the best solutions. Contributing to the situation is a recent increase in perceived fear of alien invasion, and a nativistic reaction to these fears.

Science of invasion biology
There is not a meaningful difference between the invasion process and the processes of ecological community assembly, succession and the evolution of niche differentiation by speciation. Despite this, disciplinary barriers are apparent in the differentiation of invasion biology science in unmanaged and managed habitats: agricultural weed biology and invasive plant biology are often separated in the scientific academy. Both these realms are unified by disturbance as a prime motivator of change in community structure. The scale of habitats in time and space is continuous; and all communities are inter-related and inter-dependent. Agriculturalists often do not completely embrace the invasion process in understanding population shifts, and ecologists studying unmanaged systems often fail to recognize the role of indirect disturbance and dependence on adjacent agricultural habitats in the larger landscape. The science of both will advance when the unifying principles underlying both types of undesirable species are acknowledged in a larger view of invasion biology.

Utilizing and exploiting beneficial plant invasive species

Weed is a plant whose virtues have not been yet discovered (attributed to RW Emerson, 1878). Imagine a world in which global warming results in Antarctic

ice melting and exposing a terrestrial habitat. What would the first higher plant invaders look like? Imagine that humans colonize Mars. What will their controlled environment plant communities look like? In either case, does there now exist plant traits that may provide answers to these two speculative questions? Would exploitation of the traits that allow invasive species to succeed provide us with better plant communities? Whether Antarctic, Martian, agricultural or scenic?

As humans alter the earth's habitats directly and indirectly, some consideration should be given to preserving and exploiting the germplasm of our best-adapted invasive and weedy species for such a future. Preservation of weedy and invasive genotypes is an emerging issue in science as novel and unique weedy biotypes are lost with the significant changes biotechnological crop introductions are causing [e.g., 15, 16]. The traits these noxious plants possess may provide novel solutions to the problems we create in expanding human communities. The only obstacle to utilizing invasive plants as sources of novel, useful traits in crops for biotechnology is our perception of what is useful, beautiful and harmful.

Other ecological services are provided by weeds and invasives. Purple loosestrife (*Lythrum salicaria*) is a beautiful and pleasing plant species. Zebra mussels (*Dreissena polymorpha*) have cleaned turbidity from many localities in the US great lakes (e.g., Michigan's Saginaw Bay and Lake Huron), enhancing human health and recreational value. Weeds are a major food source for indigenous wildlife bird and animal populations [17]. They provide refuge habitat to many other species, and can be alternate hosts for beneficial insects and microflora in biocontrol tactics. In addition, their vast phenotypic biodiversity is valuable in its own right.

Summary

Invasive plants have significant effects on humans and cause economic, environmental, aesthetic and biological harm to biodiversity, ecosystem function, and human welfare. The appearance of invasive plants in terrestrial and aquatic landscapes is associated with perturbations caused by human population growth and activity. Herein is posed a conjecture that a successful plant invasion is the consequence of the presence of a species possessing life history traits suitable to exploit opportunities available at a locality. Given these two conditions, a successful invader must disperse into, colonize and occupy that locality for some period of time. The last requirement is that humans must perceive some invasions as a problem. Without all these events occurring, a plant is not considered invasive. Perception of a plant as invasive is a complex, often subjective process. Inspection of public policy and reflection on human value systems provides a more systematic method of understanding how human activity creates selection pressure and opportunities for invaders. The human role in creating these opportunities includes the impact of human population

size and growth, dispersal of invasive species propagules in global trade, direct and indirect disturbance by human activity, human values and culture, and the organization of the scientific academy in researching invasion biology. Utilization and exploitation of the highly adapted traits for invasion may provide a benefit to humans, as well as provide impetus to preserve valuable germplasm resources from changes in agroecosystems with the introduction of new biotechnologies.

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Characteristics, significance, and human dimension of global invasive weeds

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Introduction

Invasive plant species have potential to damage our crops, our industries, the environment and public health. Scientists, academics, leaders of industry and land managers are realizing that invasive species are serious environmental threats for the 21st century [1, 2]. Also, invasive species are recognized as one of the leading threats to biodiversity and imposes tremendous costs on agriculture, forestry, fisheries, wetlands, roadsides, natural areas, and other human enterprises, including human health. Invasive species take a heavy economic toll with costs estimated to be $137 billion every year in the United States [3]. In 1994, the impacts of invasive plants in the United States were estimated at $13 billion per year [4].

For centuries people have moved plants, animals, and microbes around the world. Most countries now rely on plants and animals from other regions of the world in order to meet their dietary needs. People in the US also import plants and animals, and their products, as ornamental plants and pets. Organisms that have been moved from their native habitat to a distant location are typically referred to as "non-native", "non-indigenous", "exotic", or "alien" to the new environment.

There are fundamental differences in the approaches dealing with invasive plant species problem depending on the ecosystem being invaded (terrestrial, forests, and marine). My purpose is to highlight the characteristics and significance of terrestrial invasive plant species. Also, I link various aspects of the human dimension to the current status of global invasive weeds.

Invasive plants and biodiversity

Human induced biological invasions are occurring on a global scale and are beginning to blur the regional distinctiveness of the Earth's biota. That distinctiveness, which evolved over the past 180 million years as a result of the isolation of the continents, has produced and maintained biodiversity. When considered as a single phenomenon, biological invasions probably has had

greater impacts on the world's biota than more widely known aspects of global environmental change such as rising CO_2 concentrations, climate change, and decreasing stratospheric ozone levels [5, 6]. Insidious effects of invasive non-native species include displacement or replacement of native plants and animals, disruptions in nutrient and fire cycles, and changes in the pattern of plant successions [7].

In recent years, the impact of invasive species on biodiversity has also become a major concern. These silent invaders constantly encroach into preserves, parks, crop lands, wildlife refuges, and urban spaces. At a global scale, invasions by non-native plants, animals, fungi, and microbes are believed to be responsible for greater losses of biological diversity than any other factor except habitat loss and direct exploitation of organisms by humans [7]. Non-native species further threaten fully two-thirds of all endangered species. Non-natives are now considered by some experts to be the second most important threat to biodiversity, after habitat destruction [7, 8]. Native species have also been considered invasive when they spread into human-made habitats such as farms or gardens [9].

According to the US Congressional Office of Technology Assessment, there are at least 4,500 species of foreign plants and animals that have established free-living populations in the United States since the beginning of European colonization. Of that total, at least 675 species (15%) cause severe harm. In economic terms, 79 species, or 12% of total harmful species, caused documented losses of $97 billion from 1906 to 1991 [10].

The nature and distribution of invasive species has no geographical boundaries. All living organisms – bacteria, fungi, plants and other organisms – have evolved in specific areas on the Earth. Local climate, geology, soils, available water and other natural factors may influence plant or organism's invasion and subsequent establishment in a particular habitat.

Invasive plants are estimated to infest 40.5 million hectares in the United States. Every year, they spread across three million additional acres, an area twice the size of Delaware. Everyday, up to 1,862 hectares of additional Federal public natural areas in the Western continental United States are negatively impacted by invasive plant species [11].

In 1950, the number of plant introductions into the United States was estimated to be at least 180,000 [12]. In 1975, it was estimated that at least 1,800 introduced plant species had escaped into the wild, with a large proportion establishing free-living populations [13]. Currently, the Weed Science Society of America recognizes about 2,100 plant species as weeds in the United States and Canada [14]. 1,365 or 65% of all weeds in the United States are recognized as non-native in origin by the Weed Science Society of America. This does not include most weeds of natural areas. Some of the important invasive weed species in the United States are listed in Table 1.

Of the 6,741 plant species that are recognized as weeds somewhere in the world, only 2,063 species occur in the contiguous United States [15]. More than 900 non-native plant species have become established in Florida and they

Table 1. Some of the common invasive weed species in the United States[1]

Scientific name	Common name	Plant type	Habitat
Acer platanoides	Norway maple	Tree	Natural areas, landscapes
Ailanthus altissima	Tree-of-heaven	Tree	Natural areas, landscapes
Alliaria petiolata	Garlic mustard	Herbaceous	Upland, natural areas
Artemisia vulgaris	Mugwort	Herbaceous	Landscapes, ornamental
Centaurea maculosa	Spotted knapweed	Herbaceous	Prairies, grassland
Eichornia crassipes	Water hyacinth	Aquatic	Lakes, rivers and ponds
Euphorbia esula	Leafy spurge	Herbaceous	Prairies, grasslands
Heracleum mantegazzianum	Giant hogweed	Herbaceous	Upland
Lythrum salicaria	Purple loosestrife	Herbaceous	Wetland, streams
Microstegium vimineum	Japanese stiltgrass	Grass	Upland
Myriophyllum spicatum	Eurasian watermilfoil	Aquatic	Lakes, rivers and ponds
Paederia foetida	Skunk vine	Vine	Natural areas
Polygonum cuspidatum	Japanese knotweed	Herbaceous	Upland, wetland
Phargmitis australis	Common reed	Grass	Upland, wetland
Polygonum perfoliatum	Mile-a-minute	Vine	Upland, roadsides
Pueraria lobata	Kudzu	Vine	Upland
Rosa multiflora	Multiflora rose	Shrub	Pastures, old-fields and roadsides
Rubus phoenicolsius	Wineberry	Shrub	Roadsides, natural areas
Solanum viarum	Tropical Soda Apple	Shrub	Croplands, natural areas
Striga asiatica	Witchweed	Upland	Pastures, croplands and roadsides

[1]Compiled by PC Bhowmik, 2003, for presentation at the International Symposium on Ecology of Biological Invasions, School of Environmental Studies, Delhi University, Delhi, India, December 4–6, 2003

Table 2. Some of the common invasive weed species of the Tropical Regions[1]

Scientific name	Common name	Plant type	Habitat
Cromolaena odorata	Siam weed	Shrub	Forest, natural areas
Eichornia crassipes	Water hyacinth	Aquatic	Lakes, rivers and ponds
Lantana camera	Lantana	Shrub	Upland
Melaleuca quinquenervia	Melaleuca	Tree	Coastal wetlands
Mikania micantha	Miconia	Vine	Forest, cropland and landscape
Opuntia stricta	Opuntia	Cactus	Upland, landscape
Parthenium hysterophorus	Parthenium	Herbaceous	Upland
Sorghum halepanse	Johnson grass	Grass	Upland, cropland
Wedelia glauca	Wadelia	Herbaceous	Landscapes, pastures

[1]Compiled by Bhowmik PC 2003 for presentation at the International Symposium on Ecology of Biological Invasions, School of Environmental Studies, Delhi University, Delhi, India, December 4–6, 2003

constitute at least 27% of the total flora of the state [16]. Currently, it is estimated that there are 4,678 species of invasive plants in other countries that could still be introduced into the United States. Some of the important invasive weed species of tropical regions are listed in Table 2.

Characteristics and traits of invasive species

An invasive species is one that both spreads in space and has negative impacts on species already in the space that it enters. In the United States, an "invasive species" is defined by the Executive Order in 1999 [17] as a species that is i) non-native (or alien) to the ecosystem under consideration and ii) whose introduction causes or is likely to cause economic or environmental harm or harm to human health. The Order further provides that a Federal agency may make a determination that the benefits of an action, which may lead to the introduction or spread of an invasive species, clearly outweigh the potential harm caused by the species and take steps to minimize that harm [17]. This management plan is focused on those non-native species that cause or may cause significant negative impacts and do not provide an equivalent benefit to society.

In general, invasive woody plants tend to have small seed size, a short juvenile period, and a relatively short interval between seed crops that produce a high number of seeds [18]. Invasive plants (regardless of their origin) tend to have many similar biological attributes relating to high reproductive potential and stress tolerance. Some of the common traits are: i) rapid seedling growth and early maturation, ii) ability to reproduce at an early stage, iii) ability to reproduce by vegetative propagules as well as by seeds, iv) ability to produce viable seeds, v) seed dormancy ensuring periodic germination, vi) diverse dispersal mechanisms and high dispersal rate, vii) high photosynthetic rates, viii) ability to tolerate wide range of environmental conditions, ix) ability to tolerate high habitat disturbance, and x) vigorous growth allowing to compete aggressively with native species.

Invasiveness of plant species is dependent upon species traits, habitats, environmental stress and other biological factors. It has proven difficult to identify particular traits that are consistently associated with the tendency of plant species to invade [19]. Knowing history of past invasiveness may be the best predictor on invasiveness of a species in a new habitat. This suggests that some plant species are more invasive than others but does not explain which traits encourage invasiveness (see Chapter 2, this volume).

Pathways of species introduction

Introduction means the movement, by human agency, of a species, subspecies, or lower taxa (including any part, gamet or propagule that might survive and

subsequently reproduce) outside its natural range. Their movement can be either within a country or between countries. Biological invasions are important components of human-caused global environmental changes. Williamson and Fitter [20] estimated that only 0.1% of all plant species that are introduced outside their native ranges by humans become invasive.

Invasive species have been introduced in a variety of ways. The means and routes by which they are introduced are called invasion "pathways". People introduce exotic plants to new areas with intent and by accident by variety of means. Some species are introduced for use in gardening and landscaping, for erosion control, forage and other purposes. For instance, in the 1930s, the Civilian Conservation Corps planted kudzu vine [*Pueraria lobata* (Wild.) Ohwi.], introduced from Japan, throughout the Southeast to help stabilize soil in erodable areas. The recent intentional introduction of purple loosestrife (*Lythrum salicaria* L.) is another example of a successful plant invasion. This species was introduced to the northeastern United States and Canada in the 1800 s for ornamental and medicinal uses. Purple loosestrife has adapted readily to both natural and disturbed wetlands. It is replacing many of the native plant species and its environmental impact is enormous.

The role of a species within an ecosystem is a direct result of changing community processes and lead to alternatives of community composition and structure. Vegetative reproduction is often important for establishment and spread of many species in terrestrial environments and also for dispersal in aquatic habitats. Disturbance of successively advanced communities and then slow recovery rate promote the invasion of many introduced species [21]. Common habitats for invasive species can be grouped as natural areas, roadsides, wet lands, lakes/ponds, and agricultural areas. Not all non-native (introduced or alien) species are harmful. In fact, the majority of species cultivated in agricultural lands in the US are introduced species.

Intentional introductions

Alien or exotic plants are introduced intentionally for a great variety of purposes. A large proportion of important crops are grown in areas outside their natural distribution for economic reason and as a way to feed the world population. Exotic plants can be introduced for many uses, including food use, forestry use, soil improvements, ornamental plants, cover crops and other uses. Numerous ornamental plants have also been introduced in the US and some of the species are invading natural areas (Tab. 3). In India, many plants have been introduced as cover crops or for other purposes (Tab. 4). Introduced exotic species, however, can pose a risk to biodiversity when they naturalize and penetrate conservation areas. Tall fescue (*Festuca arundinacea* Schreb.), a native European, has been planted as a pasture grass in North America. It has naturalized and invaded remnant prairies, replacing the once diverse natural herbaceous community [22].

Table 3. Ornamental species invading natural areas in the United States[1]

Plant type	Scientific name	Common name	Habitat
Trees	*Acer platanoides*	Norway maple	Native sugar maples
	Ailanthus altissima	Tree-of-heaven	Stream banks/Displace native vegetation
	Melaleuca quinquenervia	Melaleuca, Cajeput	Fresh water wetlands
	Tamarix ramosissima	Salt cedar	Stream banks
Shrubs	*Berberis thunbergii*	Japanese barberry	Woodlands, young forests
	Cytisus scoparius	Scotch broom	Grasslands, roadsides
	Euonymous alata	Burning bush	Open woods, pastures
	Lonicera maackii	Amur honeysuckle	Open to shaded areas
	Rosa multiflora	Multiflora rose	Pastures, old fields and roadsides
	Schinus terebinthifolius	Brazilian pepper	Wetlands, savannahs, prairies and abandoned fields
	Spiraea japonica	Japanese spiraea	Stream banks, roadsides and forests
	Taxus cuspidata	Japanese yew	Woodlands, young forests
Herbaceous	*Lathrum salicaria*	Purple loosestrife	Wetlands, river banks, lake shores and ponds
	Polygonum cuspidatum	Japanese knotweed	Riverbanks, wet areas
	Potentilla erecta	Erect cinquefoil	Grasslands, and forests
	Vinca minor	Periwinkle	Shady areas, forests
Grasses	*Arundo donax*	Giant reed	Fresh water
	Cortaderia spp.	Pampas grass	Open sandy soil in coastal areas
	Imperata cylindrica	Cogongrass	Roadsides, pastures, wetlands, savannas and forests
	Phalaris arundinacea	Reed Canary grass	Wetlands
Vines	*Celastrus orbiculata*	Oriental bittersweet	Open woods, roadsides/overtopping native species
	Lonicera japonica	Japanese honeysuckle	Smothers small trees and shrubs/overtopping
Aquatic plants	*Eichhornia crassipes*	Water hyacinth	Lakes, waterways
	Hydrilla verticillata	Hydrilla	Lakes and rivers

[1] Compiled by Bhowmik PC, 2004

Table 4. Intentional introduction of some weeds to India[1]

Scientific name	Common name	Introduced from	Purpose
Chromolaena odorata	Siam weed	Tropical areas	Cover crop
Eichnonia crassipes	Water hyacinth	South America	Ornamental
Lantana camera	Lantana	Many countries	Ornamental
Mikania micantha	Miconia	Malaysia	Cover crop
Opuntia stricta	Opuntia	Australia	Hedge plant
Phaseolus labatus	Phaseolus	USA	Cover crop
Sorghum halepanse	Johnson grass	USA	Forage crop

[1] Presented at the International Symposium on Ecology of Biological Invasions, School of Environmental Studies, Delhi University, Delhi, India, December 4–6, 2003

Accidental introductions

Many of the alien agricultural weed species have been accidentally introduced as contaminants of crop seeds. Despite the Federal Seed Act, weeds continue to arrive in the USA as seed contaminants. Similar contaminations of alien plant species have been identified in many countries in the world. Soil-inhabiting species can be introduced by shipping soil or by soil attached to plant material. Machinery and vehicles are often shipped from place to place without cleaning. Depending on their uses, they may carry soil and plant material. Historically, military equipment has resulted in several introductions of harmful species, such as the golden nematode (*Globodera rostrochinensis)* into the USA [22].

Impacts of invasive species on society

Species inhabiting outside their historic areas of distribution often escape various checks, such as natural enemies, that normally limit their population growth. They may impact native species, through predation, herbivory, resource competition, aggression or hybridization [23]. They can displace and even cause the extinction of unique variants or races, resulting in an irreparable loss of genetic diversity [24].

Invasive species have enormous impacts on our society including economic, social, and ecological aspects. According to a recent survey by the US Department of the Rangelands in the West, western wildlands are being lost from grazing land at a rate of 1,840 hectares per day to invasive plants such as leafy spurge (*Euphorbia esula* L.) and yellow starthistle (*Centaurea solstitialis* L.). In 1996, they indicated a 14% annual increase in area infested. If weeds continued to spread at this rate, it was predicted that over 13 million hectares of western wildlands were infested with weeds by the year 2000 [8]. Purple loosestrife, a highly invasive species, can produce up to 2.7 million seeds per

plant yearly and spreads across approximately 400,000 additional hectares of wetlands each year. These strategies demonstrate the impact of an invasive species on a natural habitat.

Invasive plants damage soil and water resources. The displacement of bunch-grasses by spotted knapweed *(Centaurea maculosa* Lam.) substantially increases surface water run-off and sediment yield (soil loss). An additional 16,200 kg of soil would be lost from a 225-hectare rangeland infested with spotted knapweed in western Montana during an average 30-minute rainfall event, compared to a similar site occupied by native bunch-grasses [25].

Invasive plants may have impacts on endangered species in relation to their own habitats, competitive ability, and environmental stress factors. Rare species appear to be particularly vulnerable to the environmental changes that are brought about by non-native species. In California, it has been estimated that 30 of the state's endangered plant species are threatened by non-native invaders [7]. In Florida, Australian pine has spread to such an extent in coastal areas that it is interfering with nesting sea turtles and crocodiles [13].

Invasive plants reduce available winter forage for wildlife. Spotted knapweed invasion of bunchgrass sites in western Montana reduces available winter forage for elk as much as 50–90%. Since a highly productive foothills site in western Montana can produce an average of 2,016 kilogram of forage grass per hectare, forage loss from spotted knapweed can be as high as 1,315 kilogram per hectare [25].

Human and sociological dimensions

The human or sociological dimension in relation to species invasion is not often examined for its significance. The human dimension is considered to be the elements or social factors that are influenced by human actions in our society. Historical perspectives, economic impacts, educational component, sociological stature, political acceptance of the stature, and regulatory aspects, including national and international laws are viewed as human dimensions. In reality, the human dimension has significantly impacted the current status of global invasive species.

Historical status of invasive plant species

The importance of invasive species changes over time as we continue to identify and assess many of the invasive species. This status may be inflicted by many aspects of the human dimensions.

Kudzu (*Pueraria montana* var. *Iobata* (Wild.) Maesen & S. Almeida) demonstrates why the historical information can be important. Kudzu is a tall-climbing perennial vine from eastern Asia. The Japanese government first exhibited kudzu as an ornamental vine at the Philadelphia Centennial Exposition in 1876.

Soon afterwards, kudzu became valued for the fragrant purple flowers and the large hairy leaves that provided dense shade for an arbor or a screen for a fence. Later, kudzu was grown in the southern United States as a forage crop to reduce erosion and improve the soil. In 1935, the Soil Conservation Service began using kudzu as a soil binder to prevent erosion on roadside slopes and farmlands. At one time, the federal government paid as much as $20 per hectare for farmers to plant kudzu. Kudzu clubs were even formed to promote its use, including the 20,000 member Kudzu Club of America. The founder of the club christened kudzu the "miracle vine". Communities were holding kudzu festivals and crowning kudzu queens. By 1946, kudzu had been established on 1,215,000 hectares of highly erodible land across the South. By 1955, kudzu had escaped from its original planting sites and covered trees, shrubs, gardens, fences, power lines, and almost anything that stood in its path. Kudzu was listed as a common weed by the US Department of Agriculture in 1970 [26]. Today, kudzu is widespread throughout the Southeast and covers large areas with impenetrable thickets. In 1988, over 2.8 million hectares of land was infested with Kudzu. The plant poses a serious threat to timberland, because its dense foliage blocks received sunlight.

Economic impacts of invasive plant species

Many of the non-native plants have great economic importance in agriculture, forestry, horticulture and other agricultural industries and pose little or no threat to our ecosystems, while others have become invasive over a period of time. In a 1993 report of the Congressional Office of Technology Assessment, the cost to taxpayers of introduced species in the US was estimated to range from hundreds of millions through billions of dollars in each year [10]. A recent assessment in 2000 calculates the annual loss by alien invasive species to be of $336 billion in six major countries, including the United States ($137 billion), South Africa ($7 billion), United Kingdom ($12 billion), Brazil ($50 billion), and India ($117 billion) [3].

About a quarter of the USA's agricultural gross national product is estimated to be lost each year to foreign plant pests and the cost of controlling them. In the western United States, jointed goatgrass (*Aegilops cylindrica* Host), non-native species, now infests 2 million hectares of winter wheat and additional 2 million hectare of fallow land. It is spreading unchecked at a rate of 20,000 hectares or more per year. Currently, jointed goatgrass costs US farmers $45 million annually in direct yield losses and reduced grain yield. The indirect costs of jointed goatgrass exceed $90 million annually, and total losses exceed $145 million annually [27]. Jointed goatgrass is one of "The Least Wanted" alien or non-native species in the United States.

Leafy spurge, a deep rooted perennial, grows upwards of 1 m in dense patches and now infests about 1,093,500 hectares, mostly in southern Canada, and the Northern Great Plains of the United States. This highly competitive

plant often forms dense stands that crowd out most other vegetation. These infestations cause loss of plant diversity, loss of wildlife habitat, and reduction in land values. In the United States, direct livestock production losses together with indirect economic effects due to leafy spurge alone approached $110 million in 1990 [10].

Educational goals

Preventing the spread of invasive plants in the United States is a monumental task that depends on public awareness, support, and participation. Volunteer programs have been very successful in promoting public awareness and concern about invasive plants. The First National Weed Awareness Week was initiated in the United States in 2000. It was held in Washington DC. Its goal is to bring people and groups together from across the country to focus on national attention on the severe problems created by invasive weed species. This program has been very successful for the last five years in bringing together individuals and organizations interested in this event. Other volunteer programs such as "Scotch Thistle Day" in Millard County, Utah, The New England Invasive Plant Group and others have been successful.

How invasive species are viewed is molded by human values, decisions, and behaviors. This has been demonstrated by kudzu, purple loosestrife, giant hogweed (*Heracleum mantegazzianum* Sommier & Levier) and other species. The prevention and control of invasive species will require modifying behaviors, values, and beliefs and changing the way decisions are made regarding our actions to address invasive species. Education, outreach, and training programs are suggested to address issues such as: i) coordinate the development and implementation of a national public awareness campaign, emphasizing public and private partnerships, ii) identify and evaluate existing public surveys of attitudes and understanding concerning invasive species issues, iii) compilation of a comprehensive assessment of current invasive species communications, education, and outreach programs, iv) coordinate development and implementation of an international education campaign, and v) organize and host a series of national and international workshops on invasive species in different regions for policy makers.

Sociological implication

Introduced species can have economic and socio-cultural benefits that, at least until recently, have been considered to outweigh the negative effects of alien species invasions. In several countries, alien species make a major contribution to the economy. Alien tree species underpin commercial forestry in many parts of the world with pines and eucalyptus being important genera used in the tropics and sub-tropics. Many other plant species were introduced

as ornamentals mainly for their aesthetic appeal or many other purposes (Tab. 3).

Again, social impacts are driven by other factors such as the standards of policy makers and current scientific knowledge. Techniques to assess the costs and benefits of invasive species are evolving, but much remains to be done. However, the clear environmental costs due to invasions remain uncertain and are species dependent.

In many regions or countries government agencies or non-profit organizations have launched campaigns to raise awareness, but most of these campaigns have not been able to change the behavior of those whose actions could limit the impact of invasive species. Our approach should be not only to raise awareness, but also to persuade both public and policy makers to act to find solutions.

Impact on human health

Impact of a plant on human health can influence the desirability of a plant in a landscape setting. Such an example is giant hogweed recently identified as invasive species [28]. This species represents an increasing public health hazard because of dermatitis and skin irritation. This is due to secondary metabolites present in leaf or stem exudates of giant hogweed. Because of this health concern, this species receives tremendous attention from the public, academics, naturalists, and other stakeholders. Many organizations have developed special fact sheets, websites and other media events to understand and combat its spread in its natural as well as in escaped habitats.

Current regulations

Role of the federal government

A number of US federal agencies have management responsibilities for weed species, including invasive species. Some of the responsibilities include weed regulation, research, and management. The US Department of Agriculture's Animal and Plant Health Inspection Service (APHIS) works to prevent the introduction of foreign weeds as well as their establishment on private lands. APHIS cooperates with state and local agencies as well as private landowners and mangers to eradicate newly introduced weeds on private lands. APHIS also is responsible for regulating importation of biocontrol agents. In response to the economic and biological threat posed by invasive plants, 17 federal agencies have been formed by the Federal Interagency Committee for the Management of Noxious and Exotic Weeds (FICMNEW). The committee's role is to facilitate the development of biologically sound techniques to manage invasive plants on federal and private lands.

Political impact

Many countries have instituted their national programs for invasive species for awareness regarding invasion. At the International level, The Rio Convention of Biological Diversity in 1992 may have been the first to recognize the importance of invasive species. In March 1999, an International Workshop on Invasive Alien Species was held in Kuala Lumpur, Malaysia, in conjunction with the Global Invasive Species Program (GISP). This was coordinated by the Scientific Committee on Problems of the Environment (SCOPE) in collaboration with the world Conservation Union (IUCN) and CAB International. The overall aim of GISP was to assemble the best available data on various issues encompassing invasive alien species problems.

In 1997, 500 scientists and resource managers wrote to the United States Vice President and requested action on invasive species. Their letter stated: "We are losing the war against invasive exotic species, and their economic impacts are soaring. We simply can not allow this unacceptable degradation of our Nation's public and agricultural lands to continue". An interagency team was launched in response to develop a comprehensive and coordinated strategy for the problem. They prepared a review of the issue with recommendations foremost among them was that an executive order be issued providing standards and a framework for ongoing action.

In response to the threats posed by invasive species and the challenges to minimizing their spread, the President of the United States of America issued Executive Order 13112 (Order) on Invasive Species, February 3, 1999 [17]. The Order applies to all Federal agencies whose actions may affect the status of invasive species. It requires agencies to identify such actions and to the extent practicable and permitted by law 1) take actions specified in the Order to address the problem consistent with their authorities and budgetary resources; 2) not authorize, fund, or carry out actions that it believes are likely to cause or promote the introduction or spread of invasive species in the United States or elsewhere unless, "pursuant to guidelines that it has prescribed, the agency has determined and make public its determinations that the benefits of such actions clearly outweigh the potential harm caused by invasive species; and that all feasible and prudent measures to minimize risk of harm will be taken in conjunction with the actions" (Executive Order 13112). Although the Order applies to all Federal agencies, most of the duties required by the Executive Order are the responsibility of the eight Council members. Given the scope and complexity of the invasive species problem, it is necessary to prioritize actions to deal with the most pressing invasive species problem first.

The Order established a National Invasive Species Council (NISC). The council is made up of the President's Cabinet from the Department of State, Treasury, Defense, Interior, Agriculture, Transportation, Commerce, Health and Human Services, and the Environmental Protection Agency, and the US Agency for International Development. The Order also called for an Invasive

Species Advisory Committee (ISAC) representing a broad spectrum of scientific, commercial and conservation interests.

The initial major function of NISC has been to work in consultation with ISAC to prepare a National Management Plan (NMP) for all invasive species. A draft of this plan was released for an official 45-day public comment period on 2 October 2000. In 2001, the Council released the National Invasive Species Management Plan. The Plan recommends specific action items to improve coordination, prevention, control and management of invasive species by the Federal agency members of the Council. It also included a timetable for specific actions for restoration of infested sites, for research and education, for information management and for interagency coordination and international cooperation.

To prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause, the Executive Order 13112 consisted of the following: Section 1. Definitions; Section 2. Federal Agency Duties; Section 3. Invasive Species Council; Section 4. Duties of the Invasive Species Council; Section 5. Invasive Species Management Plan; Section 6. Judicial Review and Administration. Only the Section 1 will be illustrated here as follows:

Section 1: Definitions

a) "Alien species" means, with respect to a particular ecosystem, any species, including its seeds, eggs, spores, or other biological material capable of propagating that species, that is not native to that ecosystem.
b) "Control" means, as appropriate, eradicating, suppressing, reducing, or managing invasive species populations, preventing spread of invasive species from areas where they are present, and taking steps such as restoration of native species and habitats to reduce the effects of invasive species and to prevent further invasions.
c) "Ecosystem" means the complex of a community of organisms and its environment.
d) "Federal Agency" means an executive department or agency, but does not include independent establishments as defined by U.S.C. 104.
e) "Introduction" means the intentional or unintentional escape, release, dissemination, or placement of a species into an ecosystem as a result of human activity.
f) "Invasive Species" means alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health.
g) "Native Species" means, with respect to a particular ecosystem, a species that other than as a result of introduction, historically occurred or currently occurs in that ecosystem.
h) "Species" means a group of organisms all of which have a high degree of physical and genetic similarity, generally interbred only among themselves, and show persistent differences from members of allied groups of organisms.

i) "Stakeholders" means, but is not limited to, State, tribal, and local government agencies, academic institutions, the scientific community, nongovernmental entities including environmental, agricultural, and conservation organizations, trade groups, commercial interests, and private landowners.
j) "United States" means the 50 States, the District of Columbia, Puerto Rico, Guam, and all possessions, territories of the United States.

Future policies

Legal impacts

It is recognized that isolated and unilateral action by individual States can never be enough to manage the full range of activities and processes that generate invasions. Effective management requires not only national legal frameworks but also concerted bilateral, regional, or global action based on common objectives and joint international agreements. Regulations are necessary to implement policy, set principles, rules and procedures, and provide a foundation for global, regional and national efforts.

Currently, there are more than 50 global and regional soft law instruments dealing in one way or another with alien species [22]. They cover terrestrial, marine, freshwater, wetlands and coastal ecosystems as well as processes and pathways that generate introductions [29]. International instruments are often, though not always, fairly general in character. National legislation and regulations are necessary to operationalize these instruments in national legal systems. National policy makers should seek to develop a structural legal framework to address all the issues concerning alien species. Such legal frame work has been included under the Executive Order in the United States in 1999. In general, National frameworks should be established, streamlined or strengthened to: i) harmonize objectives, 2) standardize terminology, 3) implement measures to prevent unwanted introductions, iv) support mechanisms for early warning systems, v) provide management measures, including the restoration of native biodiversity, and vi) promote compliance and accountability.

Prediction of species invasiveness

Question may be asked: Which traits enable a species to invade a new habitat? How can we predict the invasiveness of a plant species? The leading theory for the exceptional success of invasive plants is their escape from the natural enemies that hold them in check, freeing them to utilize their full potential for resource competition [30]. Invasiveness of many terrestrial plant species is explained by allelopathic suppression of neighboring plants [31, 32]. This has been proposed as an alternative theory for the success of some invasive plants (see Chapter 2, this volume).

Can we predict the invasiveness of a plant species? Many have attempted to characterize a successful invader [33–35]. But no one seems to agree on the general characteristics common to invasive species, and some believe that these traits as described earlier have little value in prediction of invasiveness. In general, plants with aggressive potential vegetative reproduction potential may be invasive in a new environment. However, Pyšek [36] found that clonal plants account for only 36% of the non-native plant species established in central Europe. This suggests that clonal growth is not the only factor associated with invasiveness.

Different traits favor invasiveness in different habitats [37]. Factors that render habitats invasible include low intensities of competition, altered disturbance regimes and low levels of environmental stress. These factors probably often interact. Invasive potential can be classified as "highly invasive", moderately invasive" and "potentially invasive". Using multiple logistic regressions, Scott and Panetta [38] found that for agricultural weeds introduced from southern Africa to Australia the highest level of variation was explained by weed status in native region. They predicted the future status of a number of recently arrived or not yet introduced species. In general, it was agreed that species known to be invasive elsewhere in the world under similar climatic conditions were perhaps the indicators of future invasive potential.

According to Parker [39], the invasiveness of a plant species could be predicted as follows: Invasive potential A (rhizomatous, climbing, small and readily dispersed seed), Damage potential B (competitive, toxic, allelopathic), Geography potential C (the magnitude of range of geography or ecologies to be invaded), and Entry potential D (mode of entry either deliberate or accidental). These parameters are then considered as the product of A*B*C*D, to estimate a plant invasive potential. In this approach, inclusion of C and D combined with major predictive characteristics of weeds imparts an improved means for predicting the invasiveness of alien species. As we understand more and more on the biology of many of the invasive weed species, we would be able to make progress in developing a good predictive model on invasiveness of species.

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Environmental consequences and economic costs of alien species

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Introduction

Assessing the environmental damage and loss of biodiversity due to alien species invasions worldwide is complicated by the fact that only 1.5 million species of the estimated 15 million species on earth have been identified and described. The total number of introduced species in the United States is estimated to be more than 50,000 species [1]. More than 120,000 species of plants, animals, and microbes have invaded just six nations studied (United States, United Kingdom, Australia, South Africa, India and Brazil) and these are causing enormous ecological and economic damage and control costs [2].

Given the number of species that have invaded these six nations, it is estimated that nearly 500,000 alien species have been introduced into the modified ecosystems on earth. Many introduced species, such as corn, wheat, rice, plantation forests, domestic chicken, cattle, and others are beneficial and now provide more than 99% of the world food supply with a value of more than $5 trillion per year [3]. These non-indigenous crop and livestock species originated in various geographic regions of the earth (Tabs 1 and 2), such as the chicken from South Eastern Asia (Tab. 2). Other successful uses of alien species have been landscape restoration (Norway maple), biological pest control (valelia coccinelid beetle), sport (carp), pets (dogs and cats), and food processing (yeasts). In the US the introduced species provide a value of approximately $800 billion per year [3]. However, alien species are known to cause major economic losses in agriculture, forestry, and several other segments of the world economy; they also negatively impact ecological integrity [1].

The low diversity of world crops (0.006% of the plant species) and world livestock (0.1% of mammal species) presents the benefit of increased efficiency, but also serious risks such as increased vulnerability to diseases and invasive species. Increased biodiversity would offer some natural protection to crops and livestock from alien species including disease pathogens. Especially in need of protection are pollinators that are essential for about one third of US and world crops. Each year US port inspections find 13,000 exotic plant diseases while checking only 2% of incoming freight. Both crops and live-

Table 1. Major crops that provide approximately 90% of the US and world's dietary energy supply (DES) [Food and Agriculture Organization of the United Nations, 1961–1999] and their origins

Crop	% DES	Source	Origin
Wheat	23	FAO	S.W. Asia (Syria, Jordon, Turkey)[a]
Rice	26	FAO	China (Middle Yangtze Basin)[b]
Maize	7	FAO	Mexico[c]
Potatoes	2	FAO	South America (Andean Mountains)[d]
Sweet potatoes	2	FAO	South America (Peru, Equador)[e]
Millet and sorghum	2	FAO	China, Abyssinia; Abyssinia[f]
Beans	2	Est.	Central America[g]
Banana/plantain	2	Est.	S.E. Asia, Western Pacific[h]
Cassava	2	Est.	South America (Brazil, Peru)[i]
Pigeon pea	2	Est.	India[f]
Lentils	2	Est.	Near East[j]
Cowpea	2	Est.	India, Abyssinia[f]
Yam	2	Est.	West Africa, Asia[e]
Proso millet	2	Est.	Eastern or Central Asia[j]
Peanut (groundnut)	2	Est.	South America (Brazil)[k]

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stock are vulnerable, especially since in each case we depend upon a narrow band of species.

In the recent past, the rate and risk associated with alien species introductions have increased enormously because the human population and human activities altering the environment have escalated rapidly [1]. Currently there are nearly 6.5 billion humans on earth and approximately a quarter of a million people are added to the world population every 24 h [4]. Large numbers of humans are traveling faster and farther while more goods and materials are being traded among nations (globalization) [3, 5]. These human activities are increasing the spread of alien species of plants, animals, and microbes worldwide.

Table 2. Major livestock groups that provide approximately 90% of the US and world's dietary energy supply (DES) from livestock

Livestock	% DES	Source	Origin
Cattle	30	Est.	Near East[a]
Sheep	20		Asia, Europe[a]
Poultry (chickens)	15		Southeast Asia[b]
Hogs	15		Eurasia, Middle East[a]
Goats	10		Asia[a]
Buffalo	10		Asia, Africa[a]

[a] Breeds of Livestock. Department of Animal Science. Oklahoma State University.
  http://www.ansi.okstate.edu/breeds (6/20/03)
[b] IACUC Learning Module. (2001) Arizona State University.
  http://www.ahsc.arizona.edu/uac/iacuc/poultry/poultry.shtml (6/20/03)

This study assesses the magnitude of some of the environmental and economic impacts caused by alien plant, animal, and microbe invasions in the United States and other nations.

Alien species in the United States

Alien invasive species cause major environmental and economic problems worldwide. In the United States alien species are causing an estimated $120 billion in damages and control costs per year (Tab. 3). The groups causing the most damage include crop weeds, rats, cats, plant pathogens, weeds, and human diseases. These alien species are also the major cause of the reduced biodiversity in the United States, estimated to account for 40% of the extinctions [6].

Crop weeds

In crop systems, including forage crops, about 128 species of intentionally introduced crop species have become serious weed pests [7]. Most weeds are accidentally introduced with crop seeds, from ship-ballast, soil, or from various imported plant materials [1]. Introduced weeds are a greater problem than native weeds and this is one reason why they dominate the weed species in crops [1].

In US agriculture, weeds cause a reduction of 12% in potential crop yields. In economic terms this reduction represents about $18 billion loss in crop production annually, based on crop potential value of all US crops worth more than $150 billion/year [3]. Based on the estimate that about 73% of the weeds are non-indigenous [8], it is likely that about $13 billion of these crop losses are due to introduced weeds (Tab. 3).

Table 3. Estimated annual costs associated with some alien species introduction in the US (see text for details and sources) (x millions of dollars)

Category	Total number of non-indigenous species	Losses and damages	Control costs	Total
PLANTS	25,000			
Purple loosestrife		----	----	45
Aquatic weeds		10	100	110
Mealeuca tree		NA	3–6	3–6
Crop weeds		13,000	2,000	15,000
Weeds in pastures		1,000	5,000	6,000
Weeds in lawns, gardens, golf courses		NA	1,500	1,500
MAMMALS	20			
Wild horses and burros		5	NA	5
Feral Pigs		800	0.5	800.5
Mongooses		50	NA	50
Rats		19,000	NA	19,000
Cats		17,000	NA	17,000
Dogs		620	NA	620
BIRDS	97			
Pigeons		1,100	NA	1,100
Starlings		800	NA	800
Sparrows		200	NA	200
REPTILES & AMPHIBIANS	53			
Brown tree snake		1	11	12
FISH	138	5,400	NA	5,400
ARTHROPODS	4,500			
Imported fire ant		600	400	1,000
Formosan termite		1,000	NA	1,000
Green crab		44	NA	44
Gypsy moth		NA	11	11
Crop pests		7,000	500	7,500
Pests in lawns, gardens, golf courses		NA	1,500	1,500
Forest pests		2,100	NA	2,100
MOLLUSKS	88			
Zebra mussel		----	----	1,000
Asian clam		1,000	NA	1,000
Shipworm		205	NA	205
MICROBES	20,000			
Crop plant pathogens		11,000	600	11,600
Plant pathogens in lawns, gardens, golf courses		NA	2,000	2,000
Forest plant pathogens		2,100	NA	2,100
Dutch elm disease		NA	100	100
LIVESTOCK DISEASES		14,000	NA	14,000
HUMAN DISEASES		NA	7,500	7,500
TOTAL		$120,308.5		

In US pastures, 45% of weeds are alien species [8]. US pastures provide about $10 billion in forage crops annually [9], and the estimated loss due to weeds is $2 billion [10]. Since about 45% of the weeds are alien [8], the approximate forage losses due to non-indigenous weeds are nearly $1 billion each year. According to Interior Secretary Bruce Babbitt [11], ranchers spend about $5 billion each year to control invasive alien weeds in pastures and rangelands, but these weeds continue to spread (Tab. 3).

Vertebrate pests

The English or house sparrow (*Passer domesticus*) and the European starling (*Sturnus vulgaris*) were introduced into the United States. The English sparrow was introduced in 1853 to control the canker worm. Both birds have become agricultural pests, together causing an estimated $1 billion per year in crop damages [1] (Tab. 3). Pigeons, introduced for agricultural production, foul structures both urban and rural and have a role in spreading human and livestock disease; the damage caused by pigeons is estimated at $1.1 billion per year.

Other serious vertebrate pests in the United States include rats and mice. Their numbers are estimated to be more than 1.25 billion and they cause more than $19 billion in damages and control costs per year (Tab. 3). There are about 63 million pet cats in the US plus 30 million feral or wild cats. These cats kill more than 570 million birds per year with an estimated value of $17 billion per year (Tab. 3).

Crop insects and mite pests

Pest insects and mites destroy about 13% of potential crop production representing a value of about $20 billion in US crops [12]. Based on the fact that about 40% of these pests are alien species [8], the alien pests cause over $7 billion in crop losses each year (Tab. 3).

Furthermore, about 360 alien insect and mite species have become established in US forests [13]. Insects cause the loss of approximately 9% of forest products amounting to $7 billion per year [3, 14]. Because 30% of the pests are alien species, annual losses attributed to them are about $2.1 billion/year (Tab. 3).

Crop plant pathogens

US crop losses due to all plant pathogens total approximately $18 billion per year [3]. With 65% of all plant pathogens being alien species [8], an estimated $11 billion per year can be attributed to alien plant pathogens (Tab. 3).

In US forests, more than 20 non-indigenous species of plant pathogens attack woody plants [13]. Approximately 9% or a total of $7 billion per year of forest products are lost due to plant pathogens [3, 14]. Assuming that the proportion of alien plant pathogens in forests is similar to that of introduced insects or about 30%, then approximately $2.1 billion in forest products are lost each year to non-indigenous plant pathogens in the United States (Tab. 3).

Livestock pests

Microbes and other parasites were introduced when various species of livestock were brought into the six nations (see introduction). In addition to the hundreds of pest microbes and parasites that have already been introduced, there are more than 60 additional microbes and parasites that could easily invade the United States and become serious pests to US livestock [15]. A conservative estimate of the losses to US livestock from alien microbes and parasites is approximately $14 billion per year (Tab. 3).

The current threat of bioterrorism has brought a call from the American Association of Veterinary Laboratory Diagnosticians to establish an Animal Disease Diagnostic Network that would link local, state and federal (USDA) in a communication system to enhance quick response to natural and or intentional contamination of livestock. The proposed start up cost of this network is estimated to be $85 million with yearly additional costs of $22 million [16].

Conclusion

More than 50,000 non-indigenous species of plants, animals, and microbes have invaded the United States. An estimated 20–30% of the introduced species are pests and cause major environmental problems [17]. Although relatively few of these species become serious pests, some species inflict significant damage to natural and managed ecosystems and cause public health problems. There is a complex of ecological factors that allow alien species to become abundant and emerge as ecological threats in their new ecosystem. These include: alien plant or animal species introduced without their natural enemies (e.g., purple loosestrife); the development of new associations between alien parasite and host (e.g, AIDS virus and humans); effective predators in new ecosystem (e.g., feral cats); artificial and/or disturbed habitats that provide favorable ecosystems for the invasive aliens (e.g., weeds in crop and lawn habitats); and invasion by some highly adaptable and successful alien species (e.g., water hyacinth and zebra mussel).

This study documents that economic damages associated with non-indigenous species invasions in the United States to be $120 billion per year (Tab. 3). Precise economic costs associated with some of the most ecologically damaging alien species are not available. Cats and feral pigs, for example, have

been responsible for the extinction of various animal species. Yet, for these pest animals, only minimal cost data are known. Also, it is impossible to assess the value of a species forced to extinction, although it is estimated that 40% of extinctions in the US are caused by alien species. If we had been able to assign monetary values to species extinctions, losses in biodiversity, ecosystem services, and aesthetics, the costs of destructive non-indigenous species would undoubtedly be several times higher than the reported $120 billion per year. Yet even this understated economic loss indicates that alien species are extracting a significant environmental and economic toll in the United States and worldwide. The calculated dollar cost *per capita* for the losses incurred due to biological invaders in the United States is approximately $420 per year.

Approximately 99% of all crop and livestock species are non-indigenous. These alien crops (e.g., corn and wheat) and livestock (e.g., cattle and poultry) are currently vital to maintaining world agriculture and the food system; yet the lack of biodiversity in crops and livestock leaves them, in turn, highly susceptible to invasive plants, animals and microbes. The benefits of some non-indigenous species do not diminish the enormous negative impacts of other non-indigenous species on agricultural and on other managed and natural ecosystems.

A real challenge lies in preventing further damage to natural and managed ecosystems worldwide from invading alien species, especially with rapid world population growth and increased human activities. The United States has taken steps to protect the environment from biological invaders. For example, President Clinton issued an Executive Order on 2 February 1999 allocating $28 million to develop the Interagency Invasive Species Council. The purpose of this agency is the creation of a plan to mobilize the federal government to defend the United States against non-indigenous species invasions. This analysis suggests that a few million dollars spent on preventing future introduction of potentially harmful alien species in the United States and other nations will avoid billions of dollars in losses to agriculture, forestry, and other aspects of our managed and natural environment worldwide.

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