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The Effects of Invasive Plants on Biodiversity Across Spatial Scales

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WASHINGTON UNIVERSITY IN ST. LOUIS

Division of Biology & Biomedical Sciences

Evolution, Ecology & Population Biology

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The Effects of Invasive Plants on Biodiversity Across Spatial Scales

by

Kristin Irene Powell

A dissertation presented to the
Graduate School of Arts and Sciences
of Washington University in
partial fulfillment of the
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who have taught me to work hard to achieve my goals.

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ABSTRACT OF THE DISSERTATION

The Effects of Invasive Plants on Biodiversity Across Spatial Scales

by

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Washington University in St. Louis, 2013

Associate Professor Tiffany M. Knight, Chair

Although introduced plant species are often considered to be one of the most notable anthropogenic threats to biodiversity, their influence on biodiversity remains controversial. Some studies have shown large declines in biodiversity in plant-invaded areas, whereas others have noted that plant invasions are rarely implicated as the cause of species extinctions. This dissertation aims to synthesize this seemingly conflicting literature on the effects of invasive plants on biodiversity. The overarching hypothesis in this research is that the effect of invasive plant species on biodiversity is scale-dependent, and the discrepancy among studies can be explained by a difference in the scales of investigation at which these studies take place. In addition, the processes by which invasive plants influence community structure leads to slow, long-term extinction dynamics that mask likely future plant extinctions.

In Chapter 1, I used a meta-analysis to examine the influence of invasive plants on plant biodiversity. The meta-analysis showed a negative relationship between the effect size of an invasive plant on biodiversity (i.e., species richness) and the spatial scale at which the data were collected. Next, in Chapter 1 and 2, I developed a framework that generated testable predictions about why invasive plants cause scale-dependent biodiversity loss. This framework linked the shifts in plant biodiversity to scale-dependence by using the species-area relationship. In Chapter 2, I tested the framework by conducting surveys of species-area relationships in habitats with and without invasive plants in three disparate ecosystems—a temperate forest, sub-tropical forest, and tropical forest. In all three ecosystems, species in invaded habitats accumulated faster with area than species in uninvaded habitats, revealing smaller effects of invasive plants on the loss of biodiversity with increasing spatial scale. Results showed that scale-dependent biodiversity loss was due to sampling effects (i.e., a loss of individuals), as well as larger negative effects on the abundance of common species compared to the abundance of rare species. In Chapter 3, I further investigated changes in community structure by exploring the demographic processes that result in differential effects on common versus rare native species in habitats invaded by *Lonicera maackii* (Caprifoliaceae) in Missouri, United States. The overall population growth of common species was consistently more negatively affected than that of rare species. This was due to larger declines in common species' reproduction and greater sensitivity of their population growth to declines in the proportion of reproductive individuals. Finally, in Chapter 4, I established field and greenhouse experiments to test which abiotic conditions are altered by the presence of *L. maackii*. The results of these experiments showed that *L. maackii* significantly reduce light levels that reach the forest floor and that rare species tend to be more shade-tolerant than common species.

This dissertation synthesizes literature on the effects of invasive plants on biodiversity and provides a framework for how to approach biodiversity loss and predict future extinctions in the context of species commonness and rarity. Overall, my research reconciles the differences observed among local and broad-scale effects of invasive plant species on biodiversity.

INTRODUCTION

Background

Human population growth and demands on natural resources have led to mass extinctions of species and a loss of global biodiversity (Barnosky et al. 2011). Biodiversity loss has consequences for natural populations, communities, and ecosystems. For example, current biodiversity loss can change community resilience to future disturbances, as well as cause declines in ecosystem functions and services that benefit human welfare and provide economic and societal value (Chapin III et al. 2000, Krauss et al. 2010, Mace et al. 2012, Cardinale et al. 2012). Thus, understanding the processes that determine patterns of biodiversity loss in native communities, as well as ways to preserve and restore biodiversity in the face of many anthropogenic factors, has become a leading motivator in ecological studies (Brooks et al. 2006, Worm et al. 2006, May 2010).

Although it is often clear that anthropogenic factors decrease biodiversity, the magnitudes of these effects are variable across studies. One important cause of this variation is differences in the spatial scale at which these studies are conducted. The effects of anthropogenic factors on biodiversity are often scale-dependent. The number of species observed increases with area in a nonlinear, decelerating pattern known as the species-area relationship (SAR) (also known as a species accumulation curve). The shape of this relationship depends on the density of individuals, the relative abundances of species, and the spatial distribution of species. Anthropogenic factors that alter species' densities, relative abundances, and/or species' spatial distributions will alter the shape of a community's species accumulation curve, thus causing the effect size of anthropogenic factors on biodiversity to depend on spatial scale. The consequences of biodiversity loss for communities and ecosystems will depend on the amount of biodiversity loss across spatial scales (Bond and Chase 2002, Srivastava and Vellend 2005).

One of the leading anthropogenic threats to biodiversity is biological species invasions (Mack et al. 2000, Pimentel et al. 2001, Barney and Whitlow 2007). The transport of exotic species across historically distinct boundaries and the "ecological explosion" of individuals as they spread across a landscape are phenomena that have long been recognized in ecology (Elton 1958) but are increasingly frequent with expanding globalization (Mack et al. 2000). The majority of exotic species introductions have occurred through human-mediated, and often intentional, assistance. For example, exotic species are introduced for pet trades, horticultural and ornamental purposes, food, wildlife habitat, and habitat stabilization for economic development (Reichard and White 2001, Pimentel et al. 2005). A subset of exotic species become invasive, which I define in this dissertation as exotic species with high rates of population growth and spread that become dominant members of ecological communities (Colautti and MacIsaac 2004, also see Chapter 1's Introduction).

Invasive species often cause dramatic declines in biodiversity, as evidenced by predatory animal invasions and native biodiversity loss on islands (e.g., Fritts and Rodda 1998, Courchamp et al. 2003). However, the effects of invasive *plant* species on biodiversity is less clear (Davis 2003, 2009). While some studies have shown large, negative effects of invasive plants on resident biodiversity (Vilà et al. 2011), others point out that invasive plants rarely, if ever, cause regional or global species extinctions (Gurevitch and Padilla 2004, Sax and Gaines 2008, Stohlgren et al. 2008).

The overarching hypothesis of this dissertation is that the effect of invasive plant species on biodiversity is generally scale-dependent. Accounting for spatial scale when evaluating the relationship between invasive plants and biodiversity loss will reconcile the equivocal conclusions about the threat of invasive plant species and help provide a framework that is currently lacking to explain the effects of invasive plants on native biodiversity (Ricciardi et al. 2013). Notably, studies that find dramatic losses of biodiversity are usually conducted at small spatial scales (from about 0.5m^2 to 300m^2) (e.g., Allen and Knight 1984, Huenneke et al. 1990, Alvarez and Cushman 2002, Adams and Engelhardt 2009, Hejda et al. 2009), and studies that find few or no species extinctions are usually conducted at broad spatial scales (often at state, island, or regional levels).

Studies that explore the effects of invasive plants on biodiversity often describe biodiversity using a summary statistic (e.g., a diversity index such as Simpson's diversity or species richness, which is the total number of species in a defined area). However, species richness alone is an exceptionally poor descriptor of biodiversity because its values are highly sensitive to the spatial scales at which it is measured (Lande 1996, Chase and Knight 2013). Thus, a decline in species richness from an invasive plant does little to predict or inform current or future extinctions at other spatial scales.

In this dissertation, I first determined (using a literature synthesis and surveys of plant communities) that invasive plant species cause scale-dependent losses in biodiversity. Invasive plants have smaller effects on species richness with increasing spatial scale. Second, I developed conceptual frameworks that explored why invasive plants have scale-dependent effects on biodiversity loss. Third, I tested the frameworks by surveying uninvaded and invaded plant communities, and I determined empirically that invasive plants cause scale-dependent biodiversity loss because they decrease the total number of individuals in invaded communities (i.e., cause a sampling effect). Finally, I used a case study of one invasive plant, the mid-story forest invader *Lonicera maackii* (Caprifoliaceae), to explore native species' population dynamics and life-history traits that underlie changes in species' abundances in the presence of a plant invader.

Community Framework

Patterns of biodiversity loss across spatial scales can be explored using the relationship between species richness and area, known as the species-area relationship (SAR). The SAR is one of the most well-studied patterns in ecology (Arrhenius 1921, Schoener 1976, Lomolino 2000). The most common formulation of the SAR is the power law, $S = c * A^z$, where S is species richness, A is area or spatial scale, and c and z are curve-fitting parameters. When this equation is log-transformed, $\log S = z * \log A + \log c$. In the log-transformed SAR, z is the slope of the line describing the rate that species accumulate with area (i.e., higher z describes a faster accumulation of species with increasing area). Thus, in the context of invasive plant species, the effects of invasive plants on biodiversity will be scale-dependent if the presence of invasive plants changes the z of a community relative to when invasive plants are absent.

To understand the effects of invasive plant species on scale-dependent biodiversity loss, it is essential to understand how invasive plants alter three fundamentally different but non-mutually exclusive patterns. Specifically, diversity and species richness at any given spatial scale are determined by (1) the commonness and rarity of species (i.e., the species-abundance distribution), (2) the total number of individuals in a community, and (3) the aggregation (i.e., spatial distribution) of individuals and species (He and Legendre 2002).

The species-abundance distribution (SAD) describes the abundances of each species in a community. The SAD ranks species based on their absolute or relative (i.e., proportional) abundance from common to rare (Whittaker 1965). For the purposes of this dissertation, I describe species' abundances in terms of numbers of individuals. A community is usually made up of a few common and many rare species, often described by a lognormal or log-series distribution (McGill et al. 2007). The shape of the distribution of a SAD is called evenness. Changes in the evenness of the relative SAD will alter the slope of the SAR (z) (He and Legendre 2002, Green and Ostling 2003, Tjørve et al. 2008). An invasive species can make the SAD of a native community more even (i.e., all species have more similar abundances) or less even (i.e., many individuals of a few common species and few individuals of many rare species). As such, increasing evenness will increase z and decreasing evenness will decrease z (e.g., He and Legendre 2002).

The total number of individuals in a community also determines biodiversity across spatial scales. This is also known as the sampling effect. A sampling effect describes how common and rare species are affected by an invasive plant under a neutral model of loss of individuals. All species experience the same proportional decline in abundance. All else being equal, a loss in the number of individuals in a community (in this case from competition with an invasive plant) will result in a loss of species (Preston 1962), and will increase the slope of the SAR (z) (Preston 1962, Olszewski 2004).

Aggregation describes the spatial distribution of species across a landscape, including interspecific species aggregation and intraspecific species aggregation. Aggregation can occur because of a variety of factors, including dispersal limitation, clumped abiotic resources, and population dynamics such as density-dependence and allee effects (e.g., Janzen 1970, Condit 2000, He and Gaston 2003). In general, high aggregation, in which species are clumped in space, will result in low diversity at small scales, but increase the slope of the SAR (z) through high species turnover known as beta-diversity. Low aggregation, in which the individuals of each species are evenly dispersed across a landscape, will result in high diversity at small scales, but decrease the slope of the SAR (z) (Chase and Knight 2013). However, this relationship is also dependent on the spatial scale of investigation.

Population Framework

Changes in species' abundances and distributions that occur at the community level are driven by differential effects of invasive species on species' population processes. A species' ability to withstand biotic and abiotic changes induced by the presence of an invasive plant could be related to a variety of factors. These factors include their dispersal and immigration ability between uninvaded and plant-invaded habitats, their population dynamics and life-history strategies, and other species traits that allow them to cope with the environmental conditions that result from a plant invasion.

Population-level studies also inform long-term predictions about temporal biodiversity loss and allow us to separate the potential processes by which an invasive plant influences the population dynamics of native species. Both of these are informative to management of native ecosystems. Population growth rate (λ) describes whether a species' population size is declining, increasing, or stable over time, and can inform whether the effects of invasive plant species are creating long-term extinction debts in which a species' current population size is masking future extinction (Tilman et al. 1994). Decomposing how invasive plants influence a species' population dynamics reveals which vital rates (i.e., growth, survival, and reproduction) are being affected by the plant invader, as well as which vital rates are contributing to changes in overall population growth rate (Caswell 2001).

Chapter Overview:

Chapters 1 and 2 of this dissertation address the scale-dependent effects of invasive plants on biodiversity. They also address the community-level abundance and distribution patterns that cause scale-dependent biodiversity loss. These chapters synthesize data on plant invasions across the globe, while Chapters 3 and 4 focus on one specific invasive plant, *Lonicera maackii* (Caprifoliaceae, Amur honeysuckle). Chapters 3 and 4 address the population-level processes and mechanisms that underlie the effects of invasive plant species on resident species' abundances.

In Chapters 1 and 2, I tested the hypothesis that biodiversity loss caused by invasive plant species is scale-dependent. Most studies on the effects of invasive plant species are only conducted at one spatial scale. Thus, in Chapter 1, I synthesized data across 76 studies using a meta-analysis to examine the relationship between spatial scale and the effects of invasive plants on biodiversity. I also developed a conceptual framework that explored the role of the species-abundance distribution (SAD) in scale-dependent biodiversity loss. This framework generated testable predictions about the scale-dependent effects of invasive plant species.

In Chapter 2, I further developed and tested the conceptual framework set forth in Chapter 1. I surveyed pairs of uninvaded and plant-invaded communities across the United States. Invaded communities were dominated by one of three forest invaders, including *Morella faya* in Hawai'i, *Lonicera maackii* in Missouri, and *Dianella ensifolia* in Florida. These surveys allowed me to determine which community-level patterns (see Community Framework section) cause scale-dependent biodiversity loss. Large, negative effects of invaders on species richness dampened with increasing spatial scale. I showed that faster accumulation of species with area in invaded habitats was due to strong sampling effects on the numbers of individuals in a community. Though the shape of the species-abundance distribution did not change between uninvaded and plant-invaded communities, species composition was significantly altered. Common species became relatively rare while rare species became relatively common, showing the plant invaders had larger proportional negative effects on common species compared to rare species.

In Chapters 3, I focused on the population-level consequences of *L. maackii* invasions for seven rare and common native species in Missouri oak-hickory forests. By exploring the population dynamics of pairs of common and rare plants, I was able to evaluate the long-term effects of an invader on species coexistence. I also evaluated the role of native species' longevity in explaining the effects of *L. maackii* on native species' population dynamics.

Finally, in Chapter 4, I quantified the abiotic mechanisms that differed between uninvaded and *L. maackii*-invaded habitat types. Using field environmental data and a controlled greenhouse experiment, I also determined which abiotic differences explained changes in species' abundances and population growth rates. I also determined if rare and common species possessed functional traits that allowed them to better cope with environmental conditions in invaded habitats.

The goal of this dissertation was to explain discrepancies about the effects of invasive plant species on biodiversity. I showed that plant invaders negatively affect native biodiversity despite few extinctions at broad spatial scales. I linked small and broad scale plant-invasion studies by approaching plant invasions from a theoretical community and population standpoint. I provided the first study to examine the effects of a plant invader on the population dynamics of multiple species in a community. Overall, this dissertation research used theoretical, empirical, and meta-analytic tools to provide a framework that can predict biodiversity loss across spatial scales and understand long-term consequences of plant invasions.

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CHAPTER 1

A Synthesis of Plant Invasion Effects on Biodiversity Across Spatial Scales

by

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Abstract

Invasive plant species are typically thought to pose a large threat to native biodiversity, and local-scale studies typically confirm this view. However, plant invaders rarely cause regional extirpations or global extinctions, causing some to suggest that invasive species' influence on native biodiversity may not be so dire. We aim to synthesize the seemingly conflicting literature in plant invasion biology by evaluating the effects of invasive plant species across spatial scales.

We first conducted a meta-analysis on the effects of invasive plants on the species richness of uninvaded and invaded communities across a range of spatial extents. We then discussed studies that consider the role of invasive plants on regional spatial scales for which such meta-analyses are not possible. Finally, we developed a conceptual framework to synthesize the influence of invasive species across spatial scales by explicitly recognizing how invasive species alter species-occupancy distributions.

We found a negative relationship between the spatial extent of the study and the effect size of invasive plants on species richness. Our simulation models suggest that this result can occur if invaders, either proportionately or disproportionately, reduce the occupancy of common species to a greater degree than rare species.

Future studies should consider the influence of invaders on the abundance and occupancy-level changes in native species to inform how invasive plants will influence native species richness relationships across spatial scales. This approach will allow greater predictive ability for forecasting changes in biodiversity in the face of anthropogenic biological invasions and will inform invasive species management and restoration.

Introduction

Among the many threats to global biodiversity, the transport of species across historically distinct biogeographic boundaries remains one of the most enigmatic (Facon et al. 2006, Barney and Whitlow 2008, Moles et al. 2008). Some introductions have lead to dramatic declines in biodiversity of native species and the functioning of ecosystems, such as the extinctions that have resulted from predation of non-native animal species on previously enemy-free oceanic islands (e.g., Savidge 1987, Fritts and Rodda 1998, Courchamp et al. 2003). However, the effects of introduced plant species on patterns of biodiversity are more equivocal (Davis 2009). Some studies have shown large declines in biodiversity in areas that are heavily invaded by introduced plants, leading some to conclude that such invasive species are one of the most important threats to biodiversity (next to habitat destruction) across the planet (Wilcove et al. 1998, Pimentel et al. 2001, Pauchard and Shea 2006). Others have noted that plant invasions are rarely implicated as the cause of species extinctions either regionally or globally (Sax et al. 2002, Gurevitch and Padilla 2004, Maskell et al. 2006, Stohlgren et al. 2008). Davis (2003) pointed out that the majority of extinctions caused by introduced species are caused by intertrophic interactions rather than competition within trophic levels (e.g., by invasive plants) and suggested that overall, most introduced plant species are rather innocuous. These disparate views have percolated into the public realm, and along with a variety of other piecemeal evidence, have incited a number of popular articles to ask if invasive species are really that bad (Burdick 2005, Zimmer 2008).

A variety of contentious terms are used to describe species that are introduced outside of their historical biogeographic range (Richardson et al. 2000, Colautti and MacIsaac 2004), but for the purposes of this paper, we will categorize them into two broad classes: (1) *exotic species,* a subset of which may be *naturalized* and reproduce self-sustainably, which generally represent a small fraction of the community in which they are introduced and typically have negligible influence on the communities in which they inhabit, and (2) *invasive species*, which have high rates of population growth and spread, can often become dominant members of the community, have negative influences on native species, and often alter the functioning of ecosystems. In this article, we focus on invasive species, which more often have negative consequences on local communities (Mack et al. 2000); exotic species are often relegated to marginal or novel habitats (e.g., urban areas) and can in actuality increase the biodiversity of a given region.

The mechanisms by which introduced plant species can become invasive are varied and are the subject of many reviews and syntheses (e.g., Facon et al. 2006, Richardson and Pyšek 2006). Thus, we only very briefly give an overview of those mechanisms here, as they relate to the primary subject of our review—the influence of invasives on patterns of biodiversity. Invasive species can either be "passengers" or "drivers" of environmental change (Didham et al. 2005, MacDougall and Turkington 2005). If passengers, invasive species become dominant as a result of human-mediated habitat degradations (e.g., frequent disturbance), disfavoring native species and either directly favoring nonnative species' traits, or indirectly favoring them due to the reduction of native biodiversity (Byers 2002). If drivers, invasive species dominate as a result of a variety of related mechanisms generally having to do with their traits. For example, invasive species may possess traits that make them relatively unique among species in the native community, such as having novel weapons (Callaway & Ridenour 2004) or novel resource use (Funk & Vitousek 2007). Regardless of whether they are drivers or passengers, the presence of an invasive species in a community is generally associated with concomitant lower species diversity than that observed in uninvaded communities (e.g., Holmes and Cowling 1997, Alvarez and Cushman 2002, Adams and Engelhardt 2009, Hejda et al. 2009, but see Fischer et al. 2009).

However, there is discrepancy among ecologists on how they perceive the negative influence of invasive species on biodiversity, with some suggesting they are a great threat to biodiversity in the short- and long term (Wilcove et al. 1998), whereas others more recently have suggested their overall influence on global biodiversity patterns will be negligible (Rosenzweig 2001, Davis 2003, Sax and Gaines 2008).

In this article, we synthesize the disparate perspectives of the influence of invasive species on patterns of biodiversity. Our overarching thesis is that the influence of invasive species on biodiversity is generally scale-dependent. That is, at small spatial scales (e.g., samples taken from plots less than ~100m^2), the influence of invasive species on biodiversity is large, whereas at broader spatial scales, even in the same system, the influence of invasive species on biodiversity is lower. We first use a meta-analysis of observational and experimental studies to explicitly show that invasive species typically reduce native species richness, but that the strength of this effect weakens as the spatial scale of the study increases. Next, we use a simple patch-occupancy model to show that this result is expected under most realistic scenarios of native species evenness patterns and invasive-species' effects on the occupancies of rare versus more common native species in the region. Invasive species potentially change the overall structure of species' relative abundances and occupancies in a spatial context and thus change the slope of the species-area relationship [*contra* Rosenzweig's (2001) fundamental assumption]. While this synthetic view reconciles the influence of invasive species on biodiversity at small and broad spatial scales, there remains much to be understood about the overall influence of invasive species on biodiversity, and we conclude with some possible avenues for future research directions.

Effects of Invasive Plants Across Spatial Scales

A Meta-analysis of Invasive Species Effects

We conducted a meta-analysis on the effects of invasive plants on biodiversity by examining total plant species richness (i.e., all native and exotic species) as well as native plant species richness. We compared their influence across studies that varied in their spatial extent to test the hypothesis that the negative influence of invasive plants should decrease with increasing spatial scale. We used the reduction in species richness caused by the presence of a dominant invasive species as our measure of effect size.

Although studies on the community-level effects of invasive plants are sometimes considered scarce (Alvarez and Cushman 2002, Hejda and Pyšek 2006), we found 76 such studies. We began with ISI Web of Science and Google Scholar searches using a combination of the following keywords or phrases: community, diversity, impact, invasi*, plant, and species richness. We also examined the citations from those papers, which allowed us to find several more studies.

We included both experimental (removal or addition of invasive plants) and observational studies that compared species richness among invaded and uninvaded habitats in close proximity. We also included observational studies that used distance from invader or gradients of percent cover of the invader. In such cases, we used plots at the extremes (i.e., nearest and farthest from invader, lowest and highest percent cover). For studies conducted across multiple years, we used the final year of data. For studies in multiple seasons, we used the season in which the majority of the plant community was present. We excluded studies that focused on invader effects on only small subsets of the species present in the community (e.g., only woody seedlings).

We collected information from each study on average species richness with and without invaders [data extracted from text, tables, and figures using the software ImageJ (Rasband 1997-2009)]. We used these data to obtain a log response ratio effect size (*lr*) between uninvaded and invaded plots [*lr* = ln(*uninvaded species richness*) - ln(*invaded species richness*)], which provides information on the proportional difference in richness with and without invaders and has minimal sample bias compared to other metrics (Hedges et al. 1999). We also calculated another popular effect size metric, Hedges' *d*, and found similar (but weaker) relationships (see Appendix 1) and so only report *lr* here for brevity.

After excluding studies that did not provide measures of variance, we incorporated 57 studies into our meta-analysis, which led to 125 data points because some studies included multiple invasive species, multiple sites, and/or multiple habitats. Of the 125 data points, 110 were observational, and 15 were experimental. Of the 110 observational data points, only six data points from three studies compared species richness before and after invasions; the rest compared invaded areas relative to spatially controlled uninvaded areas. Although unlikely, this could have served as a comparative limitation if invaded and uninvaded habitats differed in environmental characteristics other than the presence of the focal invasive species. The online supplemental data [see online Supplemental Data for Powell et al. (2011)] contains the data obtained for the meta-analysis, including the focal invasive plant(s), focal invasive plant growth form, location of the study, type of study (i.e. observational vs. experimental), sample size, spatial scale at which the data were collected, and the mean and variance of the effect sizes.

The majority of studies only presented species richness at a single spatial scale, and thus we were not able to do within-study comparisons of invader's effects across spatial scales. However, we can test the hypothesis of scale-dependent effects of invaders across studies by regressing the effect size of invasive species relative to the spatial scale on which the data were collected. We conducted linear mixed models, with log spatial scale (m^2) as the independent variable and effect size as the dependent variable weighted by the inverse of the variance of each study, v_j (Gurevitch and Hedges 2001). We also conducted an unweighted version of the model in order to evaluate whether the incorporation of all 76 studies qualitatively changed our results. We calculated r^2 of the regression models by dividing $Q_{regression}$ (heterogeneity explained by the model) by Q_T (total heterogeneity). Analyses were conducted in MetaWin version 2.1 (Rosenberg et al. 2000).

As predicted, we found a negative relationship between *lr* and spatial scale ($Q_{regression}$=20.01, r^2=0.10, slope=–0.20, P<0.001, Fig. 1.1), suggesting scale-dependent effects of invasive plants on species richness. Using only native species richness did not qualitatively change our results. Incorporating all 72 studies on the effects of invasive plants also revealed a negative relationship between *lr* and spatial scale ($Q_{regression}$=6.08, r^2=0.08, slope=–0.20, P=0.014).

The majority of case studies (99/125) were conducted at relatively small spatial scales ≤ 25m^2, where there was a large amount of variation in the *lr* effect size (ranging from –0.26 to 2.98) that was not well explained by spatial extent. This variation was also not explained by other independent variables that we examined, including the average species richness in the uninvaded plots and the growth form of the focal invader. In addition, we found no evidence of publication bias using two separate approaches: (1) we found a funnel-shaped distribution of sample sizes, as expected with no publication bias (Palmer 1999), and (2) we found no relationship between the magnitude of the effect size and the impact factor of the journal where the study was published based on the 2009 or 5-year average ISI Journal Citation impact factor (See Appendix 1 for graphical and statistical results). However, some of this variation was explained by the magnitude of dominance of the invasive species, which was highly variable among studies (ranging from 8–100 percent cover). To examine the effect of invasive species' dominance, we investigated the subsample of studies from which we could discern the relative dominance (i.e., percent cover) of the focal invasive species. When a range of percent cover was given, we used the midpoint, whereas when a minimum percent cover was reported, we used that minimum value. We found a positive relationship between *lr* and the percent cover of the invasive species ($Q_{regression}$=9.02, r^2=0.08, P=0.003, Fig. 1.2).

Despite the influence of the degree of dominance of the invasive species on its effect size, there remains a large amount of unexplained variation in effect sizes. This variation could be due to several factors, such as ecosystem-level effects of the focal invader (Vitousek and Walker 1989, D'Antonio and Vitousek 1992) and time since invasion. Further, other site- and landscape-level factors unique to each case study may interact with, exacerbate, or dilute the effects of the focal invasive species at the plot-level, including historical factors, spatial extent of the invasion, and the size of the regional species pool in uninvaded areas.

Invasive Species' Effects at Broader Spatial Scales

Although our meta-analysis was able to discern scale-dependent effects of invasive species on native species richness, all of these experimental and observational studies were conducted at relatively small scales, whereas the process of extinction takes place at much broader scales. At broader biogeographic scales, the effects of an invader are difficult to evaluate since these studies typically use presence/absence data for both the invader and the native species from large, national or global databases such as the IUCN Red List (Atkinson and Cameron 1993, Lonsdale 1999, Vié et al. 2008, but see, Maskell et al. 2006, Vilà et al. 2010). From such data, studies often conclude that many naturalized invaders are present, but no native species have gone extinct from the introduction of plant competitors (Sax et al. 2002, Davis 2003, Maskell et al. 2006, Sax and Gaines 2008, Tsai et al. 2010), even in locations that are infamous for being devastated by species invasions, such as remote oceanic islands (e.g., Hawaii; Denslow et al. 2009). However, the presence and effects of the invader are likely to only occur in a subset of the spatial scales under consideration.

A number of authors have recognized the difficulty in causally linking broad-scale extinctions of native plants to effects of invasive plants because species invasions typically correlate with concomitant anthropogenic factors including habitat destruction, changes in fire regimes, climate change, pollution, and infectious diseases (Davis 2003, Didham et al. 2005, 2007, Gurevitch and Padilla 2004, Smith et al. 2006). However, the lack of evidence of plant invaders causing extinctions is still surprising given the levels of dominance invasive plants can reach, as well as the population-level declines and local extinctions that they cause (see meta-analysis section). It is possible that these declines could lead to plant extinctions in the future (Sax and Gaines 2008, Corlett 2010), but extinctions take many decades, centuries, or longer for regional or global extinction to occur for these plant species. For example, a federally endangered endemic plant, Tidestrom's Lupine (*Lupinus tidestromii*), is restricted to less than 15 populations in coastal Northern California (United States), and is declining towards extinction due to indirect effects caused by the presence of invasive beachgrass, *Ammophila arenaria* (Dangremond et al. 2010). However, even in this extreme case, extinction caused by the invasive species is not projected to occur for several decades. Until it does go extinct, this species will be considered present in California and in the United States and thus not contribute to a reduction in species richness at these broad spatial scales, even though it is greatly imperiled and locally extirpated from many sites from which it once occurred. However, as we show in the next section, invasive species might be expected to have greater effects on local compared to regional extinctions under a variety of simple but realistic scenarios of community structure (i.e., species evenness) and effects on rare versus common species in a community.

A Conceptual Framework for Invasive Plant Effects Across Spatial Scales

Here, we develop a synthetic conceptual framework that incorporates two observations that have been made with regards to the influence of invasive species on native communities across spatial scales. We incorporate these observations into a simple modeling framework to illustrate how invasive species may cause local but not regional extirpations, and thus reduce local but not regional biodiversity.

1) Invasive species are often more widespread and abundant than native species in nearby, uninvaded habitats (e.g., Allen and Knight 1984, Chmura and Sierka 2006, Petsikos et al. 2007, Hejda et al. 2009, Jäger et al. 2009).
2) Invasive species reduce the local richness of native species (e.g., Christian and Wilson 1999, Frappier et al. 2003, Reinhart et al. 2005); our meta-analysis makes it apparent that invasive species generally have a strong, albeit variable, influence on patterns of biodiversity at relatively small spatial scales (Fig. 1.1).

We use a patch-occupancy model that considers a diverse native community of species that vary in their relative commonness and rarity (e.g., Preston 1962, He and Legendre 2002), and we incorporate the influence of invasive plant species on the occupancy distributions of these species. We specifically explored three scenarios:

1) Neutral effects of invasive species. Here, we assume that the invasive plant has similar negative effects on all native species at the local level regardless of the identity or relative occupancy of each native species (i.e., all native species have similar competitive abilities against the invader). In this scenario, each species is affected equally and is thus equally likely to go extinct from the presence of the invader.
2) Invasive species influence common species more than rare species. Here, the invasive plant has a larger proportional effect on native species with higher patch

occupancies. In this scenario, common species are worse competitors than rare species when in competition with the invader. This could occur, for example, due to overlapping niche space, in which the invader and common species share common resources accompanied by higher invader fitness (MacDougall et al. 2009), leading to larger declines in common species that rely more heavily on the shared resource than rare species. It is also possible that species with low patch occupancies exist in more specialized (or less common) habitat refuges that are less invasible (Huenneke et al. 1990, Marvier et al. 2004, Harrison et al. 2006) or that rare species that occupy these specialized refuges are better competitors than more generalized common species in these locations (Marvier et al. 2004).

3) Invasive species influence rare species more than common species. Here, the invasive plant has a larger proportional effect on native species with lower patch occupancies. In this scenario, rarer species are worse competitors than dominant, native species when in competition with the invader. This scenario could occur due to sharing common resources or if the distribution of rare species were restricted to habitats or micro-habitats that are *more* heavily invaded by an invasive plant, for example when invaders can invade low-nutrient sites or sites with high endemicity (Funk and Vitousek 2007, Miller et al. 2010). Rare species are sometimes poor competitors compared to more common species, leading to lower site occupancies (Griggs 1940, Kunin and Gaston 1993, Rünk et al. 2004).

To model each of these scenarios, we assigned species randomly to patches based on a regional patch-occupancy distribution (N=150 native species before invasion). Regional occupancy distributions were established by drawing each of the species (with replacement) from a lognormal distribution,

$$\Phi_j = \frac{M}{j} \exp\left\{-\frac{1}{2}\left[\frac{\log_2(j/j_0)}{\sigma}\right]^2\right\},$$

where Φ_j is the expected frequency of species occupying j patches, and M, j_0, and σ are fitted parameters (Volkov et al. 2003, Chisholm 2007). With the exception of σ, which represents the proportional evenness of the occupancy distribution, other fitted parameters were held constant with M=40 and j_0=300, and j=1 to 100 patches (e.g., the most common native species can at most occupy 100 patches and the rarest species can occupy a single patch). We simulated the invasion of a dominant invader, invading 90% of the patches, based on observation number 1 above, and causing a dramatic percent (~ 40%) of native species to decline to extinction in each patch, based on observation number 2 above. Species were driven locally extinct by the invasive species according to each one of the three scenarios described above (neutral effects, greater effects on common species, or greater effects on rare species). Each species was assigned a probability of local extinction (1) equivalent among all species, (2) proportional to their relative site-occupancy to simulate a gradient of decreasing effects of the invasive plant from common to rare species, or (3) inversely proportional to their relative site occupancy to simulate a gradient of increasing effects from common to rare species. Before invasion, we obtained α-diversity (average number of native species present in a single patch) and γ-diversity (the sum of species richness across all patches). We simulated each patch-occupancy model 1000 times and obtained 95 percentile confidence intervals for γ -diversity values to distinguish among the three different invasion scenarios. All simulations were performed in MATLAB version 7.4 (MATLAB 2007).

We first examined the expected outcomes when the region had high evenness, summarized here as Pielou's J, but specifically referring to more equivalent occupancies across species, with fewer extremely common or extremely rare species. Higher evenness was based on the lognormal patch-occupancy distribution with σ=2.4, J=0.9636, mode ≈ 19 patches occupied, where the mode is $j = j_M = j_0 2^{-\sigma^2 / \log_2 e}$ (Chisholm 2007). In each scenario, invasive species had large effects on local but not regional richness (Fig. 1.3), despite high occupancy by the invading species. This result is explained by the presence of few rare (low occupancy) species, and species were thus unlikely to be lost from all patches in the presence of the invasive species. This result is consistent with the trends we see in the literature, whereby dramatic local-scale effects of invasive species do not scale up to regional-level effects on species richness or extinctions (see earlier meta-analysis section).

Importantly, the steeper slope of the relationship between local (α-diversity) and regional (γ-diversity) scales in the presence of invasive species implies higher β-diversity in the presence of invasive species. That is, because $\gamma=\alpha\beta$, if α is affected more than γ with invasive species, then β is higher. On the surface, this seems to conflict with the common observation that invasive species commonly homogenize species composition among localities (homogenization is often equated with low β-diversity) (McKinney and Lockwood 1999). However, these seemingly opposing observations can be consistent by recognizing that β-diversity is calculated among all localities, whereas species compositional differences are generally calculated as pair-wise differences among communities, and thus cumulative versus pairwise β-diversity patterns can have opposing signs (Anderson et al. 2011).

When we allowed the initial evenness of species to be lower (i.e., more rare species), the scaling of the effects of invaders on regional-level extinctions and γ-diversity differed across the three scenarios. Specifically, with lower evenness (σ=10.0, J=0.8761), the relative influence of the invasive species on common versus rare species determines the overall outcome in invasive species' effects on γ-diversity. If common species are affected proportionately more than rare species, γ-diversity was unaffected by the invader (or can even be higher in some cases when the invader is included in calculations of species richness) (Fig. 1.4A). Alternatively, when the effects of the invader were neutral, or when rare species are more affected than common species, extinction was more prevalent at the regional level, leading to overall reductions in γ-diversity (Fig. 1.4B-C). When the effects were neutral, there was approximately an equal loss of species at both the local and regional scale (Fig. 1.4B), whereas when rare species were proportionately more affected than common species, there was a much greater absolute loss of species richness at the regional scale (Fig. 1.4C) as a result of homogenization of species across patches.

An important implication of our results is that the differential effects of invaders on common and rare native species (or even neutral effects) can strongly alter the slope of the species-area relationship (Fig. 1.3, 1.4A, and 1.4C). This is in contrast to Rosenzweig's (2001) fundamental assumption that invasive species do not alter the slope of the provincial species-area relationships and thus would not be expected to alter patterns of species diversity across scales. If instead, abundance and occupancy distributions are shifted in the presence of invasive species, we should expect concurrent increases or decreases in the slope of the species-area relationship (Tjørve et al. 2008) and thus a potentially strong influence of the presence of invasive species on biodiversity scaling.

Overall, we can generalize the effects of invaders along a spectrum of proportional influence on common versus rare species (Fig. 1.4D). As the effect of the invader changes from proportionately greater effects on common to neutral to proportionately greater effects on rare species, the potential for extinctions at the regional level increases, so long as the overall patch occupancy is relatively uneven (i.e., a large number of low occupancy species). However, it is clear from this simple analysis that for invasive species to be able to drive species regionally extinct, and thus significantly reduce γ-diversity, a very specific and potentially rather unlikely set of conditions must be met. In particular, the system must have a large number of low-occupancy (rare) species, and those rare species must be strongly and disproportionately influenced by invasive species relative to the more widespread, common species. In all other combinations of conditions, we would instead expect a larger observed effect of invasive species at local relative to regional spatial scales, as we observed in our meta-analysis and literature review above.

A wide range of parameters could be altered in this model, including changes in the number of overall patches, pre-invasion native species richness, maximum occupancy levels of native species, and the identity of the invading plant species that could create differences in their level of dominance and competitive ability (Ortega and Pearson 2005). We chose parameters we considered to be realistic for species occupancy distributions and highly invasive species. If we alter these parameters, some of the qualitative results seen in Fig. 1.4A-C will change but will follow similar principles. For example, as we show in contrasting Fig. 1.3 versus Fig. 1.4, high evenness (i.e., few endemic and highly cosmopolitan species) in the system will result in qualitatively different results than from systems with low evenness (i.e., high endemicity) (Fig. 1.4). This difference is expected because higher species' occupancies buffer against regional extinctions.

Our conceptual framework and model is intended to be a very simple depiction of how different invasive species' effects on native communities could lead to differential patterns of species richness and extinctions at local and regional spatial scales. As a result, it is lacking in several potentially quite important aspects of the way invasive species might influence native communities in more realistic scenarios. These include the elements of time, stochastic extinction, local abundance versus regional occupancy relationships, environmental heterogeneity, and multiple anthropogenic forces that may synergistically affect the extinction of species.

However, our intention is to emphasize, in the simplest way possible, our overall thesis that the influence of invasive species can greatly depend on the proportional effects of invaders on rare and common native species, regardless of other co-varying factors. For example, within patches, some species are much more locally abundant than others. If locally rare species also have low patch occupancy or if locally common species have low patch occupancy, invasive species should cause higher extinctions, moving the system to the right end of the extinction spectrum (Fig. 1.4D). On the other hand, if locally rare species have high patch occupancy or locally common species are also the most widespread, invasive species should cause fewer regional extinctions, moving the system to the left end of the spectrum (Fig. 1.4D). Similarly, environmental heterogeneity could either provide refuges for rare species through patches of less-invasible habitat or conversely, increase the influence on rare species if they occupy more invasible habitat. In addition, environmental heterogeneity could influence the regional occupancy of the invader based on habitat preferences. Though not explicitly modeled, these factors are implicitly incorporated into the model through the influence of invaders on rare versus common species. Lastly, if extinctions caused by plant invaders are exacerbated by other anthropogenic forces such as habitat destruction (Didham et al. 2007), there could be an overall decrease in the patch occupancy of a majority of the species, creating more uneven communities that are more vulnerable to regional extinctions.

Variation in the invaders' effects across spatial scales requires explicit recognition of how shifts in the dominance of invaders should influence the abundance and/or occupancy of native species at local scales, and how local-scale extinctions will scale up to broader scales. Using species-abundance and species-occupancy distributions, we can determine the expectation for species losses under a null/neutral model and the likelihood of observing large effects of invaders on species richness at broad spatial scales. In the following section, we provide some suggestions for incorporating these population-level changes in native species' abundance and/or occupancy into future research.

Discussion: A Prospectus for Future Studies

We found a negative relationship between the effect of invasive plant species and spatial scale, synthesizing disparate views in the literature about the effect of plant invaders on biodiversity. This result parallels a recent study by Gaertner et al. (2009), who conducted similar analyses for 11 studies in Mediterranean ecosystems, finding a negative relationship between the loss of species richness and spatial scale. We use a conceptual model to illustrate that these patterns might be expected under a variety of assumptions of species occupancy patterns and invasive species' effects. An important line of future research lies in examining species occupancy patterns and invasive species' effects on rare versus common species in the field to determine if these patterns are consistent with those in our model. If so, then we would suggest that our conceptual framework provides a general explanation for the larger effects of invasive species on biodiversity of local compared to regional spatial scales.

We suggest that a thorough investigation of the effects of invasive species across spatial scales will provide important insights into the causes and consequences of invasive species' effects on native biodiversity. The effects of a single plant invasion on biodiversity across spatial scales (e.g., measuring the species-area relationship) is rarely utilized as a tool for understanding whether focal invasive plant species cause changes in the rate of species accumulation with increasing area (i.e., the slope of the species-area relationship). For example, Jackson (2005) evaluated the effects of an invasive grass, *Cenchrus ciliaris*, across relatively small spatial scales (from 1 to 64m^2) and found an increase in the slope of the species-area curve in *Cenchrus*-invaded habitats, revealing faster rates of species accumulation with increasing area in invaded relative to uninvaded habitats. This lead to smaller losses of species richness with increasing spatial scale, as we observed in our meta-analysis. However, whether this is a generalizable pattern is unknown, as relatively few other studies have taken the same approach (Rejmánek and Rosén 1992, Michelan et al. 2010). To evaluate whether focal invading plants cause consistent patterns of scale-dependence in the loss of biodiversity, we suggest evaluating how scaling of richness is influenced by plant invaders across varying habitats and growth forms.

Evaluating species abundance and occupancy distributions across a continuous spatial extent in the presence and absence of invasions allows one to investigate how these patterns change in the presence of a dominant invasive plant species at different spatial scales of investigation. For example, Farnsworth (2004) investigated occupancy distributions of invasive plants in habitats occupied by rare species to evaluate the direct and indirect threat of invasion on rare plant populations. Invasion-driven shifts in the relative abundance and occupancies of common and rare species could help to explain scale-dependent effects of invasions on biodiversity, as well as changes in the slope of the species-area relationship in invaded habitats. They could also help forecast invasion-induced extinctions (Sax and Gaines 2008). For example, as illustrated by our conceptual model, a larger decline in abundance and occupancy of common species will result in a faster accumulation of species with increasing spatial scale, leading to relatively small losses of diversity at broad spatial scales (Fig. 1.4A). On the other hand, a larger decline in the abundance and occupancy of rare species can lead to a homogenization of the community, a slower accumulation of species with increasing spatial scale, and larger declines in species richness at broader spatial scales (Fig. 1.4C). If naturally occurring rare species are generally less affected by the presence of plant invaders, we should expect less dramatic declines in species richness than if rare species are a target for local extinction, but have yet to manifest these extinctions at broader spatial scales. We also emphasize the importance in comparing these proportional losses in common versus rare species to null models that account for sampling effects caused simply from the large declines in the numbers (and biomass) of native species in invaded habitats (e.g., Linneman and Palmer 2006, Schutzenhofer and Valone 2006). Sampling effects alone can lead to scale-dependent effects of invasive species without any selective effects on common or rare species by increasing the slope of the species-area relationship (Preston 1962).

If declines in native species abundance and occupancy distributions differ from those that are expected from sampling effects, understanding the mechanisms behind differential species effects will be essential for a general understanding of how invasive species alter the patterns of native species diversity, and for the management of native species and restoration of habitats. For example, it is possible that some native species possess life history traits that allow them to cope with environmental changes associated with dominant plant invaders (Chabrerie et al. 2010), such as shade tolerance (Myers and Kitajima 2007) and growth under low-resource conditions (Daehler 2003). Investigating whether these traits are associated with patterns of abundance and occupancy relationships of native species can help pinpoint conservation strategies for groups of species.

Summary statistics of native communities in response to the presence of invasive species, such as evenness and diversity, provide some information about community-level changes to native species (e.g., Brown et al. 2006, Hejda and Pyšek 2006). However, these summary statistics lack the population-level insight needed to gain a more complete understanding of invasive species influences on the native flora. Communities are typically less even when heavily invaded compared to uninvaded habitats (Olden 2006, Hejda et al. 2009) because of the presence of an invader with a much higher abundance than the most common native species. However, exactly how the evenness of the resident community changes with the invader is less clear. It is possible to observe increased evenness when common species are more affected by invasive species or when rare species are driven extinct by invasive species, leaving extant common species with more even abundances. Thus, understanding the influence of invasions from a population perspective on species that vary in their relative abundances is of utmost importance (Ricciardi 2004, Comita et al. 2010).

To gain a more general understanding of the effects of invasive plant species on biodiversity, meta-analyses on (meta-) population-level studies evaluating the relative influence of invaders on common and rare plants are needed. Such meta-analyses could include reductions in the abundance of rare and common species, as well as changes in their life-history traits (e.g., growth, fecundity) and consequent changes in their population growth. Meta-analyses could reveal which species are facing unsustainable increases in extinction probability due to deterministic and stochastic processes from lower local population sizes (abundance) and/or altered meta-population dynamics (occupancy). The trajectory of plant extinctions due to invasive species can be better understood with knowledge of (meta-) population-level shifts of common and rare species as a supplement to what we currently understand from information on species richness alone.

Conclusions

Changes in the relative abundances and occupancies of common and rare species due to the influence of invasive species will likely be a more telling measure of their influence on both local- and broad-scale biodiversity patterns. Though we will likely not be able to predict time frames for species loss, changes in the abundance and/or occupancy of native species will enable us to target species of concern in invaded communities as well as evaluate how to restore invaded communities. For example, if common species are more negatively affected by plant species invasions, restoration may be a more straightforward process since common species tend to be easily obtained for restoration as well as more easily established than rarer species. Common species are sometimes overlooked in restoration goals, but in the case of the effect of invasive plant species, may actually be facing equal or greater threats than rare species and cannot go unnoticed (Gaston 2010). With a solid conceptual framework and set of expectations for the current and future consequences we face from plant invasions, we will be better able to address the needs of preservation of native biodiversity at the intersection of an overwhelming number of anthropogenic forces.

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Figure 1.1. Significant negative relationship between log spatial scale (m^2) and the log response ratio effect size, *lr*, of a focal invader on species richness (*lr* = ln(*uninvaded species richness*) - ln(*invaded species richness*)) using a weighted, mixed-model regression. Each point represents a case study of invasive species' effects at the plot level. The fitted regression line includes all study types, including observational (i.e., comparing plots with and without invaders) and experimental (i.e., removal and addition) studies (n=125, $Q_{regression}$=20.01, r^2=0.10, slope=-0.20, P<0.001). Circles represent observational studies, triangles represent removal studies, and squares represent addition studies.

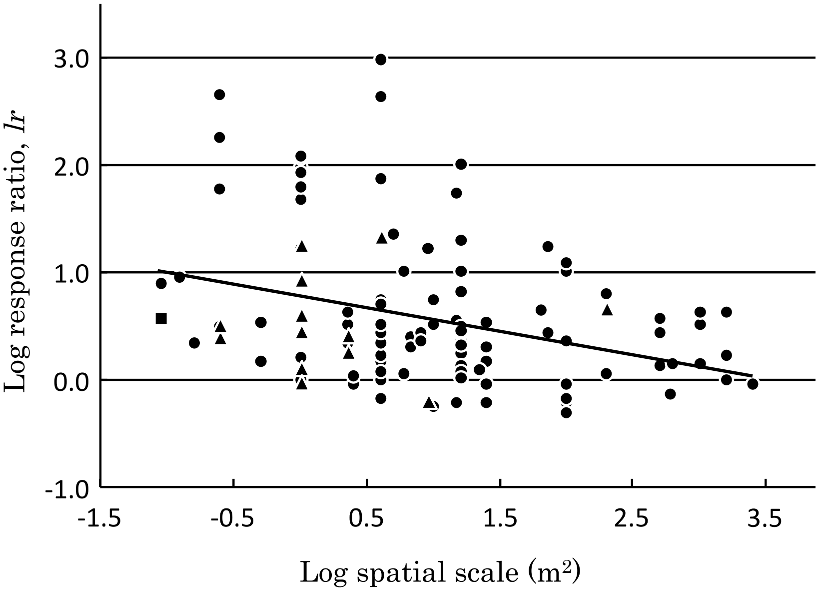


Figure 1.2. Three-dimensional visualization of the negative relationship between log spatial scale (m^2) and the log response ratio, *lr*, of the effect of a focal invader on species richness, and the positive relationship between *lr* and percent cover of the focal invader in invaded plots. Each point represents a case study that included a measure of invader percent cover at the plot level (n=92). Points change color from black to red with decreasing percent cover.

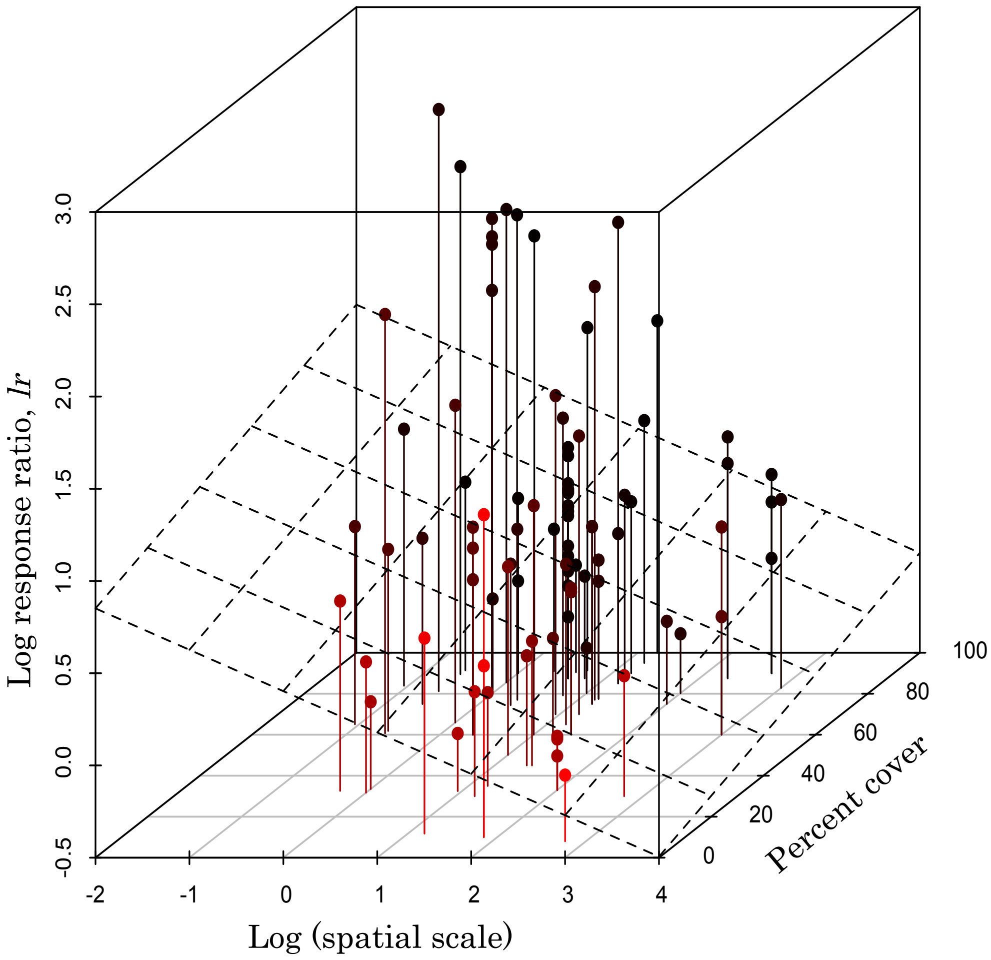


Figure 1.3. Invader effect on the loss of native species richness at local (α-diversity) and regional (γ-diversity) scales. Results were based on a patch-occupancy model, in which species' occupancies were drawn from a highly even lognormal distribution. Each species was assigned to patches randomly based on the regional patch-occupancy distribution, and their location remained fixed. We simulated a loss of native species at the local scale due to the colonization of a dominant invader. We observed no significant differences in γ-diversity among neutral losses of native species, a greater local loss of common species, or a greater local loss of rare species (see main text for more details).

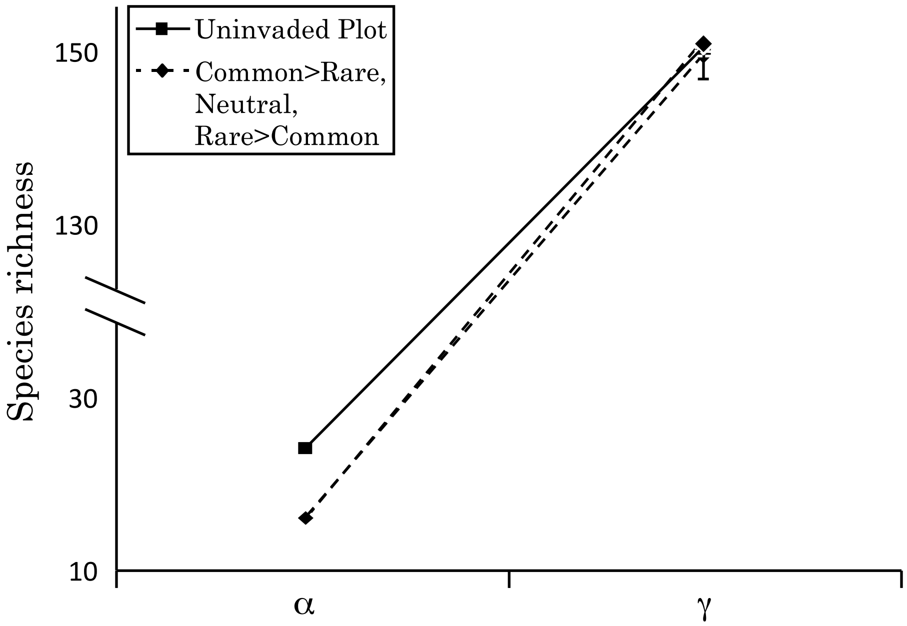
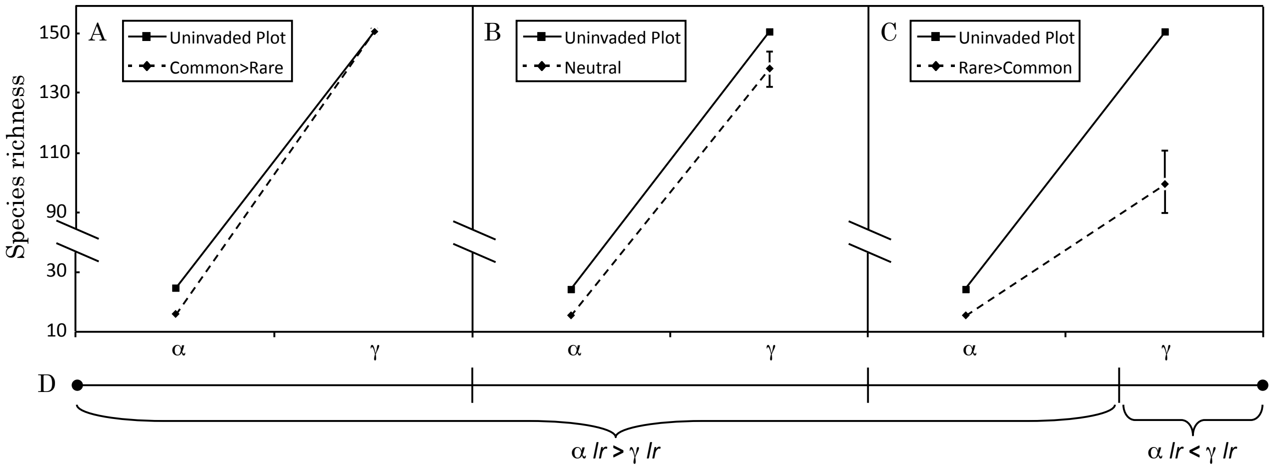


Figure 1.4. Invader effect on the loss of native, resident species at local (α-diversity) and regional (γ-diversity) scales. Results were based on a patch-occupancy model, in which species' occupancies were drawn from a relatively uneven lognormal distribution with Pielou's *J*=0.8761). With lower evenness, γ-diversity is determined by the relative influence of the invader on common versus rare species. (A) When common species are proportionately more affected than rare species, γ-diversity is equal to or greater than γ-diversity before invasion. (B) When all species are equally affected by an invasion, the effect on γ-diversity is approximately equal to the effect on α-diversity. (C) Only in the very specific case of rare species being greatly more affected than common species in conjunction with a highly uneven regional occupancy-distribution, will the log response ratio effect size, *lr*, of γ-diversity be greater than α-diversity. (D) The effect of an invader along a spectrum ranging from greater effects on common species to greater effects on rare species. Again, only at the far right end of the spectrum, would it be likely to see a larger effect (i.e. greater log response ratio, *lr*) of plant invaders at broad spatial scales compared to local spatial scales (see the conceptual framework section for more details).



CHAPTER 2

Invasive Plants Have Scale-Dependent Effects on Diversity by Altering Species-Area Relationships

by

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Abstract

Although invasive plant species often reduce biodiversity, they rarely cause plant extinctions. We surveyed paired invaded and uninvaded plant communities from three biomes. We reconcile the discrepancy in biodiversity loss from invaders by showing that invaded communities have lower local richness, but steeper species accumulation with area than that of uninvaded communities, leading to proportionately less species loss at broader spatial scales. We show that invaders drive scale-dependent biodiversity loss through strong neutral sampling effects on the number of individuals in a community. We also show that nonneutral species extirpations are due to a proportionately larger effect of invaders on common species, suggesting that rare species are buffered against extinction. Our study provides a synthetic perspective on the threat of invasions to biodiversity loss across spatial scales.

Main Text

Many empirical studies show dramatic reductions of native biodiversity in the presence of invasive species (Gaertner et al. 2009, Powell et al. 2011, Vilá et al. 2011). However, evidence that invasive species cause native species extinctions is rare, although it might be expected given the overwhelming evidence of their negative effects (Sax et al. 2002, Gurevitch and Padilla 2004, Maskell et al. 2006, Stohlgren et al. 2008). Although invasive predators and parasites are known to have caused extinctions of many species (Davis 2003), competition with invasive plants is rarely implicated in extinction (Gurevitch and Padilla 2004, Sax and Gaines 2008). In fact, in some cases the presence of invasive plants can actually increase species richness, leading to questions about whether most invasive species are really a leading threat to the conservation of native biodiversity (Sax and Gaines 2008, Davis et al. 2011).

A difference in the spatial scales of investigation might explain the controversy between studies that find reductions in biodiversity and those that find no effects or positive effects on biodiversity. Studies that find invasive-plant mediated reductions in biodiversity typically investigate small spatial scales ($<25\text{m}^2$), whereas studies that find little evidence for negative effects of plant invaders on extinctions take place at much broader spatial scales (Powell et al. 2011). We hypothesized that this discrepancy can be resolved by understanding whether and how invasive species alter the scaling of species richness with area [the species-area relationship (SAR), $S = c * A^z$, where S is species number, A is area, and c and z are constants]. Specifically, the effect of invasive species will become increasingly tempered with sampling scale if the invader decreases the intercept (c) and/or increases the slope (z) of the log-log SAR [$\log(S)=z\log(A)+\log(c)$].

We examined the scale-dependent influence of invasive plant species, which we define as the subset of nonnative plant species that have high rates of population growth and become dominant members of the community to which they are introduced (Kolar and Lodge 2001, Valéry et al. 2008, Gurevitch et al. 2011). The influence of non-native plant species that do not achieve such dominance are not as controversial and have little negative influence on species richness at any scale. We haphazardly chose three disparate, forested biomes from across the United States that are experiencing established but ongoing invasions. We chose species with disparate growth forms and physiology across biomes in order to explore possible generality of their effects on diversity. Our study systems were as follows: hardwood hammock forests in central Florida that are being invaded by *Dianella ensifolia* (cerulean flax lily), a dense mat-forming understory herb introduced from Asia and Africa (Hutchinson et al. 2011); oak-hickory forests in eastern Missouri that are being invaded by *Lonicera maackii* (Amur honeysuckle), a mid-story shrub introduced from East Asia that creates low light levels and soil allelopathy (Collier et al. 2002, Dorning and Cipollini 2006); and tropical mesic forests on the Big Island of Hawai'i that are being invaded by *Morella faya* (fire tree), a nitrogen-fixing canopy-tree introduced from Macaronesia (Vitousek and Walker 1989).

We identified multiple pairs of sites on opposite sides of each ongoing invasion front. Invaded communities were dominated (>90% cover) by the focal invader, which was present for at least 30 years (based on population structure and conversations with local managers). To minimize variation among site conditions other than the presence of the invader, paired 500-m^2 communities were identified according to the following three criteria: they were spatially proximate and occurred on similar soil and topographic conditions; they had very low densities of the invasive species but had a population structure indicative of future growth (for example, many individuals of each stage class); they had the same dominant and subdominant native over-story species, suggesting similarity in the underlying environmental conditions (Fig. A2.1).

We found a universally lower intercept (*c*) and steeper slope (*z*) of the SAR in invaded communities relative to uninvaded communities across biomes (Fig. 2.1, Fig. A2.2). Each plant invader caused large species richness reductions at small scales but a much smaller proportional reduction in species richness at broad scales (Fig. 2.1, Fig. A2.3). These patterns support our hypothesis that the discrepancy between studies that find larger or smaller influences of invasive species on native biodiversity can be reconciled by considering spatial scale.

The influence of invasive species on the slope of the SAR (*z*) results from the tension between four non-mutually exclusive mechanisms: a neutral sampling effect, nonneutral shifts in the relative abundance of species, local species extirpations, and/or shifts in the aggregation among individuals (Preston 1962, May 1975, He and Legendre 2002). First, by reducing the absolute number of individuals in invaded habitats (Vilá et al. 2011, Meiners et al. 2002, Rooney et al. 2004) invasive species can decrease *c* and increase z through a neutral sampling effect, so long as the SAR has a maximum species richness (Powell et al. 2011, Preston 1962, Olszewski 2004). Second, invasive species can alter the shape of the relative species abundance distribution (SAD) through nonneutral effects on species' abundances (Powell et al. 2011, He and Legendre 2002, Green and Ostling 2003). If native communities become more even in the presence of invaders, *z* will increase, whereas if native communities become less even, *z* will decrease. Third, both sampling effects and shifts in the shape of the SAD due to an invader can increase deterministic and stochastic local extirpations, which will decrease *z*. Fourth, the degree of intra- and interspecific aggregation of individuals within a community will alter *z* (Appendix 2, He and Legendre 2002, Green and Ostling 2003).

To dissect the relative influence of the four main mechanisms on *z*, we used null model analyses on spatially explicit abundance data collected in 50 1-m^2 plots evenly distributed within each 500-m^2 SAR plot (see Appendix 2). Because dissecting the effects of aggregation versus local extirpations requires a different type of null model, we first, separately determined whether there were differences in aggregation between invaded and uninvaded communities by measuring the bias—or difference in area under curves—between the species rarefaction (nonspatially explicit null expectation) and accumulation (spatially explicit) curves (modified from Collins and Simberloff 2009). We found no significant difference in bias between invaded compared with uninvaded communities within or across sites (paired t-tests for each plant invader, $-1.015 < t < 1.924$, $0.194 < P < 0.994$; *18*, Fig. A2.4), indicating that differences in aggregation are unlikely to be a cause of observed shifts in z. To ensure that species were not aggregated at a scale greater than what we investigated, which could change z and potentially change our observed, scale-dependent pattern in species loss, we also increased the spatial scale of our original analysis to encompass the replicated plots in each ecosystem (3 replicate 500-m^2 plots=1500 m^2 in Florida and Hawai'i and 4 replicate 500-m^2 plots=2000 m^2 in Missouri). Our analyses at these broader spatial extents confirm and extend our original results, showing even less proportional loss of species in the invaded communities relative to the uninvaded communities at spatial extents 3-4 times the size of our original study (Fig. A2.5).

We next devised a null model approach to dissect the effects of invasive species due to neutral sampling effects, local species extirpations, and shifts in the shape of the SAD (Table A2.1). In all cases, there was a large reduction in the number of individuals in the invaded community (ranging from 65 to 91% loss of individuals), which led to large increases in z due to the sampling effect (Table 2.1, Fig. 2.2). However, predicted changes in z solely due to the sampling effect were universally higher than the observed changes in z (Appendix 2, Fig. 2.2). We found that species extirpations moderated the influence of neutral sampling effects on *z*. In all invaded communities, there were fewer species in our largest sample area than expected from neutral sampling, suggesting that these species were subject to a deterministic or stochastic negative influence of small populations on extirpation. Although one site did show a more even SAD in the invaded community, species extirpations outweighed the influence of invaders on the shape of the SAD (Fig. 2.2).

Although the observed shifts in the slope of the SAR (*z*) were largely due to neutral sampling effects moderated by local extirpations, we asked whether the local extirpations might have resulted because rarer species were inherently more susceptible to invaders or, instead, simply victims of low population numbers. We examined abundance changes in each species' response to invaders and determined the deviation of their observed abundance in the invaded community relative to that expected from neutral sampling effects (Appendix 2, Chase et al. 2011). Species that were common in uninvaded communities tended to deviate negatively from abundances expected from sampling effects (they were more strongly influenced by the invader), whereas species that were rarer in uninvaded communities tended to deviate positively from expected abundances (they were less strongly influenced) (Table 2.1, Fig. A2.6). This result could have emerged from at least two non-exclusive mechanisms, including common species having greater niche overlap with invaders (MacDougall et al. 2009) and/or rare species possessing life history traits—such as shade tolerance or growth under low soil resource conditions, like soil moisture or nutrients (Daehler 2003)—that allow them to proportionately maintain their abundance in the presence of invaders (Chabrerie et al. 2010). Thus, rarer species may be more buffered from extinction than expected from neutral sampling effects. However, time-lagged extinctions due to extinction debt may lead to additional species loss (Tilman et al. 1994).

Although an examination of how hundreds of common and rare species were disproportionately influenced by invaders is beyond the scope of this study, we can glean insights by examining the traits of common and rare species at the study sites. For example, in Hawai'i, the native sedge, *Carex wahuensis*, was rare in the absence of the invader, but became proportionately more common in the presence of the invader, likely because it could tolerate lower light and/or take advantage of higher nitrogen imposed by the invasive *M. faya* (Adler et al. 1998). Likewise, in Missouri, several native species known to be shade tolerant (such as *Desmodium glutinosum* and *Trillium recurvatum*) (Bierzychudek 1982) were proportionately less influenced by the invasive *L. maacki* than were shade-intolerant species.

Overall, by explicitly focusing on scale-dependent processes, the results from our study reconcile the differences observed among local- and broad-scale effects of invasive plant species on biodiversity. Neutral sampling effects were the primary cause of decreased intercepts (c) and increased slopes (z) of the SAR. In addition, disproportionately smaller effects on rare species' abundances moderated species loss at the broadest spatial scale. Understanding the mechanisms by which invasive species shift species abundance distributions could improve our ability to forecast future invasion-induced extinctions. Although particularly harmful to native biodiversity at small spatial scales, invasive species' effects may be reversed through targeted control to increase native species abundances, at least until future extinction debt is paid.

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Table 2.1. The loss of individuals (excluding the focal invader) and Kendall's rank correlation explaining shifts in species' abundances for all sites. Kendall's rank correlations show the relationship between a species' abundance in the uninvaded community and its deviation from its expected abundance in the invaded community. Significant *P* values reflect larger negative effects of plant invaders on common as compared with rare species.

Site	Sampled site	# individuals in uninvaded community	# individuals in invaded community	Kendall's rank correlation coefficient (τ)	Kendall's rank correlation *P* value
Hawai'i	1	223	77	-0.231	0.109
	2	163	17	-0.405	0.014
	3	241	59	-0.369	0.010
Missouri	1	4378	374	-0.381	<0.001
	2	1460	228	-0.378	<0.001
	3	840	98	-0.442	<0.001
	4	4348	486	-0.407	<0.001
Florida	1*	569*	120*	-0.482*	<0.001*
	2	362	127	-0.230	0.072
	3	369	129	-0.308	0.040

*Corresponds to the Highlands Hammock State Park example shown in Fig. 2.1A.

Figure 2.1. Log-log species-area relationships (SAR) for all 10 sites across the United States. (A) Depiction of one relationship from Highlands Hammock State Park, Florida, [(B), shown in gray], highlighting how increases in the SAR slopes (z) in invaded communities lead to smaller species richness declines with increasing spatial scale. (B) Decreases in the intercepts (c) and increases in the slopes (z) of the invaded SAR for Hawai'i (invasive plant *Morella faya*: c, $t=4.702$, $P=0.042$; z, $t=15.541$, $P=0.004$), Missouri (invasive plant *Lonicera maackii*: c, $t=7.219$, $P=0.005$; z, $t=6.151$, $P=0.009$), and Florida (invasive plant *Dianella ensifolia*: c, $t=5.194$, $P=0.035$; z, $t=6.783$, $P=0.021$).

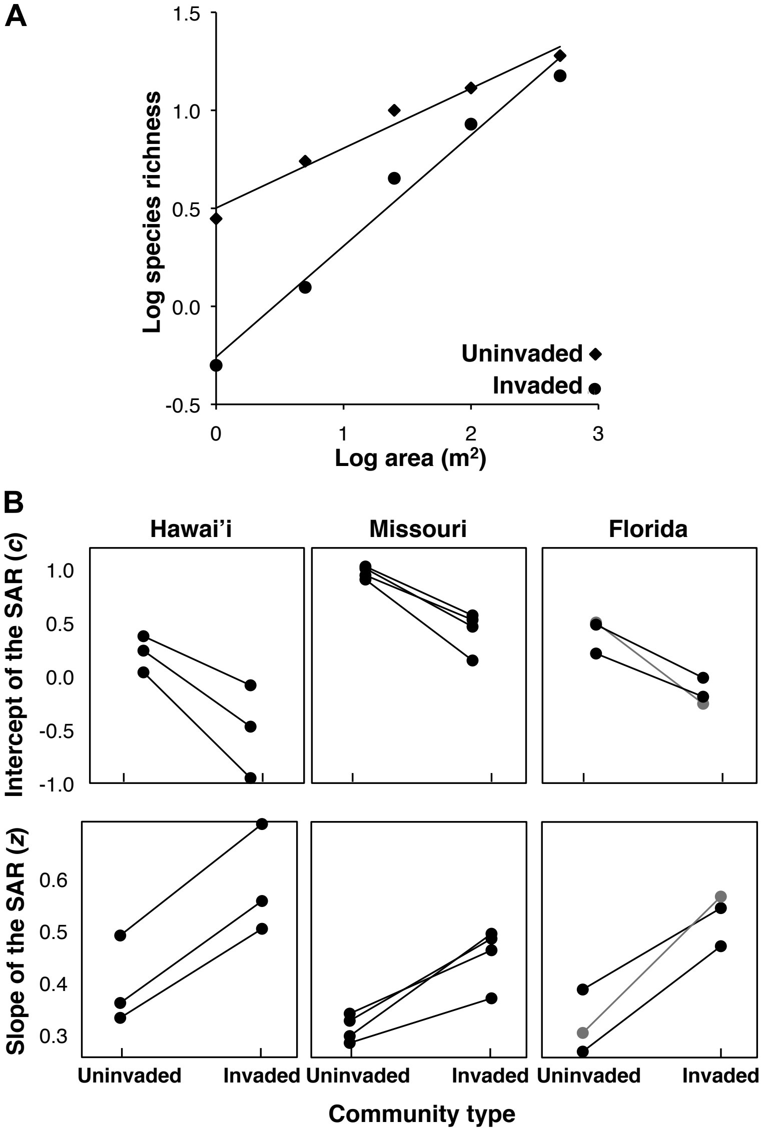
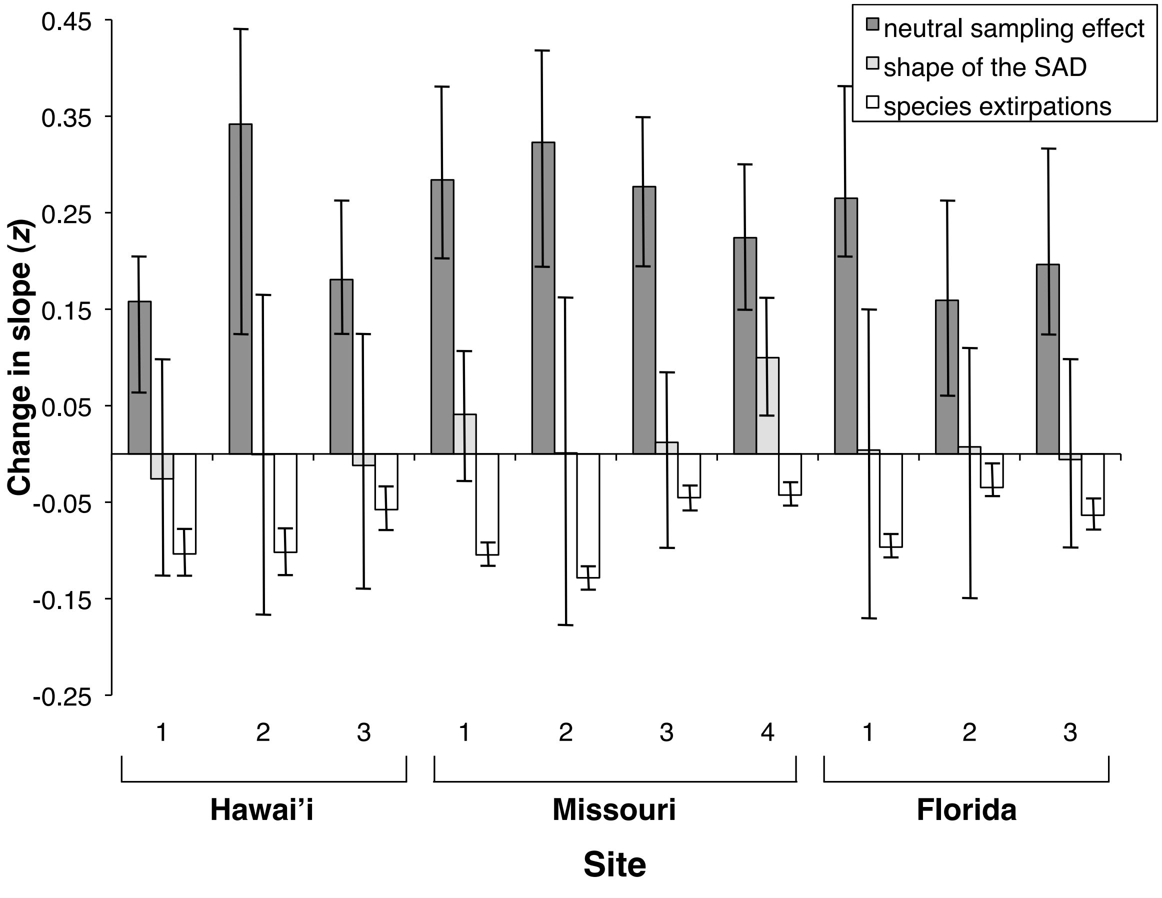


Figure 2.2. Contribution of neutral sampling effects (dark gray bars), nonneutral changes in the relative species abundance distribution (light gray bars), and species extirpations beyond those expected from sampling (white bars) to the observed difference in the slope (*z*) of the SAR between invaded and uninvaded communities. The sum of the bars for each site is equivalent to the observed change in slope between invaded and uninvaded communities across 50 1-m^2 quadrats. Positive bars contribute to a higher slope observed in the invaded relative to the uninvaded community whereas negative bars moderate the observed difference in slopes. Error bars are 95 percentile confidence intervals (see Appendix 2, Table A2.1).



CHAPTER 3

Effects of the Invasive Plant *Lonicera maackii* (Caprifoliaceae) on the Population Dynamics of Rare and Common Native Species

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Abstract

The long-term effects of invasive plants on native plant diversity and composition in part depend on how these invaders influence the population dynamics of common and rare plant species. To investigate processes underlying the long-term effects of invasive plants, we combined community-level surveys of uninvaded and invaded communities with detailed demographic studies on native plant species. We surveyed communities invaded by the exotic shrub, *Lonicera maackii,* and found that declines in plant diversity are explained by larger negative effects of *L. maackii* on the population size of locally common species relative to locally rare species. Changes in native species' population size could be due to multiple factors, including negative effects of *L. maackii* on dispersal and/or species' vital rates and population growth. Thus, we collected demographic data to parameterize matrix population models and explore the effect of *L. maackii* on the population dynamics of seven native species.

L. maackii decreases the population growth (λ) of common species more than rare species. Life Table Response Experiments (LTREs) revealed that declines in λ were due to declines in recruitment and the proportion of individuals that transition into reproductive stages. The λ of rare species was less affected overall because of smaller declines in these vital rates between invaded and uninvaded habitats, and a lower sensitivity to changes in vital rates affected by the invasion. Species that were more negatively affected by *L. maackii* also had significantly shorter median life spans. These results suggest that plant invasions will result in extinction debts, especially for short-lived and common species.

Introduction

Biological plant invasions often cause immediate declines in the abundance, richness, and diversity of resident, native plant species in local communities (Vilà et al. 2011). However, little is known about the long-term effects of biological plant invasions on plant extinctions and biodiversity. Studies have consistently demonstrated negative effects of invasive plants on the abundance and population dynamics of native plant species, and yet plant invaders have caused little to no global extinctions of native plant species (Sax et al. 2002, Gurevitch and Padilla 2004). However, many species are in decline, and it is possible that plant invaders are creating extinction debts, in which there is a time delay between invasion's effects on native plant populations and their extinction (Tilman et al. 1994, Sax and Gaines 2008, Gilbert and Levine 2013).

The time to extinction for native plant species after invasion depends on their dispersal and population connectivity (MacDougall and Turkington 2005, Gilbert and Levine 2013), initial population size, and the effect of plant invasions on population growth rates. If all species are similarly influenced by biological invasions, then rare species could have shorter extinction debts than common species because of their lower initial population sizes. However, recent studies show that the abundance of rare species tends to be proportionately less affected by plant invaders than the abundance of common species (Powell et al. 2013, Chapter 2). If the patterns in abundance reflect underlying patterns in population growth rates, then lag-times in rare species extinctions will be longer than expected based on their abundance alone.

Three, non-mutually exclusive hypotheses might explain why invaders have differential effects on the abundance of rare and common resident species. First, rare species might have higher dispersal abilities and immigration rates that allow them to sustain their population sizes in invaded habitats. However, this would be in contrast to theoretical and empirical results suggesting that rare species experience strong dispersal limitation (Volkov et al. 2003, Myers and Harms 2009). Second, common species might suffer larger decreases in vital rates and population growth rates compared to rare species in the presence of invasive species. This would be expected if common species have greater niche overlap with invaders and/or rare species possess life-history traits that allow them to cope with environmental changes associated with dominant plant invaders (Chabrerie et al. 2009), such as shade tolerance (Myers and Kitajima 2007) and growth under low-resource conditions (Daehler 2003). Finally, invasive plants could have similar effects on vital rates of common and rare species (e.g., Gould and Gorchov 2000, Leege et al. 2010), but the overall population growth of rare species may be less sensitive to changes in the affected parameters. For example, if rare species are longer-lived than common species, negative effects of plant invaders on fecundity would likely cause smaller declines in the overall population growth rate of rare compared to common species (Forbis and Doak 2004, García et al. 2008).

A demographic approach can be used to separate the processes by which plant invaders cause declines in the abundance of resident species, revealing if particular life stages are affected by invaders and how these life stages contribute to changes in resident species population growth over time (Williams and Crone 2006). There are few studies examining the effects of plant invaders on native species' demography (Lesica and Shelly 1996, Thomson 2005a, 2005b, Williams and Crone 2006, Dangremond et al. 2010). These studies find that declines in reproduction—survival of reproductive individuals, seed set, and seedling recruitment—contribute most to declines in overall population growth in the presence of a plant invader (Lesica and Shelly 1996, Thomson 2005b, Dangremond et al. 2010). However, Williams and Crone (2006) found that plant invaders altered population growth through slowing individual, vegetative growth. Reproduction appears to play a major role in the influence of invaders on native species, but it is not yet possible to make general conclusions, especially if resident species within the same habitat, such as rare versus common species, potentially experience drastically different consequences on their population dynamics from plant invaders.

All of the studies on the effects of invasive species on native species demography have examined a single focal species. Our study will be the first to investigate the effects of a plant invader on the population dynamics of multiple species and to investigate how locally rare and common resident species are influenced by plant invasions. A demographic approach will allow us to understand whether invasive plants change particular demographic parameters or a combination of all parameters of rare versus common species. It also extends our current knowledge of invasive plant competition, which focuses on changes in diversity and community structure (Levine et al. 2003), to long-term population persistence and extinction dynamics.

Our main objective was to evaluate the population dynamics of common and rare perennial herbs in uninvaded and plant-invaded oak-hickory forest habitats. Invaded habitats were dominated by *Lonicera maackii* (Amur honeysuckle), a mid-story forest shrub that is native to East Asia. We evaluated the rare and common species' declines in population growth rate (λ), sensitivity to changes in plant vital rates, and contributions of vital rates to changes in population growth. We also evaluated whether species median life span is an important life-history trait that explains differential effects on vital rates between rare versus common species (Kolb et al. 2006). In total, we parameterized and evaluated 32 matrix population models.

In this study, we address three main questions: (1) does *L. maackii* negatively affect the population growth rates and vital rates of rare and common forest herbs? (2) which vital rates contribute most to the effects of *L. maackii* on population growth rate? and (3) what is the relationship between median life span and the effects of *L. maackii* on population growth?

Methods

Study Species

The invasive plant, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae, Amur honeysuckle) is a deciduous, mid-story shrub that is native to Eastern and Northeastern Asia. It was first introduced into the United States in the late 1800's as part of a US Department of Agriculture (USDA) effort to attain commercially valuable plant species (Luken and Thieret 1996). *Lonicera maackii* was originally brought into the United States for horticultural purposes as an ornamental, and was later employed to provide bird and wildlife habitat. In the 1920's, it began to escape cultivation, and has since become a dominant invader in Midwestern woodlands, forests, and disturbed, urban habitats such as pastures and roadsides (e.g., Luken and Thieret 1996, Collier et al. 2002). *Lonicera maackii* possess life-history traits that enable it to spread rapidly and become dominant across the landscape. It is dispersed by birds (Ingold and Craycraft 1983, Bartuszevige and Gorchov 2006) and white-tailed deer (Castellano and Gorchov 2013), has high seedling survivorship (Luken and Thieret 1996), and consists of low-density, fast-growing wood (Deering and Vankat 1999). In addition, *L. maackii*'s leaves emerge in early spring and drop in late fall, resulting in an extended leaf phenology and longer growing season than all other native, Midwestern herbaceous and mid-story forest species (Trisel and Gorchov 1994). Its phenology and dense leaf canopy, both novel to Midwestern forest habitats, result in multiple biotic and abiotic habitat changes, mainly reduced light levels (photosynthetically active radiation; McKinney and Goodell 2010, Chapter 4), but also allelopathic soil chemicals (Cipollini and Dorning 2008), increased white-tailed deer abundance (Allan et al. 2010), increased apparent competition through seed predation (Meiners 2007, Dutra et al. 2011), and decreased ground temperatures (Watling et al. 2011). *Lonicera maackii* causes strong population and community-level effects, decreasing the abundance and richness of native species (e.g., Collier et al. 2002, Gorchov and Trisel 2003, see Chapter 2). Previous work by Powell et al. (2013) showed that *L. maackii* has differential effects on rare versus common species. In general, the abundance of rare species was proportionately less affected by the presence of *L. maackii* than the abundance of common species.

Study Design and Species Monitoring

We conducted this study at Washington University's Tyson Research Center in Eureka, Missouri, United States (38.522921, -90.562906). Tyson Research Center is a 2,000-acre research station consisting of old fields, prairies, glades, and oak-hickory dominated forests. We chose three oak-hickory forest sites with an ongoing *L. maackii* invasion front. By choosing invasion fronts, it is likely that uninvaded habitats adjacent to invaded habitats do not have biotic or abiotic conditions that preclude *L. maackii* invasion, but rather have just not yet been dominated by *L. maackii*. At each site, we monitored native species' demography on either side of the invasion front (i.e., in an uninvaded habitat and an invaded habitat).

The native species we monitored at each site were chosen based on their local abundance. In 2009, we surveyed species' abundances at each of the three sites by counting the number of aboveground stems of all understory forest species in 50, 1-m^2 plots in the uninvaded habitat and the invaded habitat (Powell et al. 2013). For each site, we chose perennial, herbaceous species that (1) commonly occur in oak-hickory deciduous forests and (2) were one of the rarest species and one of the most common species in the uninvaded habitat but also included enough individuals, even in the invaded habitat, to conduct demographic monitoring (Table 3.1).

At two sites, we conducted population monitoring of two native species (one rare and one common); at the third site, we monitored four native species (two rare and two common). We monitored seven species total because one species, *Ageratina altissima*, was monitored at two sites (Table 3.1). Because of the workload and the human impact on a habitat (e.g., trampling) when conducting full demographic studies on multiple species at a site, sample sizes of species larger than those presented in this study would have been difficult and affected species' population dynamics.

Because *L. maackii* causes declines in the total abundance of species (6.82, 66.59, and 14.30% loss of individuals in the three sites, respectively), as well as shifts in species composition, we had limited choices for potential species. Although we could not pair species phylogenetically in order to minimize differences in life-history traits and evolutionary history, we looked for a phylogenetic signal in species abundance by testing if more related species had more similar abundances than species sampled at random (Blomberg's K statistic, Blomberg et al. 2003). We estimated branch lengths of a phylogeny that included all the demographic studies species using the Phylocom 'bladj' algorithm. We calculated Blomberg's K and its significance (1-tailed test for greater phylogenetic signal than expected) using the R package Picante (Webb et al. 2008, R Core Team 2013). Although Blomberg's K was close to a value of one, which indicates some degree of phylogenetic conservatism in rarity and commonness, it was not statistically significant (Blomberg's K=1.032, P=0.142, also see phylogenetic tree in Appendix 3, Fig. A3.1).

We marked individuals in each population (here, we define a population as a species at a particular site and habitat type [invaded vs. not invaded]) with aluminum tags and relocated them annually to track their stage-specific vital rates, including survival, growth, reproduction, and germination. Over three years, we tracked a total of 2,680 individuals. In invaded habitats, we only tagged individuals if they were located within a 1-m^2 radius of a *L. maackii* individual and if our visual estimate of *L. maackii* percent cover was greater than or equal to 75 percent. These criteria allowed us to avoid the confounding factor that pairs of species at each site may experience differential losses in abundance from the presence of *L. maackii* simply due to occupying areas of the invaded habitat with lower or higher *L. maackii* density and/or cover.

Because of variability in species life forms, changes in an individual's size from year to year were measured using different vegetative characteristics (e.g., stem height vs. number of leaves) depending on the focal species (Table 3.1). In 2009 and 2010, we monitored individuals in all populations bi-weekly during their flowering and fruiting season (Table 3.1) to track the total number of flowers or flower heads and estimate the number of seeds per fruit or per flower head. We calculated seed dormancy and germination rates of each species by planting seeds in six seed baskets per population each year (6 pots*16 populations = 96 pots per year) and obtaining percent seed germination in the following year(s). Seed dormancy was calculated as the percent seed germination after two over-wintering seasons. Seeds were planted for 3-4 years, but with the exception of three *Trillium* seedlings in one seed basket, we did not observe any seedling germination after two years. Seed baskets were plastic 19.05-cm diameter round pots that were dug into the ground. We drilled additional holes into each pot to allow adequate water drainage (16, 2-cm holes per pot). Baskets received ambient levels of post-dispersal seed predation. We used a control, located 30 cm from each seed basket, to obtain germination rates under ambient conditions for which no additional seeds were planted. With the exception of two *Oxalis* germinates over a four-year period, no seeds of focal species germinated in the control plots.

We planted between 20-200 seeds per seed basket depending on the species and seed availability in each year. Seeds were collected from the same population in which they were planted unless we could not obtain a sufficient number of seeds. If a portion of planted seeds were collected from an unmonitored population, those seeds were spread equally across the uninvaded and invaded population seed baskets.

Matrix Population Model Construction

We built 32 stage-structured, matrix population models, one for each of the 16 populations across two transition years (2009-2010, 2010-2011), to estimate the effects of *L. maackii* on the population dynamics of rare and common species. Matrix population models describe a species' population dynamics and are constructed by using projection matrices (A) that describe a species' life cycle by dividing the tagged individuals of each species into size-specific stage classes (Caswell 2001). The number of stage classes incorporated into each matrix (A) was dependent on the focal species but included all or a subset of the following stage classes: seed bank, seedlings, small juveniles, large juveniles, and reproductive individuals (Fig. 3.1).

Each element (a_{ij}) of matrix A was calculated using the field-estimated vital rates that describe the probability of an individual transitioning from one stage class in year t to another stage class in year t+1 through survivorship, growth, and reproduction. All vital rates were modeled as density independent. Species natural densities per 1-m^2 plot in both the uninvaded (range of densities: 1.50-5.17) and invaded (range of densities: 1.86-5.15) populations were low.

The matrix population model to describe the change in population size through time is

$$N_{t+1} = AN_t \tag{1}$$

where the vector of the number of individuals in each stage class *N* at time *t* is multiplied by the matrix *A* to project the number of individuals in each stages class at time *t*+1. The deterministic, asymptotic population growth rate (λ) can also be estimated as the dominant eigenvalue of matrix *A*. If λ=1, the population size is stable through time. If λ<1, the population size is declining, and if λ>1, the population size is increasing.

The population matrix (*A*) can also be used to evaluate how small perturbations in the vital rates would affect λ. Sensitivity analysis reveals how absolute perturbations in matrix elements contribute to changes in λ, and are calculated as

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{\bar{v}_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \tag{2}$$

where the sensitivity of a matrix element (s_{ij}) is a function of the left and right eigenvectors of the matrix (*A*). Sensitivity values are proportional to the product of *i*th element of the reproductive value vector (left eigenvector, $\mathbf{v}$) and the *j*th element of the matrix stable stage distribution (right eigenvector, $\mathbf{w}$) (Caswell 1978, 2001). Elasticity analysis calculates the relative contribution of perturbations in matrix elements to changes in λ as

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = \frac{\partial \log \lambda}{\partial \log a_{ij}} \tag{3}$$

where the elasticity of a matrix element (e_{ij}) is calculated by relating logged values of λ to matrix elements.

Population Growth Rate

We compared the deterministic population growth rate (λ) within a species, between the uninvaded and invaded population, and among common and rare species at each site. To place 95% confidence intervals around λ so that populations could be compared, individuals in a population were bootstrapped. Bootstrap re-sampling is achieved by sampling individuals from the original data set with replacement, holding the sample size of the original data set constant (Meyer et al. 1986). This was repeated 1000 times to obtain 1000 λ's for each population and transition year. We obtained a median and mean λ and 95 percentile confidence intervals. Median and mean values were not significantly different for the 2009-2010 (paired *t*-test for invaded and uninvaded λ, respectively: t=-0.389, p=0.709; t=0.952, p=0.373) or 2010-2011 (t=0.033, p=0.975; t=0.917, p=0.389) transition year, and thus, only results using mean values are presented below. To compare among species at each site, we calculated the effect size of *L. maackii* on the λ of each species as

$$\Delta\lambda = \ln(\lambda^I) - \ln(\lambda^U) \tag{4}$$

where I represents the invaded population, and U represents the uninvaded population. A large, negative Δλ reveals a large, negative effect of *L. maackii* on overall population growth.

We used randomization tests to determine whether the observed Δλ's were significantly different between rare and common species (Caswell 2001, Manly 2007). We calculated an observed test statistic θ_{obs} for each transition year (i.e., 2009-10, 2010-11) as the difference between the average Δλ for the four common species and the average Δλ for the four rare species. Then, we calculated randomized test statistics θ for each transition year by randomizing the eight observed Δλ's into 70 possible combinations. The probability that the θ_{obs} is significantly different from the random θ is calculated as

$$P[\theta \leq \theta_{obs} | H_0]. \tag{5}$$

A P value ≤ 0.05 indicates that the observed difference in Δλ between common and rare species is significantly different from random.

Perturbation Analyses and Life Table Response Experiment

We conducted perturbation analyses on each population and transition year and then on each population pooled across transition years. Within-year sensitivity and elasticity analyses were qualitatively similar to data combined across years (i.e., the rankings of sensitivity and elasticity values did not change), and thus we only present results for the data pooled across years.

To determine the direct contribution of vital rates to the Δλ as caused by the presence of *L. maackii*, we used a fixed design Life Table Response Experiment (Caswell 2001). The analysis quantifies the contribution of each matrix element (a_{ij}) to Δλ by accounting for the sensitivity of the matrix element (s_{ij}) and the magnitude of change in the matrix element between the uninvaded and invaded population, or

$$\Delta\lambda \cong \sum_{ij}\left(a_{ij}^{I} - a_{ij}^{U}\right)s_{ij}. \tag{6}$$

Matrix element sensitivities (s_{ij}) for the LTRE are calculated from a matrix (A) that is the average of the uninvaded population matrix and invaded population matrix of each species. The contribution of vital rates were then grouped into six categories in order to make comparisons across species, including retrogression into previous stage classes, stasis or remaining in the same nonreproductive stage class, stasis or remaining in the same reproductive stage class, growth into a larger and nonreproductive stage class, growth into a larger and reproductive stage class, and recruitment.

Life Span Analyses

We also calculated the median life span of each species in 2009-2010 and 2010-2011. A species' life span was calculated according to the methods of Caswell (2001) using the population matrix (A) with reproduction set to zero. From A, a fundamental matrix is calculated by incorporating an additional 'death' absorbing stage and calculating the sum of the probabilities that an individual in stage class j at time 0 will be in stage i at time t. These probabilities eventually decay to zero as individuals are absorbed into the 'death' stage. We calculated a species' life span as the mean age at death of a newly germinated seedling, or the sum of the fundamental matrix elements of a seedling in stage class j (see

Fig. 3.1). We bootstrapped the individuals in the dataset to obtain a median life span. We used least-squares regression to test the relationship between $\Delta\lambda$ and life span as well as local abundance and life span. Statistical analyses for matrix population model parameters and life spans were performed in R v3.0.1 (R Core Team 2013) and MATLAB v 7.14 (MathWorks 2012).

Results

Population Growth Rate

In both transitions years (2009-2010, 2010-2011), the mean, deterministic growth rate (λ) of all species was depressed by the presence of *L. maackii* (Fig. 3.2). With the exception of *Oxalis stricta*, all common species had a significant $\lambda<1$ (i.e., mean and confidence intervals do not overlap one) in invaded populations, indicating declining populations. Conversely, the rare species did not have significant $\lambda<1$ with the exception of *Phyrma lepstostachya* in the 2010-2011 transition year, indicating population persistence (Fig. 3.2A). In addition, the $\Delta\lambda$ was consistently smaller for rare species than common species across both transition years and all three sites (Fig. 3.2B), indicating a smaller effect of *L. maackii* on the λ of rare species.

These results are generally consistent with the effect of *L. maackii* on species' local abundances, in which the abundance of rare species was less affected than the abundance of common species (Table 3.1). One exception is the common species at site 3, *Ageratina altissima*, which experienced large declines in λ, but not abundance, in invaded habitats. High *A. altissima* abundance at site 3 was due to a disproportionately high number of seedlings [excluding seedlings from the abundance survey yields an abundance effect size of 0.318 (Table 3.1)]. Indeed, we found that germination of *A. altissima* in seed baskets was slightly higher in invaded compared to uninvaded habitats (mean±std: $ge^{I}=0.076\pm0.088$,

ge^U=0.053±0.038). We did not observe differences in the seed bank dynamics of *Ageratina altissima* between invaded and uninvaded habitats (i.e., differences in percent germination after the first season of seeds overwintering).

Randomization tests compared the observed difference between the Δλ for rare and common species to the Δλ for randomly assembled groups of species. The randomization tests showed that species categories (i.e., rare or common) were significantly different from random in the 2009-2010 transition year (P=0.014) and 2010-2011 transition year (P=0.029).

Perturbation Analyses and Life Table Response Experiment

Perturbation analyses did not reveal consistent differences in the elasticity of vital rates among common versus rare species in the uninvaded or invaded habitat. Overall, matrix elements involving reproductive stages had the largest effect on λ in six of the eight uninvaded populations (Table 3.2). For example, small perturbations in growth into a reproductive stage and remaining in a reproductive stage were predicted to cause the largest changes in λ. All species had low sensitivity to recruitment values. However, species with overall high recruitment values also had high elasticity recruitment values. This is because elasticity values represent relative values that are proportional to the matrix element values. Stasis, or remaining in the same stage from time t to time t+1, also had high elasticity values (Table 3.2).

The presence of *L. maackii* affects the λ of all species by changing vital rates with high sensitivity values and by causing large changes in vital rates with relatively low sensitivity values, as shown in the LTRE (Table 3.3). Specifically, in invaded habitats, species had lower recruitment and lower probabilities of transitioning into reproductive stages compared to uninvaded habitats, and these changes contributed most to Δλ (Fig. 3.3). The λ of all species was relatively insensitive to changes in recruitment but sensitive to changes in the proportion of individuals that transition into a reproductive stage (Table 3.3). The Δλ was lower overall for rare species because rare species experienced smaller changes in these vital rates between invaded and uninvaded habitats. In addition, the λs of rare species were slightly less sensitive to changes in the proportion of individuals that transition into a reproductive stage (Table 3.3). For most species, population declines in the presence of *L. maackii* were slightly buffered by increases in retrogression and stasis in non-reproductive stages in the invaded compared to the uninvaded habitat (Fig. 3.3).

The common species *A. altissima* did not behave similarly at the two sites in which it was studied. At site 2, it suffered large declines in λ in invaded sites because of a loss in reproduction and a lower probability of transitioning into a reproductive stage class, whereas in site 3, reproduction was higher in the invaded compared to the uninvaded site. However, at site 3, *A. altissima* had a lower probability of remaining in a reproductive stage class in the presence of an invader. At site 3, the very high sensitivity of λ to changes in the probability of individuals transitioning into a reproductive stage class negated the fact that it had higher reproduction in the invaded population. Thus, *A. altissima* had high Δλ at both sites.

Life Span Analyses

Species' life span estimates in uninvaded and invaded habitats were significantly correlated with Δλ. Shorter-lived species were more negatively affected by *L. maackii* (Fig. 3.4). In uninvaded habitats, there was a significant relationship between life span and Δλ in the 2009-2010 transition year (adj. r^2=0.452,P=0.041; Fig. 3.4). However, this relationship was only marginally significant in 2010-2011 because of a more negative Δλ for *Desmodium glutinosum* (adj. r^2=0.235,P=0.126). In invaded habitats, there was a significant relationship between life span and Δλ in both transition years (2009-10: adj. r^2=0.529, P=0.025; 2010-11: adj. r^2=0.669, P=0.008; Fig. 3.4). In addition, life span in invaded habitats was negatively correlated with local abundance (adj. r^2=0.514, P=0.027).

In other words, rarer species not only had smaller declines in λ in invaded populations, but also had longer life spans.

Discussion

We investigated whether the differential effects of *L. maackii* on the abundance of rare versus common species were reflected in the effects of *L. maackii* on species' overall population growth rates. We found that the λ's of all common species were more negatively affected by the presence of the invasive plant *L. maackii* compared to all rare species (Fig. 3.2B). With the exception of *P. lepstochya*, the λ's of rare species indicate stable or growing populations despite high dominance of *L. maackii* in invaded habitats. Conversely, with the exception of *O. stricta*, the λ's of common species fell significantly below one, indicating declining populations in invaded habitats. Thus, a larger Δλ for common species also resulted in a smaller overall λ in invaded populations, confirming that changes in population growth are, in part, causing shifts in species abundance in invaded habitats.

At site 3, the common species *A. altissima* did not have large *L. maackii*-induced declines in abundance despite having a large Δλ. Unlike the common species *O. stricta* and *V. alternifolia*, *A. altissima* has wind-dispersed seeds that may facilitate its seed dispersal into invaded habitats. However, this seed dispersal must be coupled with the ability for seeds to germinate in (i.e., colonize) invaded habitats. At site 2, germination rates were low in both the uninvaded and invaded populations, likely due to heavy leaf litter in both habitats preventing the high light germination requirements (Walck et al. 1997). However, at site 3, germination rates were higher in the invaded population than in the uninvaded population. These results suggest that high dispersal of *A. altissima* into invaded site 3 allowed this species to maintain higher relative abundances than would be expected based on its Δλ.

P. lepstochya and *A. altissima* had higher reproduction in the invaded habitat compared to the uninvaded habitat at site 3 (Fig. 3.3). Greater reproduction in the invaded habitat was likely due to lower variability in reproduction across individuals in the invaded habitat. Individuals rarely flowered in the *L. maackii*-invaded habitat, but individuals that did flower subsequently reproduced and made more seeds than an average reproductive individual's seed set in the uninvaded populations. In the uninvaded habitat, more individuals flowered and reproduced, and there was larger variability in seed set across individuals (mean±std: *P. lep.*^{I}=23±1.41, *P. lep.*^{U}=11.22±5.43; *A. alt.*^{I}=327.50±146.04, *A. alt.*^{U}=312.49±566.45).

Perturbation analyses were quite similar among common and rare species. In addition, the rank order of matrix element elasticity values (e_{ij}) was similar within a species, between uninvaded and invaded populations, suggesting that a species life-history strategy remained similar between uninvaded and invaded habitats. Thus, the effects of *L. maackii* on $\Delta\lambda$ were largely due to more dramatic reductions in common species' vital rates (growth into a reproductive stage and recruitment), rather than differences in species' sensitivity and elasticity values. The vital rates that contributed most to $\Delta\lambda$ are similar to the results of previous demographic studies that evaluated competitive effects of plant invaders. Earlier studies showed that reproduction, including surviving in reproductive stages, seed set, and germination, contributed most to population declines (Lesica and Shelly 1996, Thomson 2005a, Dangremond et al. 2010). However, Williams and Crone (2006) found that λ became less sensitive to flowering in invaded habitats and found that growth contributed most to $\Delta\lambda$.

The only key difference between common and rare species in sensitivity values was that common species had a higher sensitivity to changes in the proportion of individuals that grew and transitioned into a reproductive stage class (Table 3.3). This result highlights the importance of calculating population growth rates, as declines in similar vital rates across species will not always result in the same contribution to declines in λ because of how the magnitude of the change in a vital rate relates to the sensitivity of that vital rate.

It is not rarity and commonness *per se* that led to differential effects of *L. maackii* on overall population growth. Rarity and commonness likely correlate with traits that predispose species to persisting or declining in *L. maackii*-invaded habitats. We investigated one life-history trait—longevity—that could correlate with abundance. We found that median life span was negatively associated with local, invaded abundance. This result was reflected in rare species' higher λ's in invaded habitats. Median life span also correlated with Δλ. Species with shorter life spans were more negatively affected by *L. maackii*. Species with long-lived life-history strategies were more able to cope with *L. maackii* habitat conditions.

Our research suggests that there is stronger competitive dominance between the common species and plant invader than between the rare species and plant invader. It is possible that common species have more resource-use (i.e., niche) overlap with *L. maackii*. Though forest herbs and *L. maackii* possess different growth forms, *L. maackii* might better utilize an ubiquitous resource (Corbin and D'Antonio 2010). For example, if common species thrive in high-light conditions, as does *L. maackii*, then shade-tolerant rare species may experience smaller changes in vital rates in *L. maackii*-dominated habitats where light intensity is significantly reduced (McKinney and Goodell 2010). Shade tolerance as an explanation for differential effects on rare and common species is further explored in Chapter 4.

Leege et al. (2010) also studied the effects of a plant invader in the genus *Lonicera* on rare and common species (i.e., *Trillium reliquum*, *T. cuneatum*, and *T. maculatum*). *L. japonica* had no effect on the vegetative growth or reproduction of the common or rare

Trilliums. However, the initial percent cover of *L. japonica* ranged from approximately 15-30 percent, which may have been too low to interfere with Trillium vital rates. With high percent cover of ≥75 percent, *T. recurvatum* still had the smallest average Δλ across all species in our study (Fig. 3.2B).

Recently, many researchers are using Integral Projection Models (IPMs) in place of matrix population models. IPMs use regression models and integrals to provide vital rate estimates (Easterling et al. 2000), which are more appropriate for populations that are better described by continuous sizes (e.g., height) rather than discrete sizes classes. Further, the results of IMPs are more robust to low sample sizes (Ramula et al. 2009). However, matrix population models are more straightforward for species comparisons and meta-analyses. It is not likely that using IPMs instead of matrix population models would qualitatively change our conclusions. Differential bias of matrix population models among species at a site is unlikely since sample sizes of individuals were similar (Table 3.1). A larger number of tagged individuals of *O. stricta* (Table 3.1) was not due to a larger sample size, but was due to the need to re-tag new individuals during the 2010 monitoring year.

We showed that half of the study species had declining population growth rates in the invaded habitats, while the other half was stable or increasing (Fig. 3.2A). Many of the declining species are locally common, and extinction would take a long time, allowing time for invasive species removal and restoration efforts to occur before biodiversity is lost. We predict that half of species are currently persisting despite the presence of *L. maackii*, though their population growth rates were depressed and their abundances were reduced. The likelihood of persistence over long-term time frames is therefore lower than in the absence of *L. maackii*. We confirm previous work (Gilbert and Levine 2013) that suggests that extinction-debt times for native species could be on the order of hundreds of years. Understanding how rare and common species compete with plant invaders, in addition to understanding the fundamental differences in the population dynamics of rare versus common species, will provide insights into the role of dominant species, like plant invaders, in long-term plant coexistence.

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Table 3.1. Description of rare and common species for which we conducted demographic monitoring, including species names, total abundance at each of the three monitoring sites, the number of tagged individuals used to build demographic matrix models, and growth and reproductive demographic parameters.

			Abundance (category*)[†]					
Site	Family	Species	Un-invaded	In-vaded	Abundance effect size[‡]	# of tagged plants	Measure of vegetative growth	Fruiting/ Seeding dates
1	Rubiaceae	*Galium circaezans* Michx.	30 (r)	25	-0.182	298	Stem number and height	Jun-Aug
1	Oxalidaceae	*Oxalis stricta* L.	93 (c)	62	-0.405	522	Leaf and stem number	Jul-Oct
2	Fabaceae	*Desmodium glutinosum* (Muhl. ex Willd.) A.W. Wood (aka *Hylodesmum glutinsoum*)	22 (r)	17	-0.258	361	Leaf number and leaf size	Sep-Oct
2	Asteraceae	*Ageratina altissima* (L.) King & H. Rob	172 (c)	28	-1.815	316	Stem number and height	Sep-Oct
3	Liliaceae	*Trillium recurvatum* Beck	13 (r)	9	-0.368	357	Leaf number and leaf size	Jun-Jul
3	Verbenaceae	*Phryma leptostachya* L.	54 (r)	48	-0.118	261	Stem number and height	Jul-Aug
3	Asteraceae	*Ageratina altissima* (L.) King & H. Rob	108 (c)	103	-0.047[§]	266	Stem number and height	Sep-Oct
3	Asteraceae	*Verbesina alternifolia* (L.) Britton ex Kearney	132 (c)	8	-2.803	299	Stem number, stem height, leaf number	Sep-Oct

*Abundance category refers to whether a species is locally rare (r) or common (c)

[†] Total abundance is based on 50, 1-m^2 surveyed plots in each habitat type (i.e., uninvaded, invaded)

[‡] Effect size calculated as *ln*(invaded population abundance) – *ln*(uninvaded population abundance)

[§] The effect size of *Ageratina* is unexpectedly low because of a shift in stage classes; there was an increased percentage of seedlings in the invaded population

Table 3.2. The top four ranked elasticity values (e_{ij}) of each population. Data were combined across transitions years for elasticity analyses.

			Top four elasticity values							
			1		2		3		4	
Site	Population	Species	*i,j*[*]	e_{ij}[†]	*i,j*	e_{ij}	*i,j*	e_{ij}	*i,j*	e_{ij}
1	Uninvaded	*Galium circaezans* (r)	r, r[‡]	(0.2038)	sd, sb	(0.2038)	r, j	(0.1503)	j, sd	(0.1445)
	Invaded		r, r	(0.1853)	r, j	(0.1665)	sb, r	(0.1521)	sd, sb	(0.1521)
	Uninvaded	*Oxalis stricta* (c)	sd, r	(0.4077)	r, sd	(0.3690)	r, r	(0.1238)	r, j	(0.0443)
	Invaded		sd, r	(0.2868)	r, sd	(0.2126)	r, r	(0.1183)	r, j	(0.1039)
2	Uninvaded	*Desmodium glutinosum* (r)	r, r	(0.2175)	sd, r	(0.1683)	sj, sd	(0.1458)	r, lj	(0.0900)
	Invaded		lj, lj	(0.1662)	r, r	(0.1244)	sj, sj	(0.1232)	r, lj	(0.1214)
	Uninvaded	*Ageratina altissima* (c)	sd, r	(0.2689)	sj, sd	(0.1437)	r, sd	(0.1128)	r, sj	(0.1114)
	Invaded		sj, sj	(0.3304)	lj, lj	(0.1550)	lj, sj	(0.1498)	sj, lj	(0.1164)
3	Uninvaded	*Trillium recurvatum* (r)	r, r	(0.1760)	sb, r	(0.1036)	sj, sd	(0.1036)	r, lj	(0.0916)
	Invaded		lj, lj	(0.1443)	r, lj	(0.1285)	sj, sj	(0.1142)	r, r	(0.0887)
	Uninvaded	*Phryma leptostachya* (r)	j, j	(0.3178)	r, j	(0.1799)	j, sd	(0.1602)	sd, r	(0.1581)
	Invaded		j, j	(0.3283)	sd, sd	(0.1698)	r, sd	(0.1447)	sd, r	(0.1415)
	Uninvaded	*Ageratina altissima* (c)	sd, r	(0.3128)	r, sd	(0.2179)	r, lj	(0.0806)	r, r	(0.0731)
	Invaded		r, lj	(0.2088)	sd, r	(0.1774)	lj, sd	(0.1363)	sd, sd	(0.1164)
	Uninvaded	*Verbesina alternifolia* (c)	lj, lj	(0.2154)	sd, r	(0.1265)	sj, sd	(0.1265)	r, lj	(0.1231)
	Invaded		sj, sj	(0.4130)	lj, lj	(0.1383)	sj, sd	(0.0875)	sj, lj	(0.0395)

[*] Matrix element of current stage (*j*) in time *t* and subsequent stage class (*i*) in time *t*+1

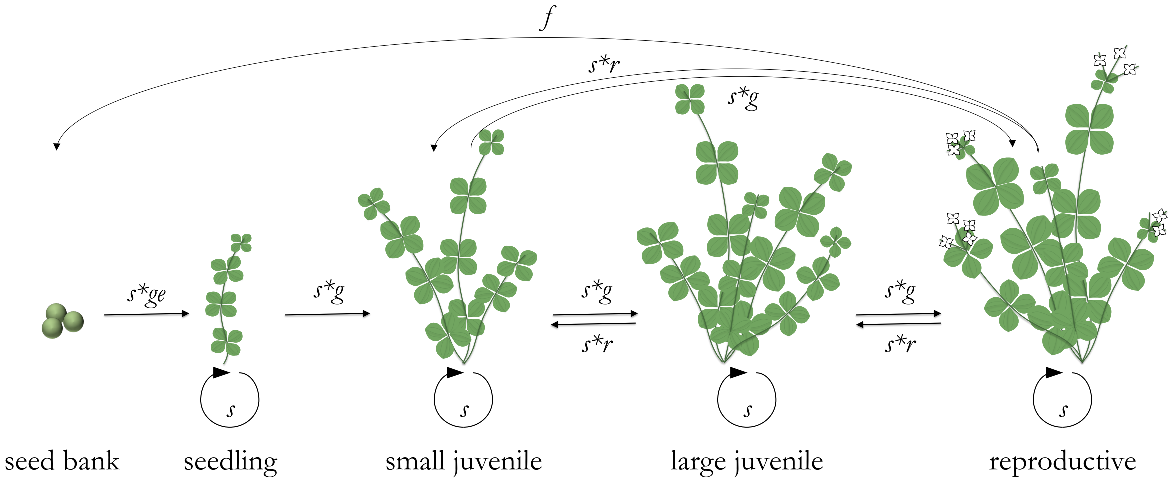
[†] Elasticity value (e_{ij}) of matrix element in previous column

[‡] Key to matrix element abbreviations: seed bank (sb), seedling (sd), small juvenile (sj), juvenile (j), large juvenile (lj), reproductive (r)

Table 3.3. Life Table Response Experiment (LTRE) of each species, broken down into the difference in matrix elements between habitat types (a_{ij}^{I}-a_{ij}^{U}), sensitivity values (s_{ij}), and contributions to population growth. LTRE values are summed by elements that describe the probability of survival but regression into a smaller stage cl ass (Retrogression), survival and stasis in the same nonreproductive stage class (Stasis (nr)), survival and stasis in the same reproductive stage class (Stasis (r)), survival and growth into a larger nonreproductive stage class (Growth (nr)), survival and growth into a larger reproductive stage class (Growth (r)), and reproduction and germination (Recruitment) (also see Fig. 3.3). Because matrix elements and sensitivity values are summed across multiple stages, the product of the values in the table does not equal the contributions. Abundance category is indicated for each species as locally rare (r) or common (c).

		Species							
		site 1		site 2			site 3		
Stage	LTRE	*Galium* (r)	*Oxalis* (c)	*Desmodium* (r)	*Ageratina* (c)	*Trillium* (r)	*Phryma* (r)	*Ageratina* (c)	*Verbesina* (c)
Retrogression	a_{ij}^{I}-a_{ij}^{U}	0.1412	0.3042	0.3691	0.3537	0.3806	0.2128	0.2324	0.3564
Stasis (nr)	a_{ij}^{I}-a_{ij}^{U}	0.1089	0.4624	0.4480	-0.1010	0.2364	-0.0187	-0.4596	0.1505
Stasis (r)	a_{ij}^{I}-a_{ij}^{U}	0.0027	-0.1947	-0.2432	-0.2883	-0.2981	-0.1282	-0.2500	-0.1563
Growth (nr)	a_{ij}^{I}-a_{ij}^{U}	-0.0734	-0.0463	-0.1212	-0.2704	-0.3288	-0.1127	-0.3951	-0.0661
Growth (r)	a_{ij}^{I}-a_{ij}^{U}	-0.1046	-0.3941	-0.4826	-0.4783	-0.1956	-0.0808	-0.1395	-0.1018
Recruitment	a_{ij}^{I}-a_{ij}^{U}	0.0165	-4.7873	-1.0305	-10.2360	-0.9393	7.9729	8.1976	-19.8052
Retrogression	s_{ij}	0.2251	0.1435	0.4395	0.4405	0.9846	0.2510	0.3067	0.4042
Stasis (nr)	s_{ij}	0.4582	0.4885	0.6497	0.6735	0.5513	0.7393	0.6166	0.8105
Stasis (r)	s_{ij}	0.3594	0.5115	0.3504	0.3265	0.2605	0.2607	0.3834	0.1895
Growth (nr)	s_{ij}	0.4804	0.6766	2.3977	1.5111	1.2810	0.5610	1.5054	2.0585
Growth (r)	s_{ij}	2.2230	4.0872	4.4742	4.9322	2.0219	8.6700	13.2696	9.0859
Recruitment	s_{ij}	0.0535	0.0571	0.0266	0.0306	0.0288	0.0142	0.0169	0.0065
Retrogression	contribution	0.0160	0.0255	0.0477	0.0341	0.0476	0.0226	0.0285	0.0417
Stasis (nr)	contribution	0.0252	0.1088	0.0895	-0.0128	0.0465	-0.0193	-0.0214	0.0543
Stasis (r)	contribution	0.0010	-0.0996	-0.0852	0.0941	-0.0777	-0.0334	-0.0959	-0.0296
Growth (nr)	contribution	-0.0353	-0.0314	-0.0892	-0.1044	-0.0556	-0.0632	-0.1359	-0.0228
Growth (r)	contribution	-0.1097	-0.7723	-0.3130	-0.5698	-0.0951	-0.3177	-0.6364	-0.1766
Recruitment	contribution	0.0009	-0.2734	-0.0274	-0.3132	-0.0271	0.1132	0.1385	-0.1287

Figure 3.1. Example life-cycle diagram and corresponding projection matrix illustrating the matrix model built for each species. Vital rates include survival (*s*), growth (*g*), regression (*r*), fecundity (*f*), and germination (*ge*) transitions. Transitions vary among species and between transition years. Subscripts refer to the current stage class (*j*) in time *t* and subsequent stage class (*i*) in time *t*+1.



		Stage class at time t				
		seed bank	seedling	small juvenile	large juvenile	reproductive
Stage class at time *t+1*	seed bank					$(f)_{1,5}$
	seedling	$(s*ge)_{2,1}$	$(s)_{2,2}$			
	small juvenile		$(s*g)_{3,2}$	$(s)_{3,3}$	$(s*r)_{3,4}$	$(s*r)_{3,5}$
	large juvenile			$(s*g)_{4,3}$	$(s)_{4,4}$	$(s*r)_{4,5}$
	reproductive			$(s*g)_{5,3}$	$(s*g)_{5,4}$	$(s)_{5,5}$

Figure 3.2. The effects of *L. maackii* on native species' overall population growth. Dashed lines separate species by site. Abundance category is indicated for each species as locally rare (r) or common (c). (A) Population growth rate (λ) for each uninvaded (circle) and invaded (square) population. Transition years were analyzed separately for 2009-2010 (open symbols) and 2010-2011 (closed symbols). Error bars indicate the bootstrapped 95 percentile confidence intervals. (B) The change in λ (Δλ) caused by the presence of *L. maackii* and calculated by equation *(4)* in the text. A larger negative value indicates a greater negative effect of *L. maackii* on λ.

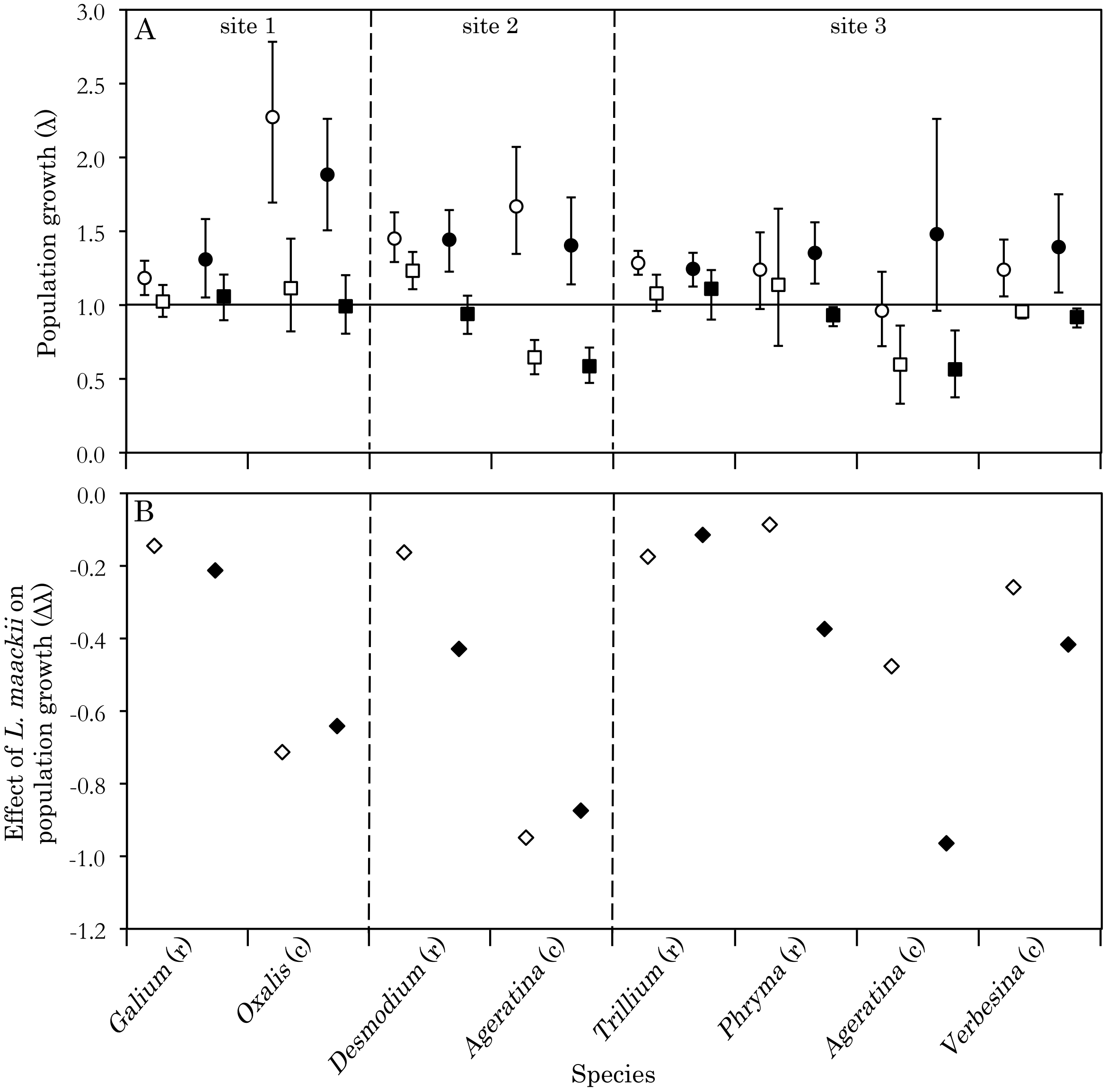


Figure 3.3. Life Table Response Experiment (LTRE) contribution of each matrix element to the change in population growth (Δλ) as calculated by equation *(4)* in the text. A large negative value indicates a large negative contribution of the matrix element to declines in λ in the invaded population. Matrix elements were summed by elements that describe the probability of survival but regression into a smaller stage class (Retrogression), survival and stasis in the same nonreproductive stage class (Stasis (nr)), survival and stasis in the same reproductive stage class (Stasis (r)), survival and growth into a larger nonreproductive stage class (Growth (nr)), survival and growth into a larger reproductive stage class (Growth (r)), and reproduction and germination (Recruitment). Dashed lines separate species by site. Abundance category is indicated for each species as locally rare (r) or common (c).

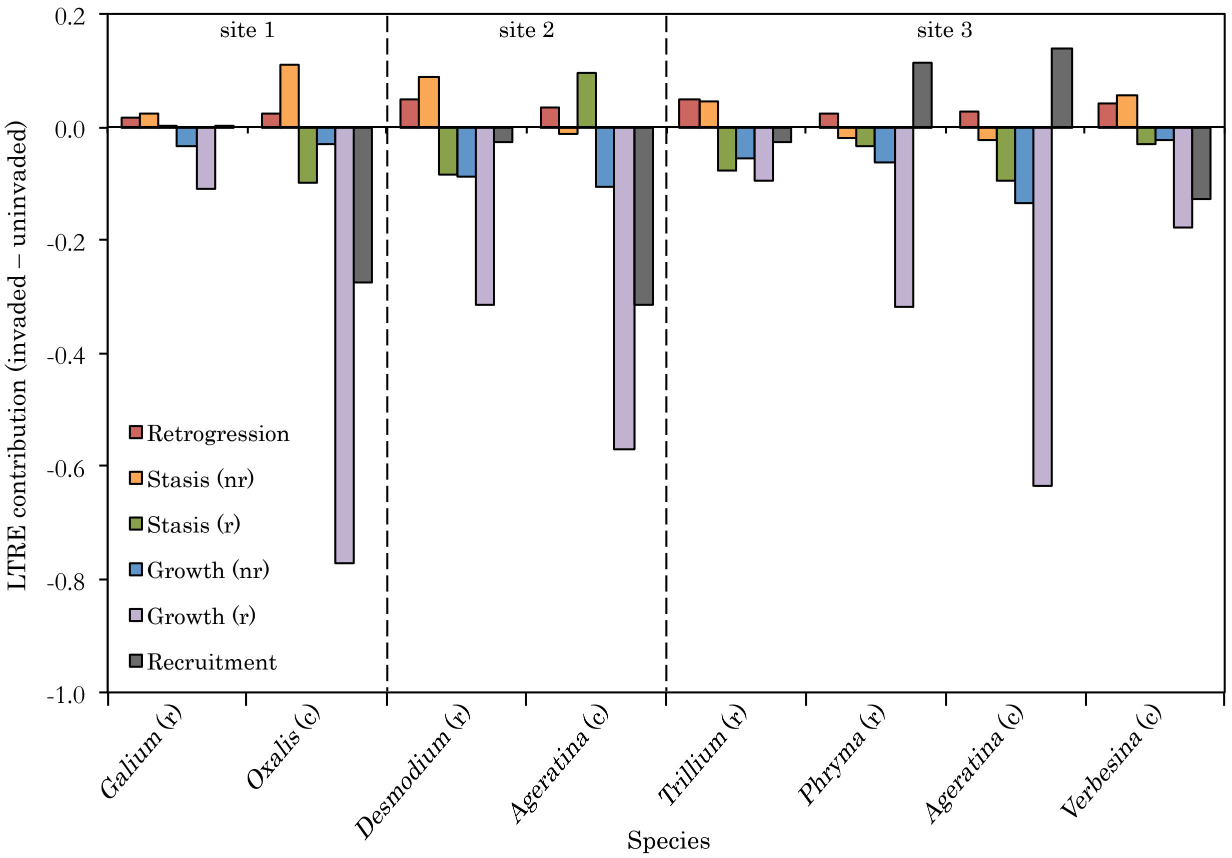
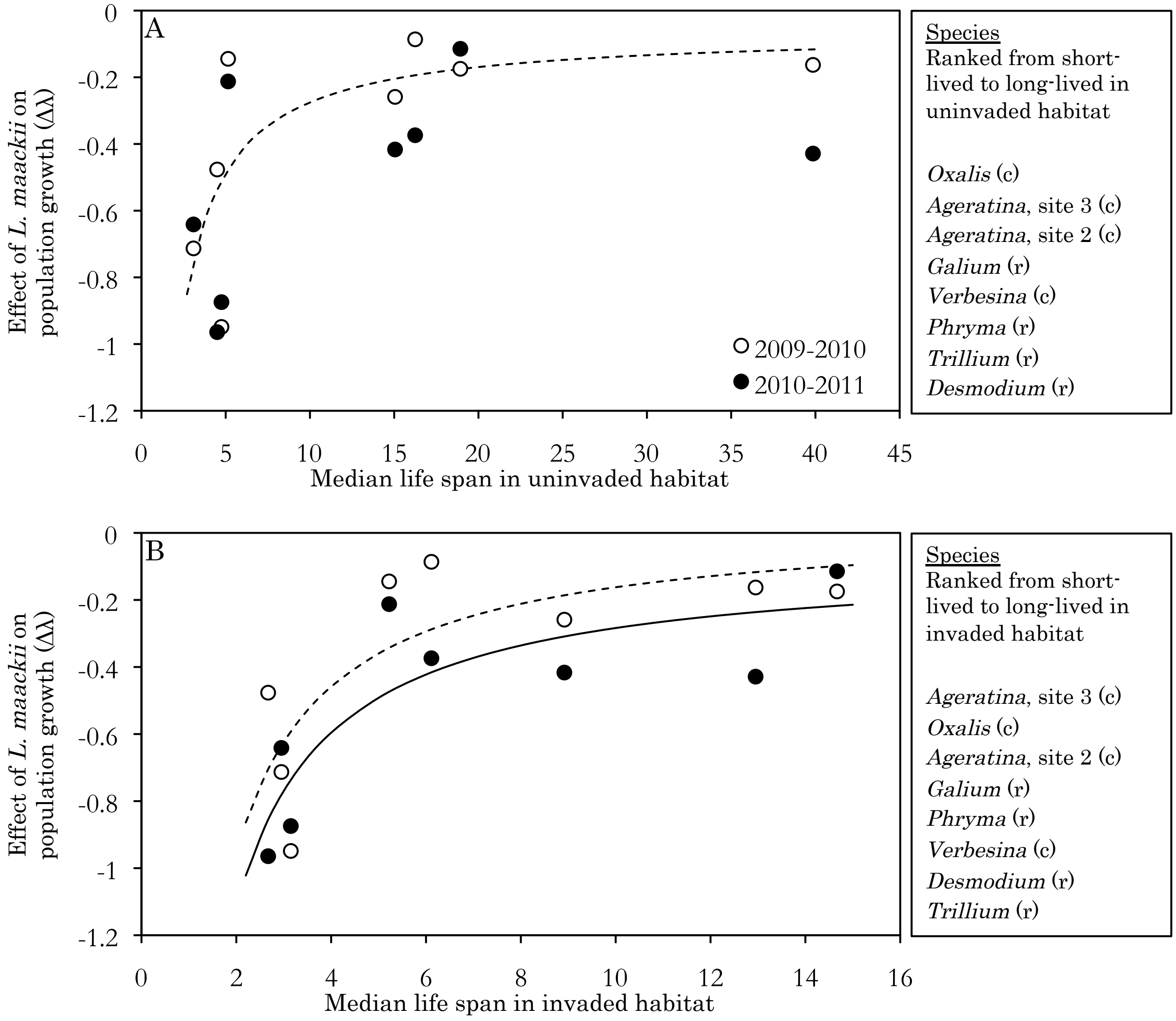


Figure 3.4. Relationship between median life span of species in (A) uninvaded and (B) invaded habitats and the effect of *L. maackii* on population growth ($\Delta\lambda$) in the 2009-2010 transition year (open symbols) and 2010-2011 transition year (closed symbols). Regression curves show significant, inverse relationships ($P < 0.05$) in 2009-2010 (dashed line) and 2010-2011 (solid line). Legends show species ranked from the shortest-lived species to the longest-lived species. Abundance category is indicated for each species as locally rare (r) or locally common (c).



CHAPTER 4

Intense Shading Explains Why Rare Species are Less Affected than Common Species in Habitats Invaded by *Lonicera maackii* (Caprifoliaceae)

by

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Abstract

While invasive plants cause declines in species diversity at local spatial scales, they cause few extinctions at broad spatial scales. In previous studies, we found that the small number of extinctions at broad scales is, in part, due to a proportionately larger effect of plant invaders on the abundance and population growth of common species as compared to rare species. We examined the mechanisms that cause shifts in species composition and declines in common species in habitats invaded by the exotic mid-story forest shrub, *Lonicera maackii*.

We first characterized the abiotic differences in uninvaded compared to *L. maackii*-invaded habitats, including differences in light, leaf litter, soil moisture, and soil nutrients. Significant differences in uninvaded and *L. maackii*-invaded habitats were mainly driven by decreases in light (i.e., photosynthetically active radiation), which resulted from dense *L. maackii* stands shading the forest understory. We evaluated whether the reduction in light was the mechanism driving species composition in *L. maackii*-invaded habitats. Using redundancy analyses, we showed that the abundance of common species in the field is best explained by high-light conditions. In addition, when grown in a greenhouse, common species had larger declines in biomass between treatments mimicking uninvaded and *L. maackii*-invaded light environments. *L. maackii* thrives in high-light conditions, and our results suggest that competitive dominance and niche overlap of a critical resource—in this case light—between *L. maackii* and common species best explains the mechanistic effects of an invasive plant on native species' composition and extinctions.

Introduction

Invasive plant literature has thoroughly documented the negative effects of dominant invasive plant species on the species richness, abundance, and diversity of native plant communities (Hejda et al. 2009, Powell et al. 2011, Vilà et al. 2011). However, there are few case studies examining the mechanisms that lead to these patterns (Levine et al. 2003, Vilà et al. 2011). We define mechanisms similar to Levine et al. (2003)—the ecosystem-level or ecological processes that generate invader effects on diversity. Identifying mechanisms will not only provide an understanding of how plant invasions lead to extinctions, but also help guide management and restoration of invaded habitats.

A common approach to identifying mechanisms that affect plant community structure is by first identifying the environmental changes that occur when a plant invades a native habitat (e.g., Vila et al. 2006, Mummey and Rillig 2006). Once an invasive plant has successfully established and become a dominant member of a native community, the biotic and abiotic environment is altered. Invasive plants transform the environment because of novel traits that differ from the native community (Vitousek and Walker 1989, Fridley 2012) and/or the amount of total biomass they add to the invaded habitat (Vilà et al. 2011, van Kleunen et al. 2011). Ecological and ecosystem-level processes are altered, and these processes feed back to influence each other as well as the resident plant community. For example, invasive plants cause changes in belowground and aboveground processes such as nitrogen and carbon cycling, soil biota and microbial activity, soil acidity and salinity, leaf litter biomass and decomposition, and allelopathic chemicals (Levine et al. 2003, Ehrenfeld 2003, Liao et al. 2008, Weidenhamer and Callaway 2010, Vilà et al. 2011). Invasive plants alter fire regimes and hydrology, such as soil moisture and water table levels (e.g., Mack and D'Antonio 2003, Zedler and Kercher 2004). Despite our knowledge of the ecosystem and ecological processes that occur in habitats where an invasive plant has established, studies rarely examine which processes cause the observed, negative effects on plant populations and communities (<5% of studies: Levine et al. 2003).

One of the most common ecological processes that occur during a plant invasion is intense shading (Braithwaite et al. 1989, Woods 2003, Reinhart et al. 2005). High invasive-plant cover causes reductions in light availability for resident plant species, and is measured as photosynthetically active radiation (i.e., light quantity) and red: far-red wavelength ratios (i.e., light quality). Shading in known to have strong influences on communities through changes in composition, plant growth, and plant survival, as evidenced through successional patterns and forest canopy gaps (Bazzaz 1979, Denslow 1987, Pagès et al. 2003, Jäger et al. 2007). Thus, light is often considered, though not always tested as, a major factor in native species population-level declines in invaded habitats (Reinhart et al. 2006).

Once environmental differences between uninvaded and plant-invaded habitats have been established, correlational analyses and experimental manipulations help determine which/if environmental variables also cause observed changes in resident plant growth and community structure (Levine et al. 2003, Reinhart et al. 2006, Truscott 2008). For example Vivrette and Muller (1977) used a combination of observational and manipulative experiments to show that most changes in environmental conditions (grazing, low moisture, light, and macronutrients) in *Mesembryanthemum crystallinum*-invaded habitats were not causing reductions in native grassland seedling diversity and establishment. Rather, high osmotic levels (from salt leaching from dried *M. crystallinum* plants) caused observed shifts in seedling distributions.

In a previous study, we found that invaders change community composition because of larger proportional declines in the abundance of common species rather than rare species (Chapter 2, Powell et al. 2013). In addition, the overall population growth of common species was more negatively affected, as compared to rare species, by the presence of the invasive forest shrub *Lonicera maackii* (Chapter 3). However, it is likely not the presence of an invasive plant or *L. maackii per se* that is causing large population-level declines in common native species; as described above, changes in species abundance and diversity is likely due to changes in the ecosystem and ecological processes that occur once *L. maackii* has invaded a habitat (Levine et al. 2003).

It is possible that larger declines in the population growth and abundance of locally common species are caused by common species being unable to cope with the altered abiotic conditions in plant-invaded habitats. Common species could have larger overlap in niche space with plant invaders, as defined by a shared common resource (Chapter 1). Thus, the mechanism causing common species' declines could be stronger direct competition with plant invaders for a shared resource, such as water availability or light, or stronger associations with a resource that is depleted by a plant invader. Common species could also lack functional traits that are necessary for tolerating abiotic conditions in plant-invaded habitats, making common species weaker competitors than potentially more specialized rare species (Marvier et al. 2004). These potential pathways leading to the decline of common species are not mutually exclusive.

Species' functional traits will influence their ability to cope with these altered, plant-invaded landscapes. To date, much of the functional trait literature has focused on comparing native and invasive species to determine why invasive plants successfully establish (Funk et al. 2008, van Kleunen et al. 2010). Some studies address species traits in the context of competition, in which individuals of native species compete against individuals of invasive species, often in a greenhouse setting (e.g., Daehler 2003, Burns 2004, Corbin and D'Antonio 2010). The main conclusion from these studies is that invasive species can have novel traits that give them an increased competitive ability, and that coexistence with natives can occur if there are other asymmetric functional differences between species (Heard and Sax 2013).

However, the functional trait literature does little to inform us about the traits that allow native species to cope with changing environmental conditions in plant-invaded habitats. Few studies have examined which life history and/or functional traits confer native species' survival in invaded habitats (Olden et al. 2004). A study conducted by Kyle and Leishman (2009) compared extant versus extinct species in invaded, riparian habitats. They found that short-lived, early colonizing species with high specific-leaf area, soft leaves, and herbaceous and therophyte life forms were characteristic of species that could co-occur with plant invaders.

We tested the abiotic mechanisms that cause changes in population and community-level patterns in *Lonicera maackii*-invaded habitats. *Lonicera maackii* (Amur honeysuckle) is a mid-story forest shrub invader in Midwestern, U.S. forests. *L. maackii* has been shown to have strong aboveground competitive effects on co-occurring plants (Gorchov and Trisel 2003, McKinney and Goodell 2010). We identified the abiotic differences between uninvaded and *L. maackii*-invaded habitats. We measured light availability, as well as other abiotic conditions that might be influenced by invasion, such as leaf litter, soil moisture, soil pH, and soil nutrients. We correlated the abiotic variables with shifts in resident species abundance and composition. We followed up our observational study with a manipulative greenhouse experiment to test how one abiotic condition—light—influences the fitness of rare and common species. Based on previous studies, we know that the abundance of common species is more affected by *L. maackii* than that of rare species. Thus, we hypothesized that rare species better cope with environmental changes created by *L. maackii*, specifically shade, through traits that confer higher shade tolerance (Valladares and Niinemets 2008).

Our goals were to (1) identify differences in abiotic conditions between uninvaded and *L. maackii*-invaded habitats, (2) determine if these differences in abiotic conditions explain variation in species composition and differential effects of *L. maackii* on rare and common species, and (3) experimentally test the quantitative effects of intense shading on the growth of rare and common species that vary in their functional traits.

Methods

Invasive Plant Study Species and Study Sites

We investigated the abiotic conditions that are created by the presence of the invasive mid-story shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae, Amur honeysuckle). *Lonicera maackii* is native to Eastern and Northeastern Asia, and began spreading into urban, woodland, and forest habitats in the Midwestern United States in the 1920's (Luken and Thieret 1996, Collier et al. 2002). *Lonicera maackii* increases shading for understory plants because it forms dense stands in forests with otherwise low vegetation cover by native mid-story species. Also, its leaf phenology extends beyond the leaf-emergence and leaf-fall dates of native species (Gorchov and Trisel 2003, McKinney and Goodell 2010). For more background on *L. maackii*, refer to *Methods: Study Species* (Chapter 3).

We conducted plant surveys and measurements of abiotic variables in eight sites across six natural areas in the greater St. Louis metropolitan region. The natural areas included Cliff Cave County Park (38.460344,-90.293505), Mastodon State Historic Site (38.381767,-90.38445), Forest 44 Conservation Area (38.524936,-90.533023), Washington University's Tyson Research Center (3 sites; 38.522921, -90.562906), Missouri Botanical Garden's Shaw Nature Reserve (38.475296,-90.80236), and August A. Busch Memorial Conservation Area (38.717126,-90.741692). At each site, we paired one uninvaded habitat with one *L. maackii*-invaded habitat in oak-hickory dominated forest. We chose habitats that occur on opposite sides of ongoing *L. maackii* invasion fronts. In addition to site replication, using invasion fronts increases the probability that biotic and abiotic differences between habitats are a direct result of the *L. maackii* invasion. With eight sites and two habitats per site, we sampled a total of 16 locations.

Abiotic Variables and Analyses

During the summer of 2010, we collected abiotic data in the uninvaded and invaded habitats. We permanently established twelve, 1-m^2 plots in each habitat. In each plot, we collected one soil core using a soil core sampler (AMS, Inc.) between the dates of 14 and 19 June. Soil cores were frozen and sent to the Soil Testing Laboratory at the University of Missouri (Columbia, MO). For each pair of uninvaded and invaded habitats, we used the soil cores to evaluate the following soil variables: pH, organic matter, and soil nitrogen in parts per million (ppm), including nitrate-nitrogen (NO_3-N), ammonium-nitrogen (NH_4-N), and organic and total nitrogen (N). We also evaluated phosphorous (P) using the Bray-1 P extraction method, potassium (K), calcium (Ca), and magnesium (Mg). In addition to soil cores, we collected information on the leaf litter depth at two points in each plot, measured as the number of leaves captured on a sharp, metal pin that we used to pierce through the litter layer (Farris-Lopez et al. 2004). Leaf litter could affect a variety of abiotic conditions, including seed germination and survival, nutrient cycling, soil temperature, and water availability (Facelli and Pickett 1991).

We measured light availability in each plot at 0.5 m above the ground, which is a height that is relevant to the understory plant community. Light availability was calculated using a quantum sensor that averages photosynthetically active radiation (PAR, $\mu mol \times m^{-2} \times s^{-1}$) over a 70-cm sensor stick (Model MQ-301, Apogee Instruments, Inc.). For consistency across sites, measurements were always taken between 10:00 and 14:00 on cloudless days. Finally, we collected soil moisture measurements in each plot over eight time periods between 25 May and 26 July. Measurements were taken repeatedly to track soil moisture over varying rainfall periods throughout the growing season. At each sampling time, two volumetric water content measurements were taken in each plot using the HydroSense® Soil Water Measurement System (Model CD620, Campbell Scientific, Inc.).

To test for differences in abiotic conditions across sites and habitats (i.e., uninvaded vs. *L. maackii*-invaded), we first visually compared data using principal component analysis (PCA) to ordinate sampled locations with scaled environmental variables (Taylor et al. 1993). We then conducted a one-way multivariate analysis of variance (MANOVA) to determine whether uninvaded and invaded habitats were significantly different, despite variation in sites. Light was log-transformed to reach assumptions of normality. Following a significant MANOVA ($P \leq 0.05$), we conducted subsequent, independent one-way ANOVAs on each environmental variable (e.g., Conner and Zangori 1998). To control for site-to-site variation, we also conducted independent paired *t*-tests on each environmental variable. We conducted a separate analysis on soil moisture because this variable was collected repeatedly over the sampling season. To determine if soil moisture varied between habitat types over time, we used a repeated-measures ANOVA with volumetric water content and habitat type as fixed factors. Greenhouse-Geisser epsilon degrees of freedom values were used to account for violations in the repeated-measures ANOVA assumption of compound symmetry.

Species Composition and Analyses

The species abundance data collected for Chapter 2 and 3 were correlated with abiotic conditions. We tested whether species abundances across sites were significantly explained by our collected abiotic variables. We then tested specifically whether common versus rare species' abundances had strong associations with abiotic variables that were altered by *L. maackii*. We surveyed species' abundances at all eight sites in each pair of uninvaded and invaded habitats. We collected abundance data on all species in a community by counting the number of aboveground stems of all understory forest species in 50, 1-m^2 plots in the uninvaded habitat and the invaded habitat. The plots were spread evenly across a 500-m^2 area in each habitat (see Powell et al. 2013).

We determined which abiotic variables were driving shifts in species composition. We first reduced the species abundance data to only include species with high replication across sites (i.e., species that were found at five or more of the eight sites). Then, the effect of abiotic variables on community composition was analyzed using redundancy analysis (RDA). RDA is a principal components method and assumes a linear relationship between the environmental variables and species' local abundances (natural log-transformed+1) (ter Braack 1994). We also tested our data assuming a unimodal relationship with a canonical correspondence analysis (CCA) (ter Braack 1986). However, the results were qualitatively very similar to RDA, and we mainly present RDA results. We calculated significance of the RDA and its ordination axes in explaining community structure using Monte-Carlo permutation tests.

To further examine how the abiotic variables explained variation in species composition, we regressed species' RDA ordination axis scores against (1) species' local abundances in uninvaded habitats across sites, and (2) the effect of *L. maackii* on species' local abundances across sites. The average effect of *L. maackii* on local abundances was calculated for each species as

$$effect\ size = \frac{\sum_1^n \ln\,(uninvaded\ site\ abundance) - \ln\,(invaded\ site\ abundance)}{n} \qquad (1)$$

where n is the number of sites where a species is present. These analyses determined whether the abiotic variables significantly explained species commonness and rarity as well as the effect of *L. maackii* on species' abundances. We determined which environmental variables correlated with the RDA ordination axes using the interset correlations, which are the correlations between the abiotic variables and WA scores (see Ter Braack 1986, McCune and Grace 2002).

Shade Greenhouse Experiment and Analyses

In 2011, we established a greenhouse experiment to test one environmental variable that is known to change in *L. maackii* stands—light (Gorchov and Trisel 2003, Cipollini et al. 2008). We tested the importance of light and shading on the growth of common versus rare species that co-occur with *L. maackii*. We conducted a factorial, species-by-light experiment in Washington University's greenhouse from 26 March to 27 May 2010. This experiment allowed us to directly manipulate the effects of reduced light on species' traits and fitness, as well as control for the other abiotic and biotic factors that are altered in *L. maackii*-invaded habitats.

We chose 11 species to use in the greenhouse experiment. The species spanned a range of average local abundances observed at our field sites. The majority of species were perennial forbs (see Table 4.1). To ensure that local abundance was not congruent with taxonomic similarity for these 11 species, we tested for a phylogenetic signal in species abundance using Blomberg's K statistic (Blomberg et al. 2003). We estimated branch lengths of a phylogeny that included the 11 greenhouse species by using the Phylocom 'bladj' algorithm. We calculated Blomberg's K and its significance (1-tailed test for greater phylogenetic signal than expected) using the R package Picante (Webb et al. 2008, R Core Team 2013).

Most species germinated under greenhouse conditions in Sun Gro Metro-Mix 30 Growing Medium after a 60-day cold treatment (Table 4.1). Three species were collected as new germinates from field conditions, including *Trillium recurvatum*, *Galium circaezans*, and *Impatiens capensis*. After germination, each individual seedling was replanted into an

11.43-cm-diamter round pot and assigned to a light treatment. Each species had 6-12 replicates (i.e., pots) per treatment (Table 4.1). We also harvested 6-12 seedlings per species at the start of the experiment to calculate an initial seedling weight.

We manipulated light quantity and quality using black, knitted shade cloth and green, coated polyester filters. We created three light treatments: high-light, medium-light, and low-light. In the high-light treatment, individual pots were not covered by any light filters. For the medium- and low-light treatments, we constructed metal frames (5m x 1m x 1.5m) that rested on top of the plant racks. The light filters and shade cloth were draped over the frames (Fig. 4.1). The medium-light treatment mimicked the average uninvaded habitat PAR (131.83±127.41). We achieved the correct red: far-red ratio as described in the literature for uninvaded forests (Griffith and Sultan 2005, Bonser and Geber 2005, Reinhart et al. 2006, Forster and Bonser 2009) using a polyester color-effect 088 filter (Lime Green, LEE Filters, see www.leefilters.com for spectral light transmission). The low-light treatment mimicked the average invaded habitat PAR (8.01±2.28). For the low-light treatment, we achieved the correct red: far-red ratio using a polyester color-effect 122 filter (Fern Green, LEE Filters). We placed an additional 80% shade cloth (PAK Unlimited, Inc.) over the color-effect 122 filter to attain the low invaded-habitat PAR levels. Grated plant racks and slits in the color filters allowed sufficient airflow for pots in all three treatments (see Fig. 4.1). We measured the air temperature directly above the pots in each treatment to ensure there were no differences across treatments (6 April: 24.45±0.21 °C, 4 May: 20.7±0.1 °C across treatments).

Individuals were randomized within a light treatment every week to avoid effects of greenhouse and bench location. At the end of the experiment, all species were destructively sampled to measure fitness traits and leaf- and plant-level functional traits that correlate with shade tolerance (Valladares and Niinemets 2008, Poorter 2009). For each species, we collected two leaves per individual to measure leaf-level traits. We measured the following variables: (1) fitness variables: stem biomass, leaf biomass, below-ground biomass, above-ground biomass, and total biomass to calculate relative growth rate (RGR; increase in total dry mass per unit time); (2) functional traits: number of branches, longest branch length, internode branch length, number of leaves, leaf thickness, leaf toughness, leaf area and mass to calculate specific leaf area (SLA; leaf area per unit dry leaf mass in cm^2g^{-1}), leaf-area ratio (LAR; total leaf area per total plant mass in cm^2g^{-1}), and leaf mass fraction (LMF; total dry leaf mass per total dry plant mass). In addition to the fitness variables and functional traits collected as response variables in each of the three light treatments, we calculated the natural log effect sizes of the response variables between each treatment (i.e., natural log difference in a response value between high-light and medium-light, high-light and low-light, and medium-light and low-light).

Because our main goal was to evaluate whether shade could explain the differential effects of *L. maackii* on common versus rare species, we conducted correlation and regression analyses to compare the greenhouse response variables to the species abundance data that was collected in the field. We used Pearson correlations and least-squares linear regression models to compare the greenhouse response variables with (1) average abundance in uninvaded habitats and invaded habitats (natural-log transformed) in the field and (2) the average effect of *L. maackii* on abundance in the field calculated using *eq. 1*. We also standardized average abundance by the average PAR at each site to account for the fact that not all species were found at the same sites and natural areas, which vary in their total light levels. The statistical analyses for the abiotic variables, species composition, and greenhouse experiment were performed in R v3.0.1 (R Core Team 2013) and SPSS v12.0 (SPSS 2003).

Results

Abiotic Variables

Paired habitats within a site were environmentally more similar to each other than uninvaded habitats across sites or invaded habitats across sites (Fig. 4.2). This suggests that habitat types within each site were paired successfully to minimize abiotic differences other than the presence of *L. maackii*. For example, habitat pairs at Shaw Nature Reserve and August A. Busch Memorial Conservation area were associated with high light and moisture conditions, while habitat pairs at Minke Valley in Washington University's Tyson Research Center was associated with high organic matter and soil nutrient conditions (Fig. 4.2). The first two principal component axes explained 63.32% of the abiotic variation among the sites and habitat types. The first principal component had large, significant component loadings for pH, calcium, potassium, NO_3-N, organic matter, and organic and total nitrogen. The second principal component had large, significant component loadings for light, moisture, leaf litter, and phosphorous (Fig 4.2).

Despite the high abiotic similarity within sites, uninvaded and invaded habitat types were still significantly different from each other (MANOVA: $F_{2,14}=33.79$, $P=0.03$). This was mainly due to lower quantities of light in invaded habitats (Table 4.2). When we accounted for site variation using a paired *t*-test, invaded habitats also had more basic soils (i.e., higher pH; Table 4.2). Soil moisture significantly changed over the duration of the study period (repeated-measures: n=8 dates, $F_{2,30}=15.206$, $P<0.001$; Fig. 4.3A), but there was no interaction between soil moisture through time and habitat type ($F_{2,30}=0.246$, $P=0.801$; Fig. 4.3B).

Species Composition

Forty-five forbs, vines, and woody seedlings were found at five or more of the eight sites and were used in multivariate analysis of community structure. The abiotic variable organic nitrogen was removed from the multivariate analyses because it was tightly correlated with total nitrogen. The linear RDA model significantly explained 90.59% of the variation in species composition (Permutations=199, F=2.41, P=0.005), and the first two ordination axes explained 42.91% of the variation in species composition (RDA 1: F=9.02, P=0.018; RDA 2: F=4.67, P=0.030; Fig. 4.4). The correlations of the abiotic variables with the ordination axes are shown in Table 4.2. The variables that were significantly different between uninvaded and invaded habitat types, light and pH, were significantly correlated with the RDA ordination axes 1 and 2, respectively (Table 4.2). Results from the CCA were qualitatively similar to those of the RDA and explained 88.71% of the variation in species composition (Permutations=199, F=1.96, P=0.005).

We found a negative, linear relationship between RDA axis 1 and a species' average abundance in an uninvaded habitat (adj. R^2=0.517, P<0.001; Fig. 4.5). We also found a negative relationship between RDA axis 1 and the effect of *L. maackii* on species' abundances (adj. R^2=0.424, P<0.001; Fig. 4.5). Common species, as well as species that were more negatively affected by *L. maackii* in the field, had lower species ordination scores. Low ordination scores were associated with high light, magnesium, and NH_4-N abiotic conditions (Table 4.2). Thus, high light, magnesium, and NH_4-N best explained the abundance distributions of common species and species that were more negatively affected by *L. maackii* (Table 4.2, Fig. 4.5). High NO_3-N conditions best explained the abundance distributions of rare species and species that were less affected by *L. maackii* (Table 4.2, Fig. 4.5).

Shade Greenhouse Experiment

Overall, species gained the least biomass in the low-light treatment and the most biomass in the medium-light treatment. This result was expected since the species grown in the greenhouse are naturally found in woodland and forest habitats rather than high-light, open habitats.

All significant correlations between species' abundances in the field and greenhouse response variables are shown in Table 4.3. Species that were more common in the field had longer branch lengths (i.e., were taller) in the greenhouse (Table 4.3). Apart from branch length, functional traits were not correlated with species' abundances in the field. In addition to having a longer branch length, common species had larger reductions in branch length, aboveground biomass, and total biomass in the low-light greenhouse treatment (i.e., a larger effect size between medium- and low-light treatments) (Table 4.3, Fig. 4.6A). In addition, species that were more negatively affected by the presence of *L. maackii* in the field experienced larger reductions in aboveground biomass and total biomass in the low-light greenhouse treatment (Table 4.3, Fig. 4.6B). RGR in the greenhouse did not significantly correlate with species' abundances due to the annual species *Impatiens capensis*, which was relatively rare in the field but experienced large declines in growth in the low-light treatment. When *I. capensis* was removed from the analyses, the effect of *L. maackii* on species' abundances in the field was positively correlated with the RGR effect size (loss of RGR from the medium- to low-light treatment; Table 4.3, Fig. 4.6C) and RGR in the medium-light treatment (Table 4.3, Fig. 4.6D).

Species did not group taxonomically by average local abundance (Blomberg's K=0.529, *P*=0.483, also see phylogenetic tree in Appendix 4, Fig. A4.1), and thus, our results were not confounded by phylogenetic similarity. Standardizing the field abundance survey data by PAR did not quantitatively change the results.

Discussion

We studied the mechanisms by which *L. maackii* affects resident plant community composition and species abundances. Based on previous research and *L. maackii*'s shrubby life form, we hypothesized that reductions in light levels would have the strongest effect on species composition. Our results supported this hypothesis. The measured, abiotic variables that differed between uninvaded and *L. maackii*-invaded habitats were light quantity and soil pH (Table 4.2). Both light and soil pH significantly explained variation in resident species composition across the study sites and natural areas (Table 4.2). However, of these two variables, only light levels explained the effects of *L. maackii* on species abundances (Fig. 4.5B).

In addition to light and soil pH, we measured soil moisture, leaf litter, and soil nutrient variables at all study locations. Overall, environmental differences among sites (i.e., natural areas) were greater than environmental differences between uninvaded and invaded habitats (Fig. 4.2). This result suggests that *L. maackii* is able to invade a variety of oak-hickory forest natural areas that have a range of environmental conditions (Fig. 4.2). Other studies confirm that *L. maackii* likely has a wide niche breadth, as its distribution is often explained by factors describing the amount of nearby urban landscape rather than within-site, environmental variables (Borgmann and Rodewald 2005, Bartuszevige et al. 2006).

Soil pH was slightly more basic in invaded habitats. Higher soil pH in *L. maackii*-invaded habitats could be caused by higher nitrate uptake or high root and leaf litter nitrogen concentrations, similar to the woody forest invader *Berberis thunbergii* (Ehrenfeld et al. 2001). *Lonicera maackii* indeed has high nitrogen concentrations and decomposition rates compared to native tree species (Poulette and Arthur 2012). Invaded habitats could also be harboring more root biomass. Though we attempted to reduce pre-invasion, environmental differences between sampled habitats, it is also possible that *L. maackii* preferentially invades habitats with more basic soils. However, in the years following our initial plant surveys, there have been significant increases in *L. maackii* in the previously uninvaded habitats (K. Powell, personal observation), suggesting that our uninvaded habitats were suitable pairs for *L. maackii*-invaded habitats.

We did not measure all possible mechanisms by which *L. maackii* could affect resident plant species. For example, *L. maackii* produces allelopathic chemicals (Trisel 1997, Dorning and Cipollini 2006, Cipollini and Dorning 2008), though these effects can be weak in the field relative to the effects of aboveground shading (Cipollini et al. 2008). *L. maackii* also influences biotic mechanisms, such as white-tailed deer abundance and pre- and post-dispersal rodent seed predation (Allan et al. 2010, Dutra et al. 2011). However, many of the understory species we surveyed are small-seeded species that likely do not experience strong differential rodent seed predation. Studies to date have focused on population-level outcomes of seed predation in invaded habitats (i.e., seed predation on one species; Orrock et al. 2008, Mattos and Orrock 2010, Dangremond et al. 2010). To investigate if biotic mechanisms play a role in differential effects of invaders on rare and common species, studies would need to investigate the role of seed predation for multiple species within a community.

In previous work, we found that the abundance of common species, as compared to rare species, is more negatively affected by the presence of *L. maackii* (Powell et al. 2013). The only variable that significantly explained differences in both the commonness and rarity of species as well as habitat types was light quantity (Table 4.2, Fig. 4.5). Rare species were associated with low-light environments. Common species were associated with high-light environments. This suggests that common species thrive in high-light conditions, and thus experience larger declines in abundance when intense shading occurs after a *L. maackii* invasion.

The greenhouse study provided a controlled test of whether common species are indeed less shade tolerant than rare species, and whether common versus rare species confer traits that allow them to survive in low light. More common species were taller (height measured as branch length) in conditions that mimicked an uninvaded habitat (Table 4.3), but experienced large declines in height when light was reduced (Table 4.3). High competitive ability is often associated with height (Falster and Westoby 2003, Violle et al. 2009), and tall plants might have a competitive advantage in uninvaded habitats. However, in the presence of a mid-story invading species, native plants will not confer a benefit from allocating resources to branch length since they cannot reach the leaf canopy of *L. maackii*. Instead, it could be detrimental for species to allocate more resources to aboveground biomass if long-term survival in low-light conditions requires belowground storage resources (e.g., Myers and Kitajima 2007). Species that were most negatively affected by *L. maackii* in the field also had the highest RGR in medium-light greenhouse conditions (Fig. 4.6). Similar to height, a higher RGR in medium-light conditions translated into a larger decline in RGR in low-light conditions. This suggests that species that are able to attain high growth in uninvaded habitats experienced the largest declines in growth in invaded habitats (Fig. 4.6, Chapter 3).

In the greenhouse experiment, species that were less affected by *L. maackii* in the field had smaller declines in RGR from the medium-light to low-light treatment. *Impatiens capensis* was the exception to this relationship (Fig. 4.6C). *I. capensis* was the only annual species in our study and has a different life-history strategy from the nine other perennial species. To ensure reproduction, *Impatiens capensis* must allocate a lot of resources to aboveground biomass, which was more affected by shade than belowground biomass. In addition, our estimate of *I. capensis'* local abundance was based on one site where the species was relatively rare, and thus we may have underestimated *I. capensis'* average local abundance in the field (Table 4.1). Unlike our field abundance data, but similar to our greenhouse study, Cipollini et al. (2008) found large significant, negative affects of *L. maackii* on *I. capensis* height, survival, and reproduction in the field.

Our results suggest that *L. maackii* has greater resource overlap with common species than rare species. We found that common species thrive in environments where light is a ubiquitous resource, whereas rare species are able to persist in low-light conditions. *Lonicera maackii* also thrives in high-light conditions, in both disturbed urban habitats and forest edges, spreading inward into forest interiors (Luken and Goessling 1995, Luken and Thieret 1996). Competitive dominance in resource use may allow *L. maackii* to successfully establish by replacing the resident common species. We suggest that the replacement of common species through niche overlap coupled with high invader fitness (MacDougall et al. 2009) might be a common strategy in successful invasions. For example, we found that common species were more negatively affected than rare species in two other ecosystems with sub-tropical and tropical forest invaders, including *Dianella ensifolia* in Florida, U.S. and *Morella faya* in Hawai'i, U.S. (Powell et al. 2013, Chapter 2). In these systems, it is also possible that common species are competitively inferior because of resource-use overlap with the focal invader, such as competition for light.

Studying the mechanisms by which plant invaders affect species composition will help prioritize restoration efforts of invaded landscapes. For example, if shifts in belowground soil chemistry and microbial communities are the main mechanism driving changes in species composition, then legacy effects could play a long-term role in whether resident species are able to re-establish in restored habitats. In the case of *L. maackii*-invaded habitats, we found that common species are mainly influenced by aboveground light competition. Thus, there should be a higher likelihood that invasive-plant removal and re-seeding of locally extinct native species will result in a successful restoration.

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Table 4.1. Description of species used in the shade greenhouse experiment, including species names, life form and life span, average local abundance, germination technique, and the number of replicates per species per each light treatment (i.e., high-light, medium-light, and low-light).

				Average abundance ± stdev*				
Family	Species	Life form	Life span	Un-invaded	In-vaded	# of sites used in abundance averages	Germina-tion technique	Replicates per light treatment
Asteraceae	*Ageratina altissima* (L.) King & H. Rob	Forb	Perennial	305.1± 606.8	35.3± 48.9	7	60-day cold treatment, 1 wk in GH†	12
Vitaceae	*Parthenocissus quinquefolia* (L.) Planch	Woody vine	Perennial	241.6± 162.5	76.9± 73.6	7	60-day cold treatment, 1.5 wk in GH	12
Oxalidaceae	*Oxalis stricta* L.	Forb	Perennial	153.8± 328.4	13.0± 24.4	6	60-day cold treatment, 1 wk in GH	12
Asteraceae	*Verbesina alternifolia* (L.) Britton ex Kearney	Forb	Perennial	133.0± 0.0	8.0± 0.0	1	60-day cold treatment, 1 wk inGH	12
Rubiaceae	*Galium concinnum* Torr. & A. Gray	Forb	Perennial	129.5± 130.8	3.5± 2.1	2	60-day cold treatment, 1-2 wk in GH	12
Rubiaceae	*Galium circaezans* Michx.	Forb	Perennial	40.0± 30.6	4.6± 9.1	7	Field collection	12
Apiaceae	*Cryptotaenia canadensis* (L.) DC	Forb	Perennial	22.0± 29.7	0.5± 0.7	2	60-day cold treatment, 1 wk in GH	6
Liliaceae	*Trillium recurvatum* Beck	Forb	Perennial	13.0± 0.0	9.0± 0.0	1	Field collection	9
Fabaceae	*Desmodium glutinosum* (Muhl. ex Willd.) A.W. Wood	Forb	Perennial	12.4± 9.6	3.8± 7.4	5	60-day cold treatment, 1 wk in GH	12
Lamiaceae	*Monarda fistulosa* L.	Forb	Perennial	10.0± 0.0	0.0± 0.0	4	1 wk in GH	12
Balsaminaceae	*Impatiens capensis* Meerb	Forb	Annual	1.0± 0.0	15.0± 0.0	1	Field collection	12

*Abundance is based on 50, 1-m^2 surveyed plots in each habitat type (i.e., uninvaded, invaded). See Methods section for further explanation

†Greenhouse (GH)

Table 4.2. The role of abiotic conditions across locations in explaining differences in uninvaded and *Lonicera maackii*-invaded habitat types (columns 2 and 3) and species composition (columns 4 and 5). ANOVA and paired t-test results followed a significant MANOVA testing differences in habitat type. Interset correlations are the correlation of each abiotic variable with RDA ordination axis 1 and RDA ordination axis 2. Significance values associated with the interest correlations show significance of each variable in the model explaining variation in species composition.

	Significant differences in habitat type		Significant differences in species' composition[‡]	
Abiotic dependent variable	F-value (ANOVA)	t-value (paired t-test)	interset correlations for RDA 1 (permutation test)	interset correlations for RDA 2 (permutation test)
leaf litter	0.888	1.478		
light (PAR[†])	71.08***	7.305***	-0.597**	
moisture	0.201	-0.773		-0.322*
pH	1.796	-1.159*		-0.770**
calcium	0.588	-1.394		-0.754
magnesium	0.001	-0.061	-0.511**	
phosphorous	0.045	1.038		0.583*
potassium	2.661	-1.711		-0.392
NO_3-N	1.519	-1.307	0.369*	-0.408*
NH_4-N	0.933	1.396	-0.569*	
organic matter	1.037	-1.614		-0.609
organic nitrogen	1.174	-1.571	na	na
total nitrogen	1.173	-1.569		-0.614

[†] Photosynthetically Active Radiation (PAR, µmol x m^{-2} x s^{-1})

[‡] Interest correlations ≥ 0.30 are shown

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$

Table 4.3. Pearson correlations of species' abundance in the field with greenhouse fitness variables and functional traits in different light treatments. Only significant correlation coefficients (r) are shown. The correlations shown in blue were only significant when the outlier species, *Impatiens capensis*, was removed from the analysis.

	Fitness variable or functional trait →	RGR† (g*growing days^{-1})	RGR ES	Branch length (cm)	Branch length ES	Above-ground biomass ES	Total biomass ES
Field abundance variable	Light treatment →	ML‡	ln(ML)-ln(LL)	ML	ln(ML)-ln(LL)	ln(ML)-ln(LL)	ln(ML)-ln(LL)
Ln (uninvaded abundance)		--	--	0.640*	0.608*	0.618*	0.594°
Ln (invaded abundance)		--	--	--	--	--	--
Effect size of *L. maackii* on abundance		0.721*	0.896***	--	--	0.649*	0.639*

†Relative growth rate (RGR)
‡Medium-light treatment (ML), Low-light treatment (LL)
°$P \leq 0.10$, *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$

Figure 4.1. Photos of the three greenhouse light treatment, including the low-light, medium-light, and high-light treatment (from left to right). The low-light treatment is shown (A) without and (B) with the 80% knitted, black shade cloth. Metal frames used to hold the green, polyester color-effect filters and shade cloth rest on the grated plant racks.

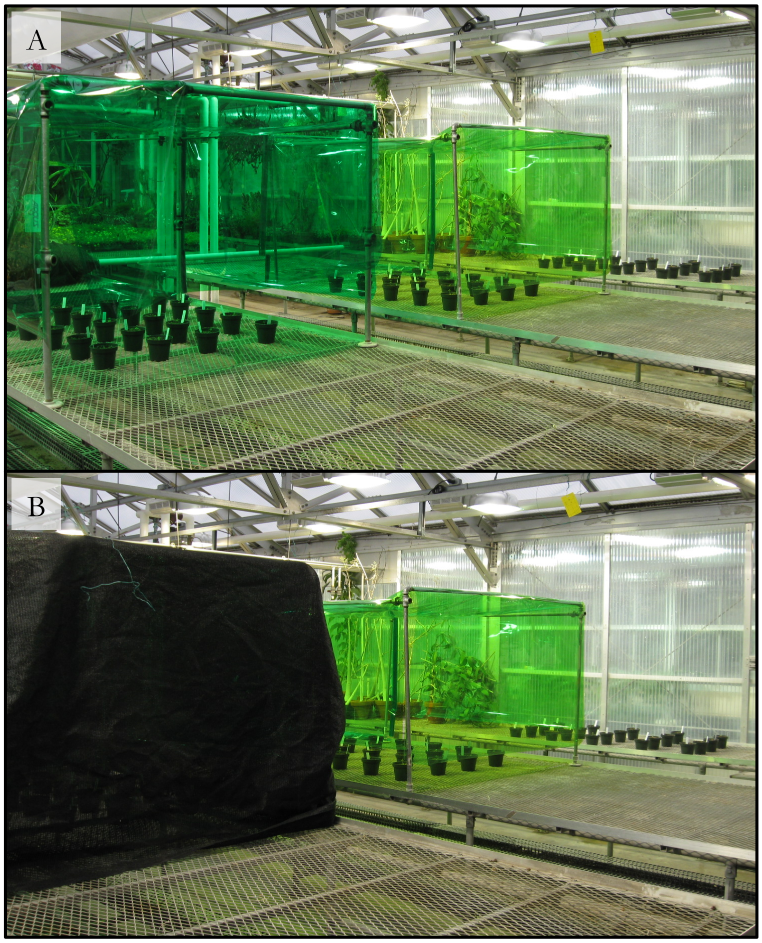


Figure 4.2. Principal Component Analysis (PCA) as defined by the first two ordination axes to visualize the abiotic variables (red) and site locations (black). The uninvaded habitat (o) and *Lonicera maackii*-invaded habitat (+) are presented for each site (Table 4.1). Based on the abiotic variables, locations group by site rather than by habitat type. The amount of variation in the data as explained by each principal component axis is shown in parentheses.

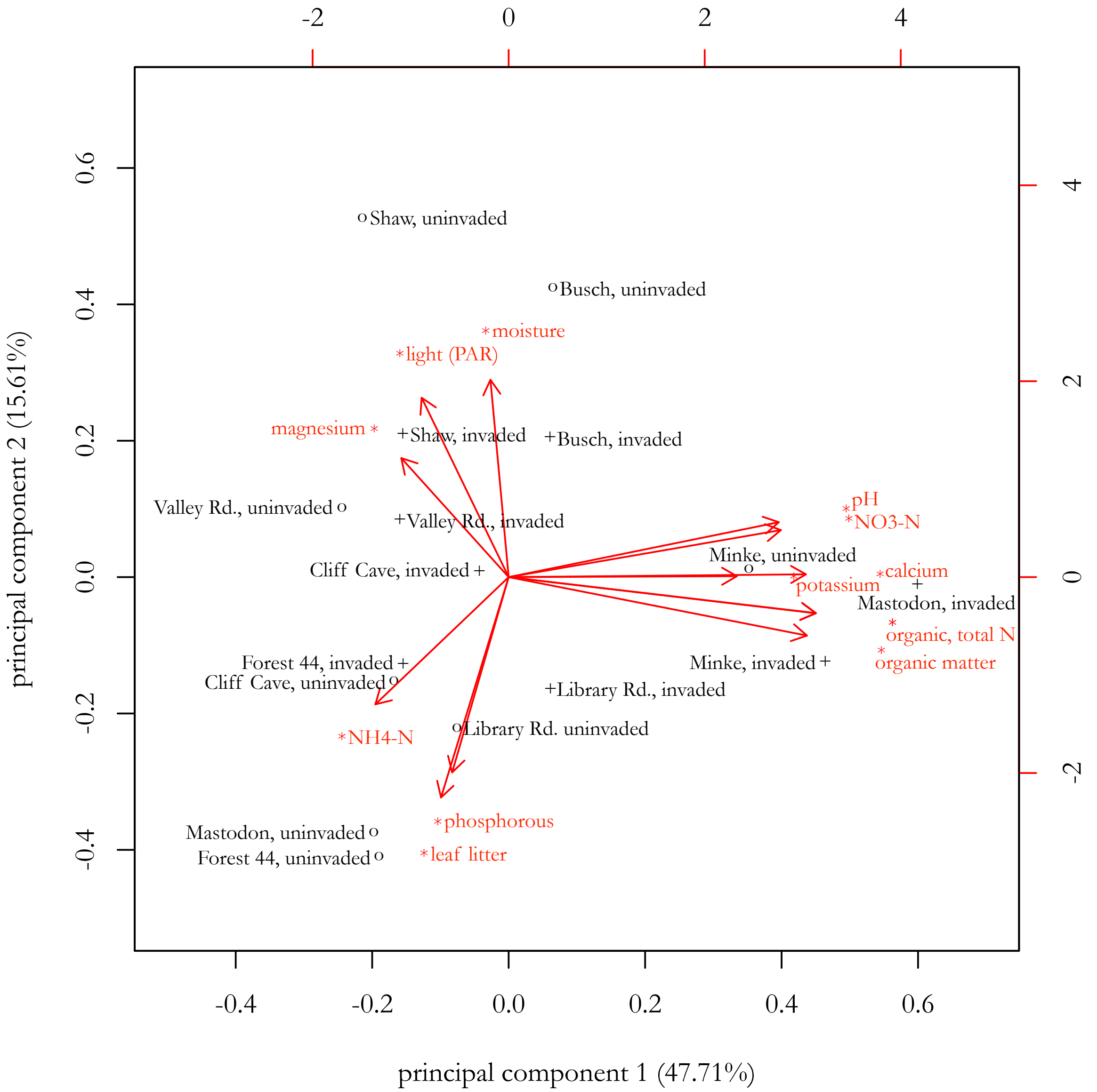


Figure 4.3. Soil moisture, defined as volumetric water content (VWC), over eight sampling dates averaged (A) within each site and habitat type and (B) across habitat types. *Lonicera maackii*-invaded (o) and uninvaded (□) habitats are shown. Error bars indicate one standard deviation.

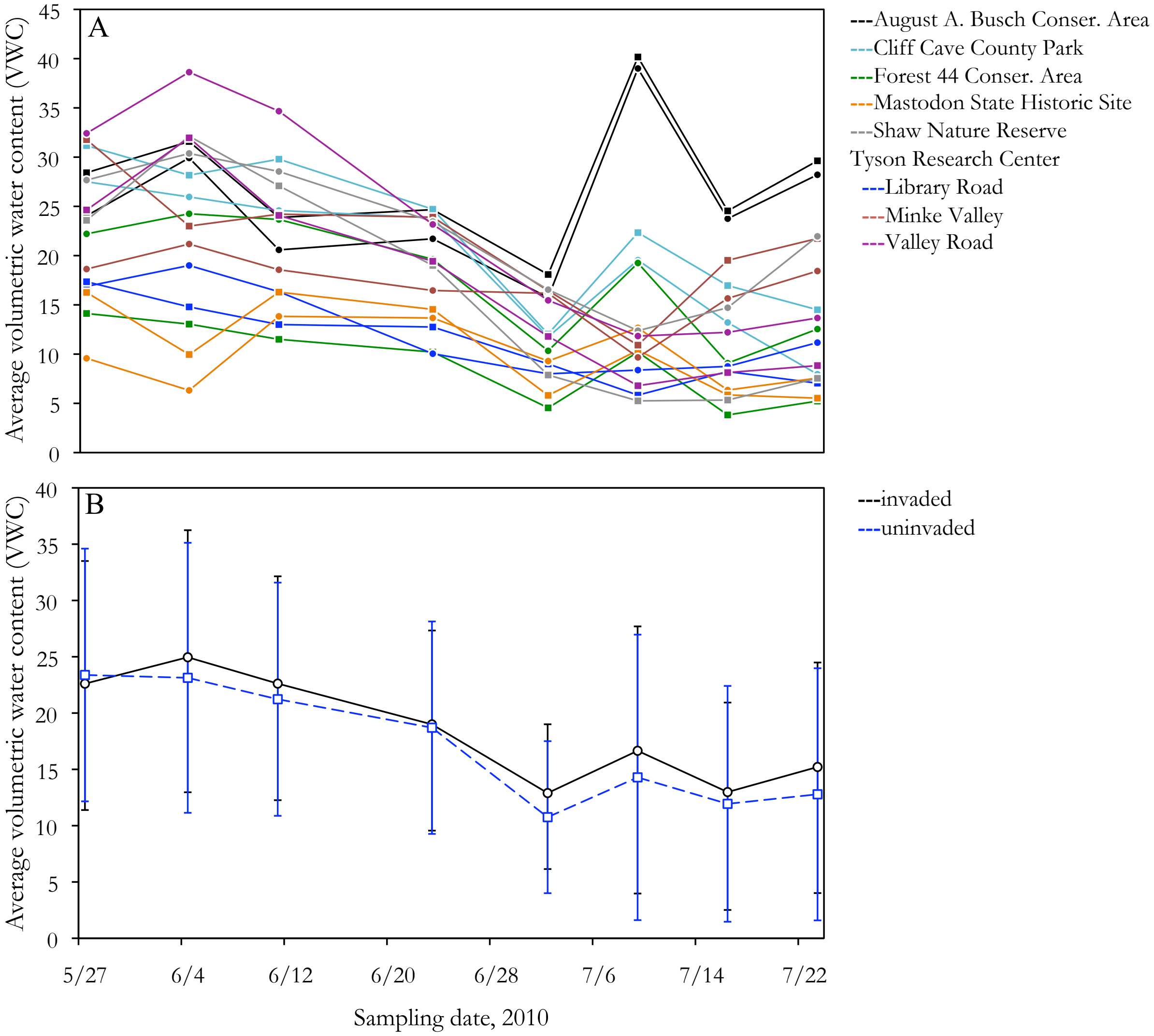


Figure 4.4. Redundancy Analysis (RDA) principal component as defined by the first two ordination axes to visualize the abiotic variables (red) and species composition (black). Species labels show the first three letter of the genus name and first three letters of the species name. The amount of variation in the data as explained by each RDA ordination axis is shown in parentheses.

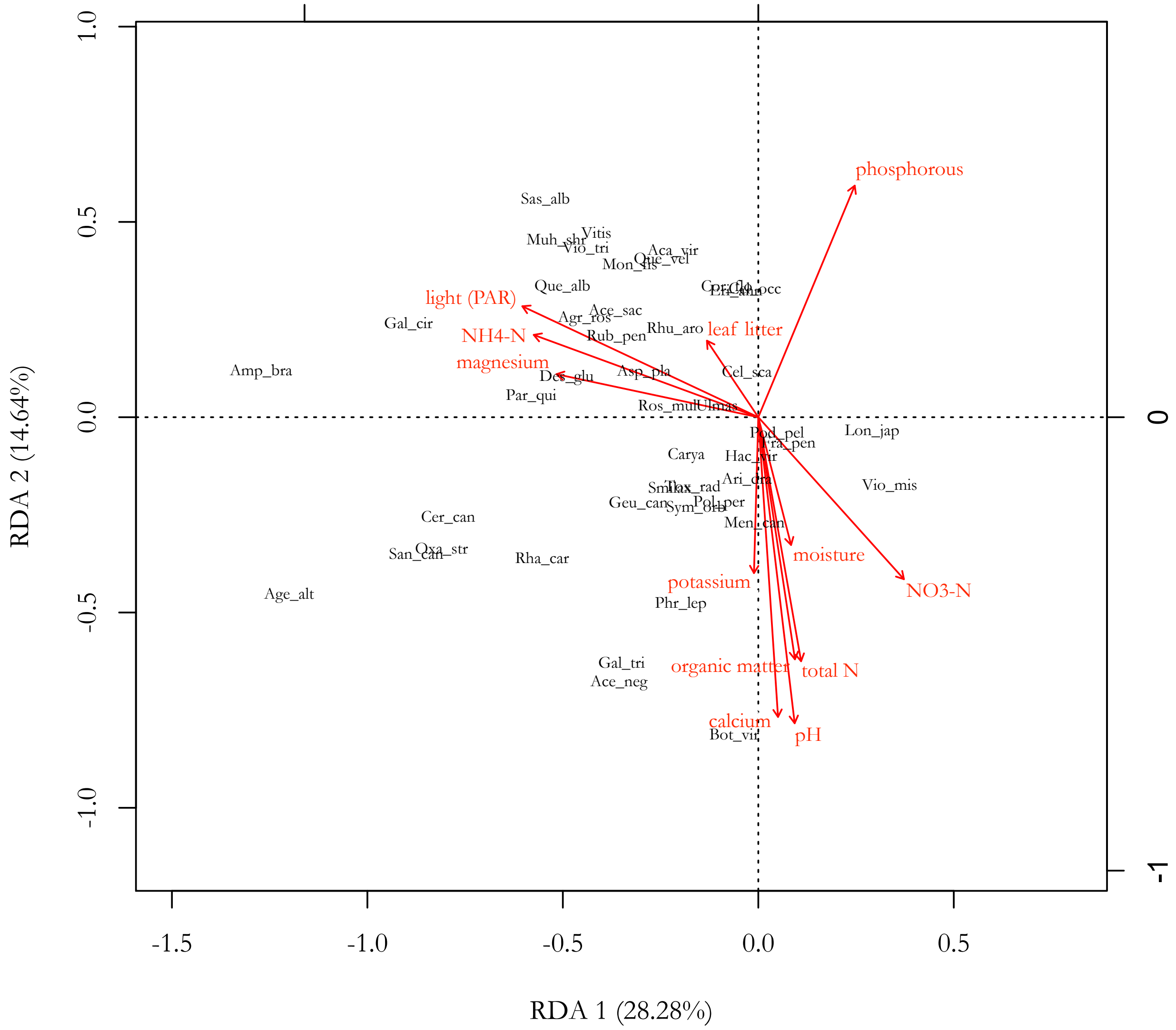


Figure 4.5. Negative relationship between species' ordination scores for RDA axis 1 and (A) local uninvaded abundance and (B) the change in local abundance in the presence of *Lonicera maackii*, calculated using *equation 1*. In 'B,' a larger effect size equates to a larger decline in abundance in the presence *L. maackii*. The abiotic variables that correlate with RDA ordination axis 1 are shown on the y-axis (also see Table 4.2, Fig. 4.4).

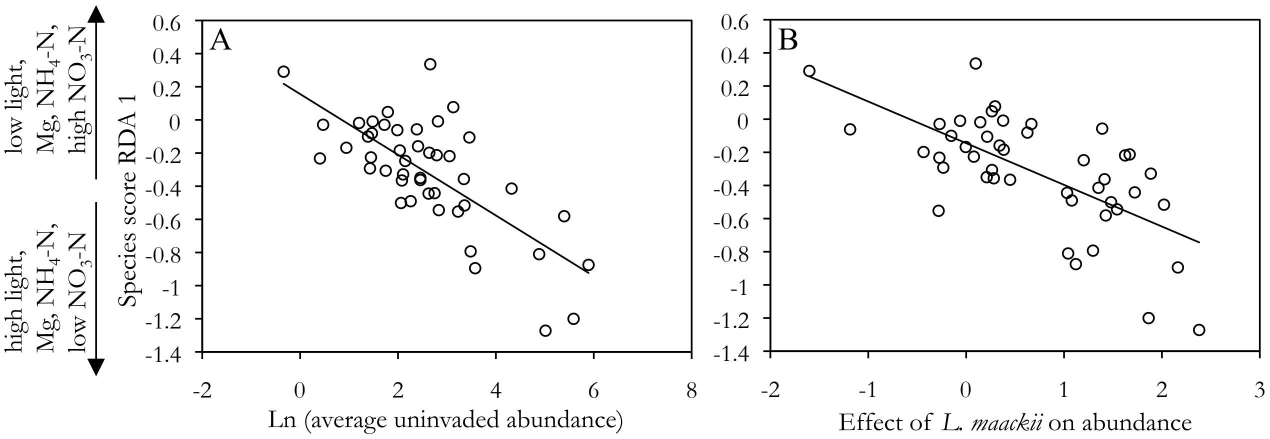
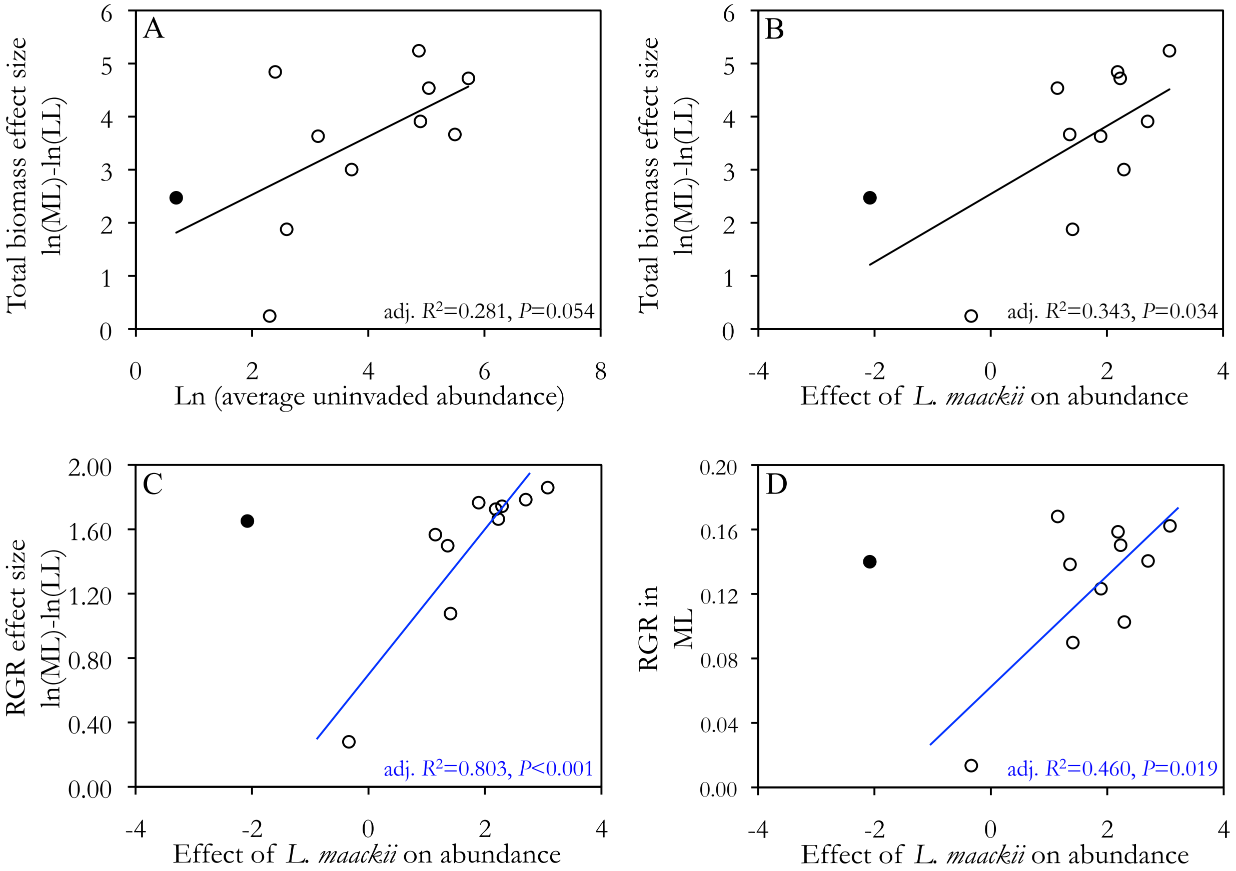


Figure 4.6. Positive relationship between plant fitness variables and species' abundances in the field. Dependent variables (y-axes) that are effect sizes are calculated as the natural log (ln) of the value in the medium-light treatment (ML) minus the value low-light treatment (LL). A larger effect size equates to a larger decline in the variable from the medium-light to low-light treatment. Lines represent significant least-squares regressions. The filled data point represents an outlier species, *Impatiens capensis*, in analyses on relative growth rate (RGR). The blue regression lines do not include the outlier.



CONCLUSIONS

The goal of this dissertation research was to integrate population- and community-level approaches to understand the effects of invasive plant species on biodiversity loss and extinction across spatial scales. I also investigated invasion-driven shifts in the abundance and population dynamics of common and rare species to understand longer-term extinction dynamics of native plants. Using meta-analyses and plant surveys, I first established that there was a scale-dependent relationship between invasive plant species and their effects on biodiversity loss. Invasive plants had smaller effects on biodiversity loss with increasing spatial scale. I then used simulation models, population demography, and experimental manipulations to determine the patterns and mechanisms by which invasive plants cause these scale-dependent biodiversity patterns and shifts in species composition.

Prior to my dissertation research, there was anecdotal evidence that suggested scale-dependent effects of invasive plants (Sax and Gaines 2008, Stohlgren et al. 2008, Vilà et al. 2011). My meta-analysis provided a quantitative test and confirmed that invasive plant species have scale-dependent effects on biodiversity. Despite a large amount of variation in the studies used in the meta-analysis (i.e., differences in invasive species growth form, habitat type, pre-invasion biodiversity levels, etc.), I found a scale-dependent signal of biodiversity loss. My dissertation, and recent research on landscape heterogeneity and meta-population dynamics, are among the few studies that investigate extinction from invasive plants across multiple spatial scales (Jackson 2005, Michelan et al. 2010, Gilbert and Levine 2013).

I drew from community ecology theory to make generalizable predications about how invasive plants affect communities across spatial scales. I first surveyed pairs of uninvaded and invaded plant communities. I showed that even when invasive plants are dominant across the study area (>90% cover), they cause smaller proportional declines in biodiversity at broader spatial scales. This is consistent with the findings of the meta-analysis. I classified the main patterns that underlie biodiversity loss (for a full description of the patterns, see the Introduction), and tested which pattern(s) caused scale-dependence. Neutral sampling effects (i.e., losses in the total number of individuals), which increase the rate of species accumulation in invaded communities, were the main cause of scale-dependent biodiversity loss.

Scale-dependence was not caused by shifts in the shape of the species-abundance distribution. However, species were being re-ranked in terms of their relative abundance. The rare species became relatively common, and common species became relatively rare. Thus, rare species, which were expected to go extinct at a faster rate than common species (if local abundance is the main determinant of extinction), are likely somewhat buffered against the high extinction rates that are expected when only taking sampling effects into account.

I tested the hypothesis that rare species have lower extinction rates than common species. I conducted case studies on the population dynamics of rare and common perennial herbs that co-occur with the exotic, mid-story forest shrub, *Lonicera maackii*. I found slow extinction trajectories, in which most rare species had stable or increasing population growth rates, even in *L. maackii*-dominated communities. Alternatively, most common species had declining population growth rates in *L. maackii*-dominated communities. All species' population growth rates declined in the presence of *L. maackii*, therefore decreasing the probability of long-term native plant persistence.

My results are optimistic and support the hypothesis that native plant extinctions are slow, which allows time to successfully restore invaded habitats.

Though my demographic study is the most comprehensive demographic work on the effects of an invasive plant on native population dynamics, it is important to note that many species, both common and rare, had too few individuals to conduct demographic monitoring. Low population sizes will increase stochastic extinction probabilities, and my results may be a conservative estimate of rates of plant population declines. In addition, recent work suggests that common and rare species have fundamentally different population dynamics, in which rare species have strong self-limitation and are able to persist despite low population sizes (Comita et al. 2010, Yenni et al. 2012). In the case of *L. maackii* invasions, common species experience the largest declines in population sizes. If common species are less able to tolerate stochastic extinction dynamics at low population sizes, their extinction rates could be higher than my demographic study suggests.

I further explored the mechanisms by which the abundance and population growth of native species decline in invaded habitats. I characterized the environmental conditions in uninvaded and invaded, *L. maackii* habitats. Light was the main abiotic variable that differed between habitat types. Light declines in invaded habitats because of shading by *L. maackii*'s dense leaf canopy. Field observations and a greenhouse experiment confirmed that common species were more associated with high-light conditions and lost more biomass than rare species when grown in low-light conditions. Thus, it is likely that light patterns drive differential effects on the abundance and population growth of common and rare species. Aboveground removal of *L. maackii*, and re-seeding of locally extirpated common species, should have high rates of success in invaded habitat restorations.

This dissertation addressed the controversial argument about the severity of the effect of invasive plant species on biodiversity loss (Davis et al. 2011). I found that a lack of plant extinctions at broad spatial scales is expected based on how invasive plants alter community structure. In addition, larger negative effects on common compared to rare species support the hypothesis that extinction debts, or lag-times in global extinctions, will take a long amount of time to manifest. Overall, this dissertation provides a framework to understand the current trajectory of plant extinctions, as well as prevent future extinctions. This framework is not specific to biodiversity maintenance in the presence of invasive species, and it can be applied to understand the patterns that underlie biodiversity loss caused by other anthropogenic forces, such as climate change and habitat loss. Future studies that investigate the patterns that underlie scale-dependent biodiversity loss, including sampling effects, species abundances, and species distributions, should explore scenarios that will help generalize the effects of invaders on biodiversity that I find in this dissertation, including exploration of different invaded habitat types, regional species pool sizes, and changing disturbance regimes.

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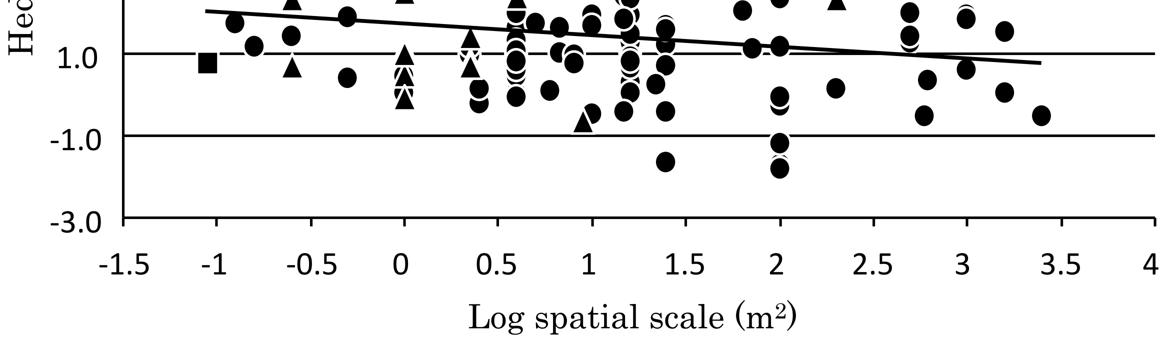
APPENDIX 1

Supplementary text and figures for Chapter 1

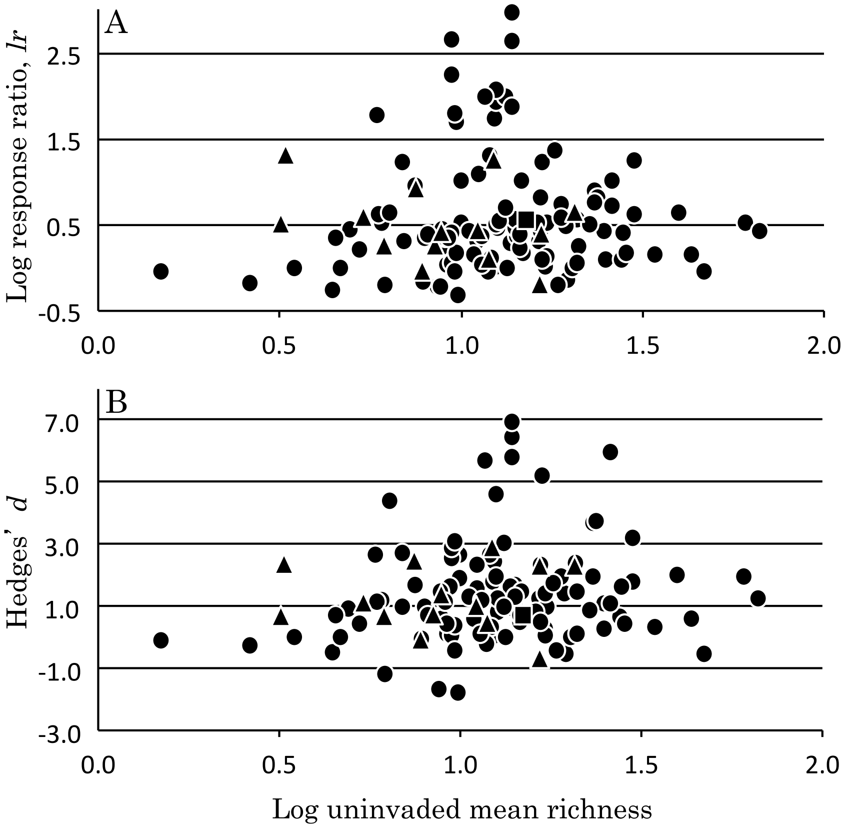
Relationship with Hedges' *d*:

Figure A1.1. In addition to the log ratio response (*lr*) of the loss of species richness between invaded versus uninvaded plots, there was a weak, yet significant, negative relationship between log spatial scale (m²) and Hedges' *d*, a standardized mean difference and unbiased effect size (see below). Hedges' $d = \frac{(\overline{X}^U - \overline{X}^I)}{S} J$, where $\overline{X}$ is mean species richness for uninvaded (U) and invaded (I) plots, *S* is the pooled standard deviation, and *J* is to correct for bias ($J = 1 - \frac{3}{4(N^U + N^I - 2) - 1}$, where *N* is sample size)). We used a weighted, mixed-model regression where each point represents a case study of invasive species' effects at the plot level. The fitted regression line includes all study types, including observational (i.e., comparing plots with and without invaders) and experimental (i.e., removal and addition) studies (n=125, $Q_{regression}$=9.18, r^2=.05, slope=-0.34, P=0.002). Circles represent observational studies, triangles represent removal studies, and squares represent addition studies.



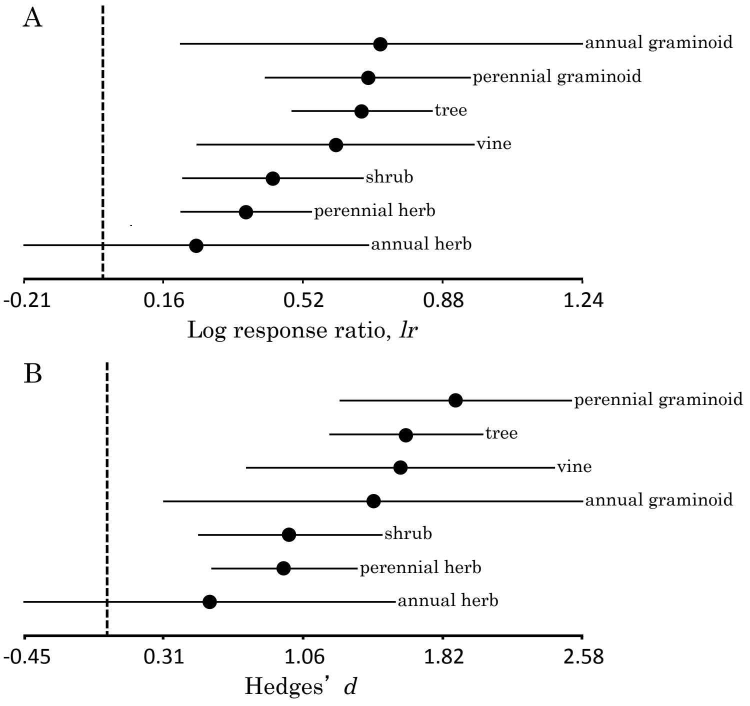
Relationship with Initial, Uninvaded Species Richness:

Figure A1.2. We tested whether there was a relationship between *lr* or Hedges' *d* and the initial species richness (logged to reach assumptions of normality) of the uninvaded plot. There was no significant relationship between effect size and uninvaded species richness (see below). We used weighted, mixed-model regressions where each point represents a case study of invasive species' effects at the plot level. We included observational (i.e., comparing plots with and without invaders) and experimental (i.e., removal and addition) studies (n=125; *lr*: $Q_{regression}=0.48$, $P=0.490$; Hedges' *d*: $Q_{regression}=3.47$, $P=0.063$). Circles represent observational studies, triangles represent removal studies, and squares represent addition studies.



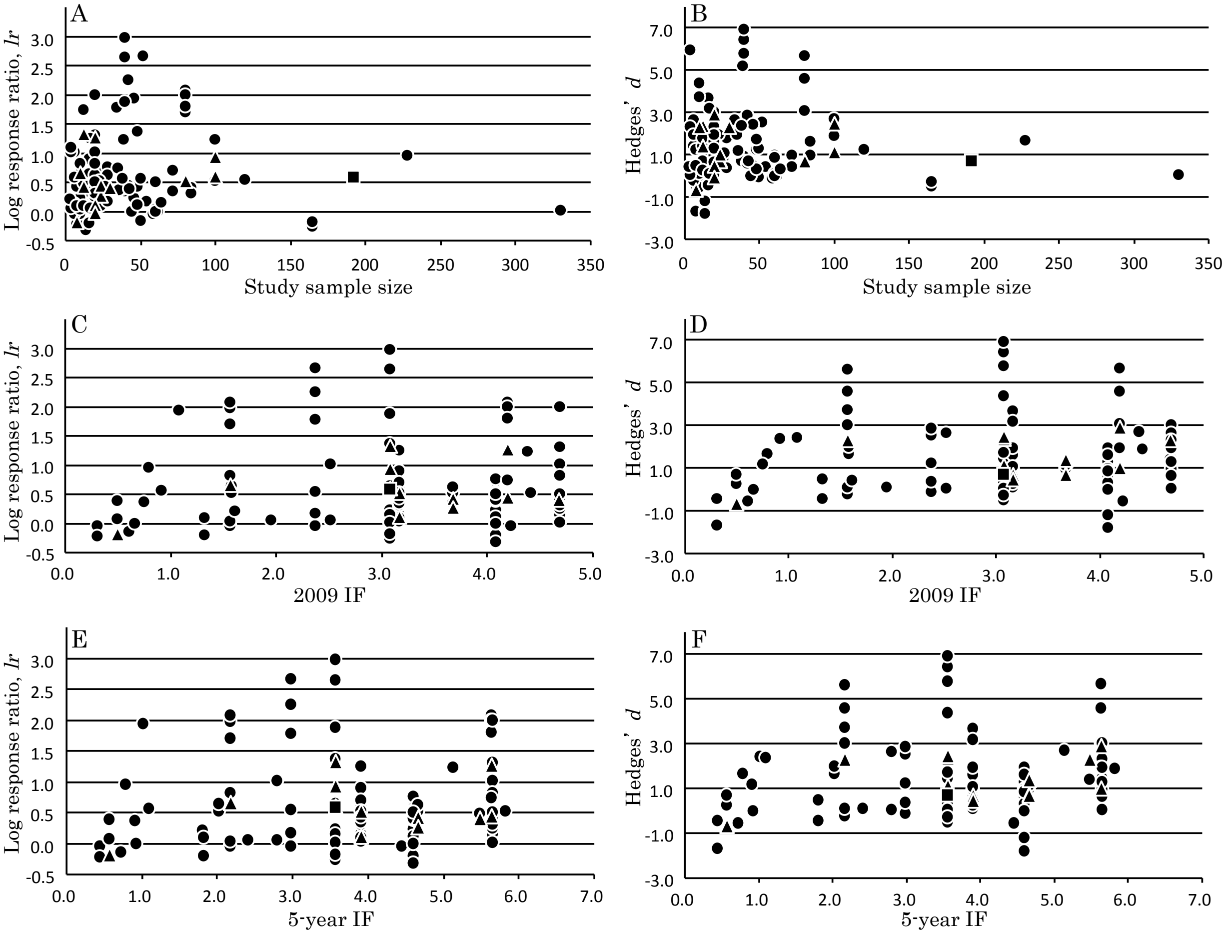
Relationship with Focal Invasive Species Growth Form:

Figure A1.3. We also tested whether growth form could explain variation across studies in the effect sizes of loss of species richness. We tested whether there was a relationship between *lr* (A) or Hedges' *d* (B) across growth forms of the focal invasive species. We excluded studies that included multiple invaders of multiple growth forms. There was high variation in effect sizes for each growth form category and no significant relationship between *lr* across growth forms. There was significant variation in Hedges' *d* across growth forms, in which perennial graminoids had the largest negative effect on species richness and annual herbs the weakest effect (see below). We used weighted, mixed-models (categorical); each point represents the mean effect size for a growth form surrounded by 95% bias-corrected bootsrapped CIs. We included observational (i.e., comparing plots with and without invaders) and experimental (i.e., removal and addition) studies (n=122; *lr*: Q_b=9.84, *P*=0.131; Hedges' *d*: $Q_{regression}$=12.57, *P*=0.050).



Publication Bias:

Figure A1.4. There were no signals of publication bias when plotting either effect size against (1) sample size of each study, in which a funnel-shaped distribution was found as expected under no publication bias (Palmer, 1999) (A-B), or (2) 2009 (C-D) and 5-year (E-F) average impact factors (IF) of the publication journal of each study using the ISI Journal Citation Report (JCR) (2009 IF *lr*: $Q_{regression}=0.25$, $P=0.614$; 5-year IF, *lr*: $Q_{regression}=1.27$, $P=0.260$; 2009 IF, Hedges' *d*: $Q_{regression}=0.180$, $P=0.671$; 5-year IF, Hedges' *d*: $Q_{regression}=1.358$, $P=0.244$).



APPENDIX 2

Supplementary text and figures for Chapter 2

Methods

Species-Area Relationship Data

To evaluate the scale-dependent effects of each plant invader on species richness, we collected data in 2009 and 2010 in Florida, Missouri, and Hawai'i, U.S. In Florida, data were collected at sites within Highlands Hammock State Park in Sebring, Florida, U.S. In Missouri, data were collected at four parks in the St. Louis Metropolitan area, including Shaw Nature Reserve, Forest 44 Conservation Area, August A. Busch Conservation Area, and Cliff Cave County Park. In Hawai'i, data were collected at sites within Hawai'i Volcanoes National Park on the Big Island of Hawai'i. At each location, we identified three to four sites, each consisting of one uninvaded and one plant-invaded community (3 locations x 3 or 4 sites/location x 2 communities/site = 20 total communities). Communities were chosen based on the location of invasion fronts of the pertinent plant invader, in which the invader was dominant in the plant-invaded community (>90% cover), and present but not dominant in the uninvaded community. Invasion fronts were ideal for pairing adjacent uninvaded and plant-invaded communities in order to minimize potential environmental differences between communities, with the exception of the presence of the plant invader. In each community, we collected data on understory plant species richness from 1 to 500 m^2 using a nested plot sampling design (Fig. A2.1, Fridley et al. 2005). All data were collected and analyzed using a paired sampling design. Original data for species richness and area are available on Dryad (doi:10.5061/dryad.qq08m).

In addition, in order to tease apart possible mechanisms underlying differences in the slope of the species-area relationship (z), we collected data on the abundance of each species in 50 evenly spaced 1-m^2 plots in each of the 20 communities. All individuals in each plot were counted and identified. Since all data in 50 1-m^2 plots were collected at a slightly later time than species-area relationship data, there were small differences in total number of species in the species-area relationship and species-abundance distribution data.

Species Aggregation Analyses

We evaluated the role of aggregation (spatial dispersion) in causing shifts in the slope (z) of the species-area relationship. For example, if native species are significantly aggregated before a plant invasion due to heterogeneous resource conditions and/or frequency-dependent interactions, the presence of a dominant invader might decrease resource heterogeneity and reduce species aggregation. Alternatively, if native species have some refuge within a heterogeneous community where the influence of invasive species is less intense, the native community would become more aggregated after invasion. If plant-invaded communities experience consistent changes in species aggregation compared to corresponding uninvaded communities, aggregation could contribute to the observed increases in z. We measured aggregation by comparing the area under the curve between rarefaction (non-spatially explicit) and accumulation (spatially explicit) curves [modified from Collins and Simberloff (2009)].

For each community, we simulated 1000 rarefaction curves by randomizing individuals within and among the 50 data plots, keeping the simulated and observed number of individuals per plot consistent. Accumulation curves were calculated by accumulating individuals as they were spatially observed in the empirical dataset. We obtained 50 accumulation curves per community, starting the collecting at each of the 50 plots and sequentially adding the nearest plot based on Euclidean distances.

We used rarefaction bias to measure the degree of aggregation in each community. Clumping among individuals within a species as well as clumping among species can contribute to the rate of species accumulation; rarefaction bias is an ideal metric of aggregation because it takes within- and among-species aggregation into account.

Rarefaction bias was calculated as the difference in area under the curves between the mean rarefaction and accumulation curves, standardized by the number of individuals in the community. A smaller bias in plant-invaded communities compared to the corresponding uninvaded communities would indicate that invaded communities are less aggregated relative to uninvaded communities. For further details, see Collins and Simberloff (2009). We also compared the mean accumulation curve to the 95 percentile confidence intervals of the rarefaction curves to look for significant differences in spatial dispersion from random. We found no significant differences in bias between uninvaded and invaded sites. In addition, we found no consistent trends in deviations of accumulation curves from random. The majority of accumulation curves fell within the 95 percentile confidence intervals of the corresponding 1000 species rarefaction curves (Fig. A2.4). Four sites show deviations of accumulation curves from random. At two Missouri and one Florida site (Fig. A2.4D, A2.4G, A2.4I), accumulation curves of invaded communities fall below the lower 95 percentile confidence intervals of the corresponding species rarefaction curves, indicating that invaded communities were more aggregated than the paired, uninvaded community.

Species could accumulate faster in uninvaded habitats relative to invaded habitats at larger spatial extents if rare species were proportionately more aggregated ('clumped') at scales greater than 500 m^2 in the uninvaded relative to invaded habitats. To test this, we increased the spatial scale of our original analyses to encompass the replicate plots in each ecosystem. Analyses at these broader spatial extents confirm and extend our original results, showing less proportional loss of species in the invaded communities relative to the uninvaded communities at spatial extents 3-4 times the size of our original study (Fig. A2.5).

Partitioning the Mechanisms Contributing to Changes in the Slope of the Species-Area Relationship (z)

We created a null model to dissect the relative influence of neutral sampling effects, the shape of the species abundance distribution (SAD), and species extirpations on changes in the slope of the species-area relationship (z). For each site, we used the same SAD data used for aggregation analyses, collected in paired, uninvaded and invaded communities. Using this abundance data, we simulated the species-area relationships of the 50, 1-m^2 plots to decompose the difference in slope observed between invaded and uninvaded communities into three components: neutral sampling effects due to a loss of individuals in invaded communities, changes in the shape of the SAD in invaded communities, and species extirpations in invaded communities, beyond those caused by sampling effects. Data were simulated using additive species-area relationships, though we saw the same general patterns in z as observed in the nested, 500-m^2 data.

Each pair of communities required four simulations to decompose the main mechanisms that drive z; the parameters used in each simulation are listed in Table A2.1. We fit a log-series distribution ($Y=(-1/\log(1-c)) * c^X/X$) to the ranked species abundances for each community to estimate the coefficient, c, that best described the relationship between relative abundance and species' rank. In simulation one, we created the species-area curve for the uninvaded community using the total number of individuals and the relative abundance of each species as described by the log-series distribution in the uninvaded community. We randomly filled 50 plots based on the number of individuals per plot in the observed data. In simulation two, we repeated this process for the invaded community, using the total number of individuals and relative abundance of species in the invaded community to randomly fill 50 plots. In simulation three, we generated a species-area curve using the total number of individuals and relative abundance of species in the invaded community. However, we removed the effects of additional species extirpations by assuming that the number of species observed at the broadest spatial scale was equivalent to the uninvaded community. In the fourth simulation, we generated a species-area curve using the relative abundance of species for the invaded community, but removed the effect of species extirpations and the sampling effect by using the total number of individuals and species observed at the broadest spatial scale for the uninvaded community (Table A2.1). We replicated each simulation 1000 times, calculated the mean species-area curve and log-log species-area relationship slope (*z*) for each simulation.

The contribution of the neutral sampling effect, the shape of the species abundance distribution, and species extirpations were computed by subtracting the slopes calculated from the four simulations in the following ways: the contribution of the neutral sampling effect was calculated as the slope of simulation three minus simulation four; the contribution of the shape of the species abundance distribution was calculated as simulation four minus simulation one; the contribution of species extirpations was calculated as simulation two minus simulation three (Table A2.1).

Species Abundance Distribution Data and Analyses

Using the same 50 1-m^2 plot data collected for analyses of species aggregation and changes in slope (*z*), we used a null model approach to evaluate the effects of plant invaders on species' abundances at each site. By using a null model, we could evaluate the deviation in the abundance of each species (in an invaded community) from the abundance expected from a neutral sampling effect alone. Deviations from the null model generally represents a stronger or weaker competitive effect of a plant invader on a particular species. Only species found in the uninvaded communities were incorporated into the null model as a conservative estimate of the effects of invaders on common versus rare species; including all species would have further strengthened the result that the abundance of rare species is less affected than the abundance of common species. For each uninvaded community, we calculated the relative species abundance distribution. Using this relative abundance distribution, we drew the number of individuals found in the paired plant-invaded community (see Table 2.1). We simulated these random draws 1000 times for each site to calculate an expected absolute species abundance distribution for the plant-invaded community, surrounded by 95 percentile confidence intervals. We then compared simulated, null model values to observed abundances in the empirical data. We repeated this process for each of the 10 locations across the United States (Table 2.1, Fig. A2.6).

We calculated the deviation of observed abundances in the plant-invaded communities from simulated, expected values based on our null model using methods similar to Chase et al. (2011). We summed the number of observed abundances that were greater than the simulated, expected abundances of each species, as well as one-half the simulated abundances equal to the observed abundance. The summed value was divided by 1000 and standardized from -1 to 1. A value of -1 is a scenario in which the observed abundance fell below all simulated abundances, and reveals a larger negative effect of the plant invader on a species than expected from a sampling effect alone. A value of 1 represents a scenario in which the observed abundance was above all simulated abundances, and reveals a smaller effect of the plant invader than expected from a sampling effect alone. The distribution of deviations for rarer species is non-normal, which is a result of the shape of the species abundance distribution. When species are rare, it becomes more likely that observed abundances fall at the extremes of the distribution of expected abundances, creating a non-normal distribution of deviations. We analyzed each site using a Kendall's rank correlation to compare the relationship between species abundance in the uninvaded community and the deviation from expected abundances in the invaded community.

Literature Cited

Chase, J. M., N. J. B. Kraft, K. G. Smith, M. Vellend, B. D. Inouye. 2011. Using null models to disentangle variation in community dissimilarity from variation in α-diversity. Ecosphere 2:1-11.

Collins, M. D., D. Simberloff. 2009. Rarefaction and nonrandom spatial dispersion patterns. Environmental and Ecological Statistics 16:89-103.

Fridley, J. D., R. K. Peet, T. R. Wentworth, P. S. White. 2005. Connecting fine- and broad-scale species-area relationships of southeastern U.S. flora. Ecology 86:1172-1177.

Table A2.1. Parameters used for each simulation to dissect mechanisms contributing to changes in the slope of the species-area relationship (*z*). Parameters were calculated from uninvaded and invaded communities using data from 50 1-m^2 plots. Simulations 1 and 2 represent observed species-area relationships, without the effects of aggregation, while simulations 3 and 4 change various parameters to test the role of neutral sampling effects (number of individuals), the shape of the species abundance distribution, and species extirpations in changes in *z*. The contribution of neutral sampling effects was calculated by subtracting the slope (*z*) of simulation 3 and 4. The contribution of the shape of the species abundance distribution was calculated by subtracting the slope (*z*) of simulation 4 and 1. The contribution of species extirpations was calculated by subtracting the slope (*z*) of simulation 2 and 3.

	Uninvaded community parameters			Invaded community parameters		
Simulation	# of individuals	shape of the SAD (using a log-series distribution)	# of species	# of individuals	shape of the SAD (using a log-series distribution)	# of species
1	✓	✓	✓			
2				✓	✓	✓
3			✓	✓	✓	
4	✓		✓		✓	

Figure A2.1. Species-area relationship sampling design. Nested-plot, vegetative sampling design from 1 to 500 m^2. Six additional 1-m^2 plots were collected within the 500-m^2 plots for ample replication at the smallest spatial scale.

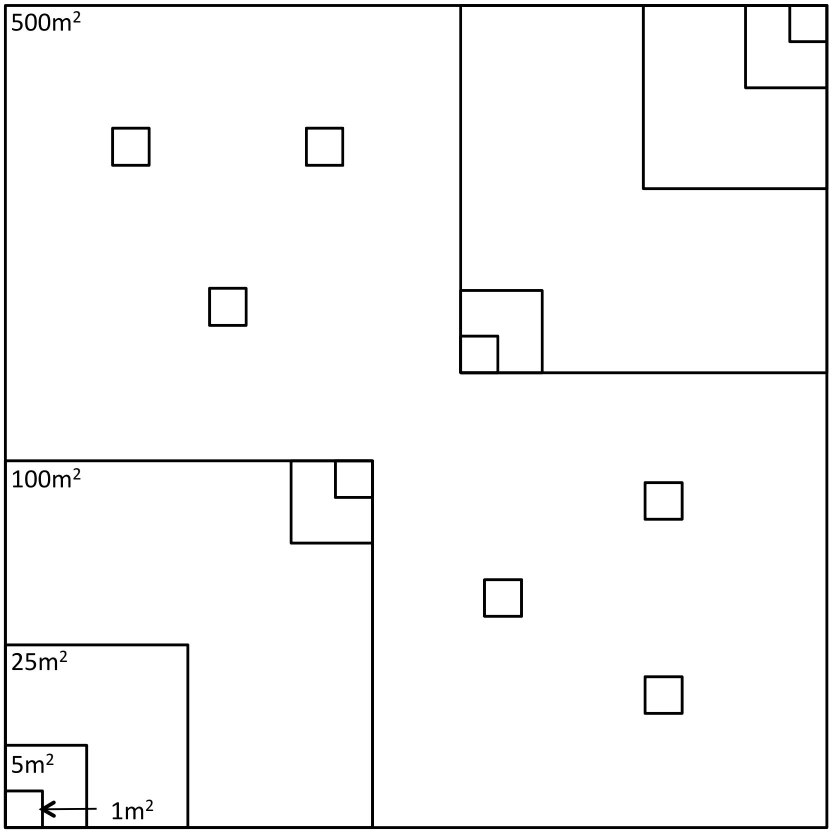


Figure A2.2. Species-area relationships for each site. Depiction of the 9 logged species-area relationships from Hawai'i (A-C), Missouri (D-G), and Florida (H-I), United States. The remaining site is shown in Fig. 2.1A. All sites show an increase in the slope (*z*) and decrease in the intercept (*c*) of the logged species-area relationship in plant-invaded compared to uninvaded communities.

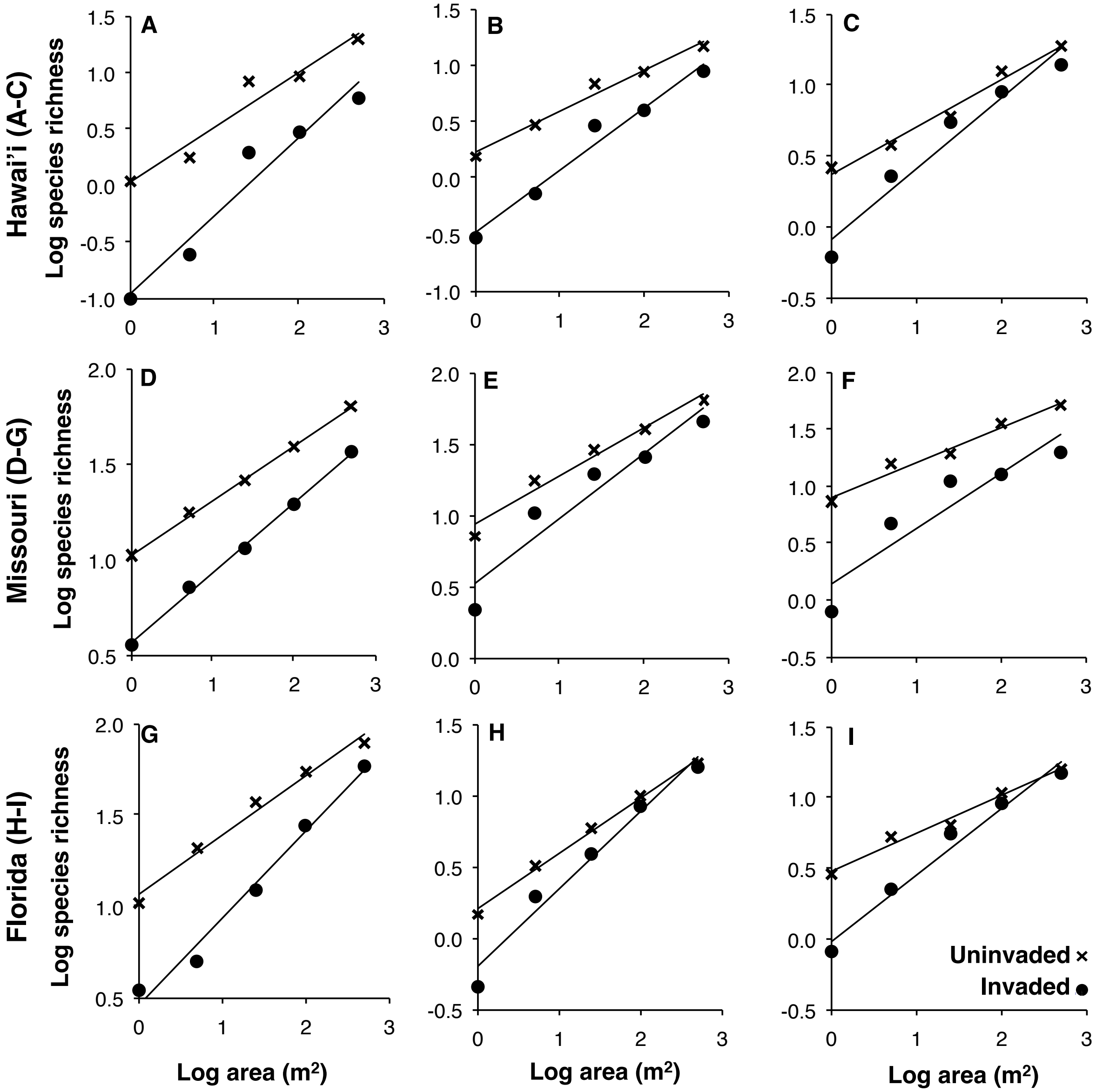


Figure A2.3. Invaders' scale-dependent effects on species richness. Declining relationship between the loss of species richness and the spatial scale at which it was measured, showing smaller losses in species richness with increasing spatial scale. Symbols represent different sites within each location (i.e., U.S. states).

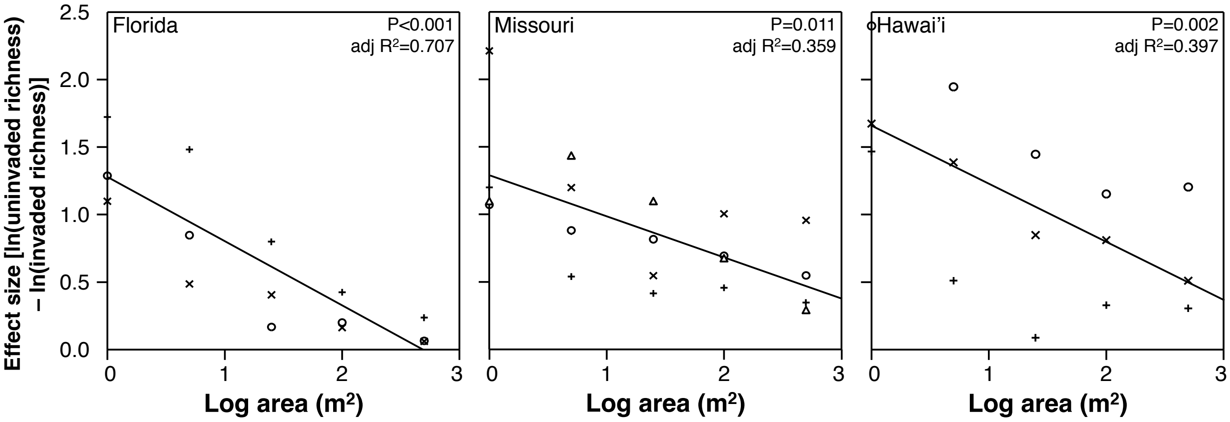


Figure A2.4. Spatially and non-spatially explicit abundance curves. Mean accumulation curves of uninvaded (black) and corresponding invaded (grey) communities, surrounded by the 95 percentile confidence intervals of the corresponding 1000 simulated species rarefaction curves. Each graph depicts one of the 10 sites in Hawai'i (A-C), Florida (D-F), and Missouri (G-J), United States. For each location (i.e., U.S. state), sites are presented in numerical order, as shown in Table 2.1. The majority of graphs show the spatially explicit, mean accumulation curve falling within the 95 percentile confidence intervals of the non-spatially explicit rarefaction curves.

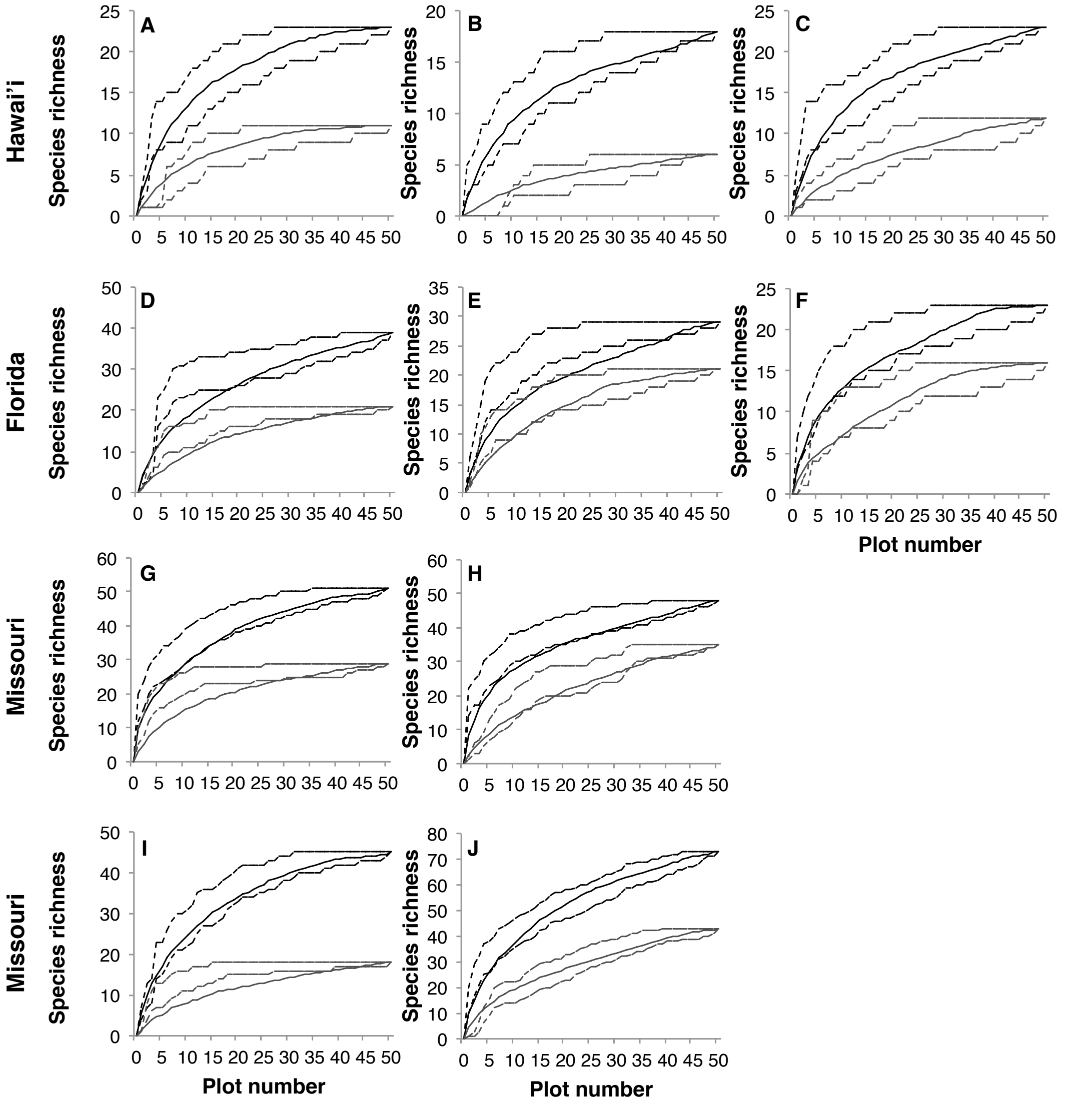


Figure A2.5. Log-log Species-Area Relationships (SARs) for each invasive plant, combined across all sites sampled for each invader in (A) Hawai'i for *Morella faya*, (B) Missouri for *Lonicera maackii*, and (C) Florida for *Dianella ensifolia*. Combining data across sites shows a consistent decrease in the intercept (*c*) and increase in the slope (*z*) of the SAR in invaded communities up to scales of 1500m^2 (in Hawai'i and Florida) and 2000m^2 (in Missouri). This result is consistent with our original result that invasive plants cause smaller proportional declines in species richness with increasing spatial scale (Fig. 2.1 and Fig. A2.2).

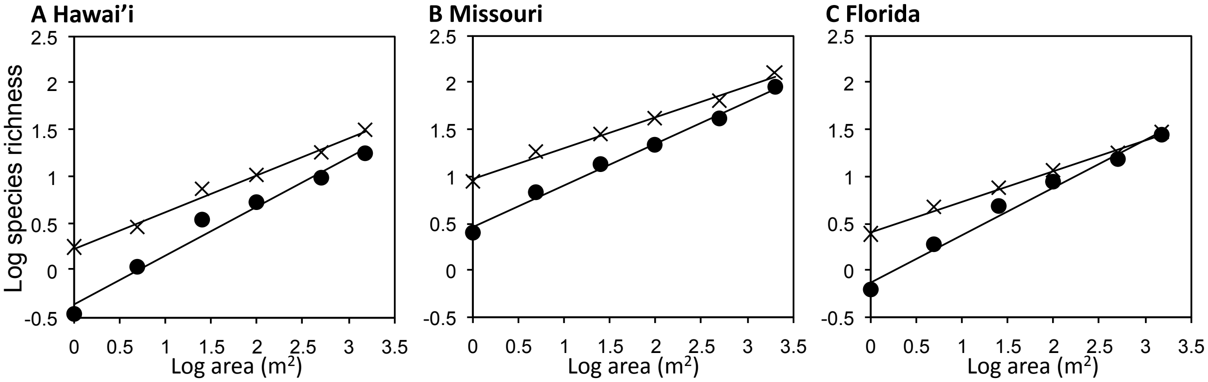
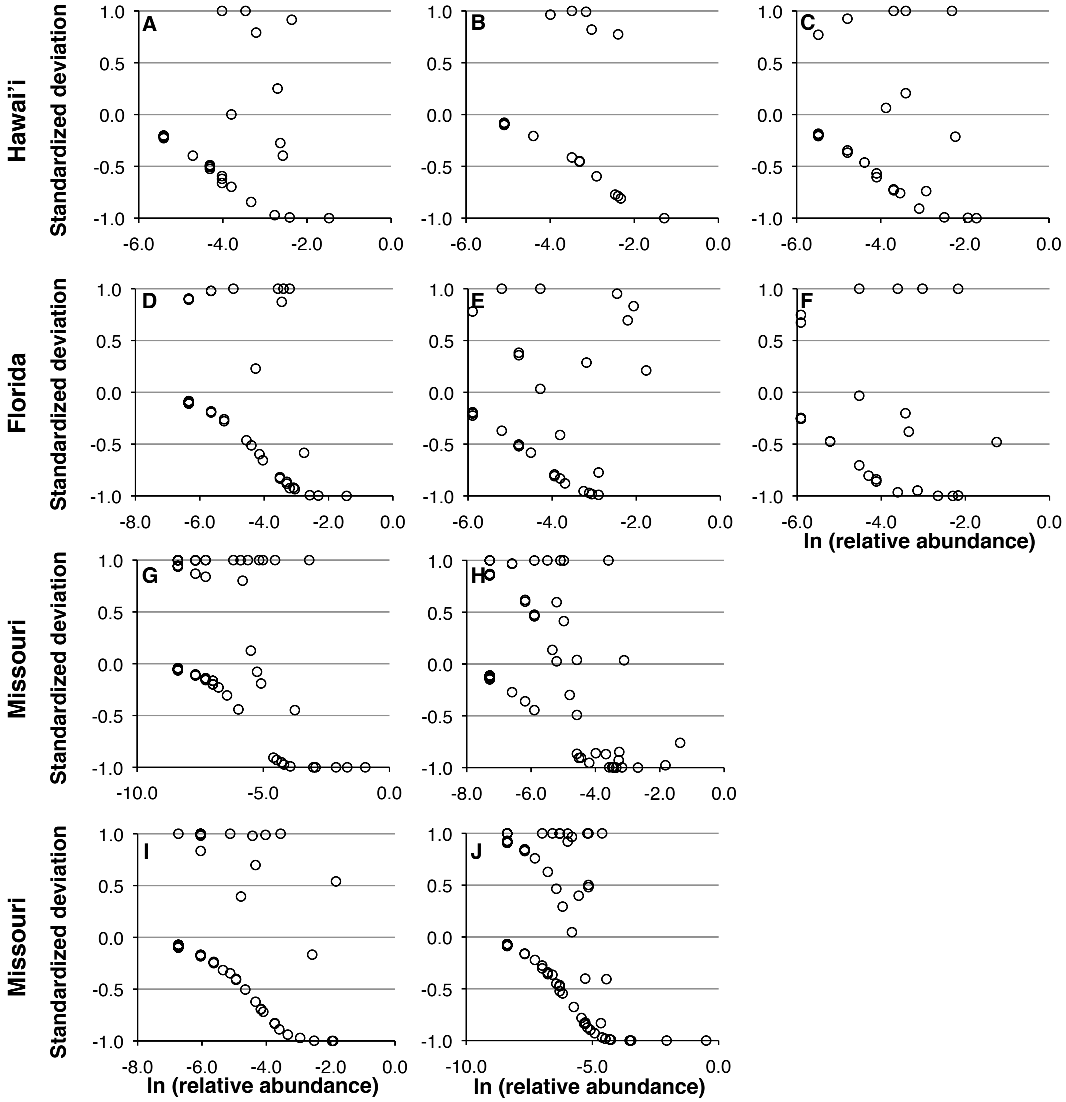


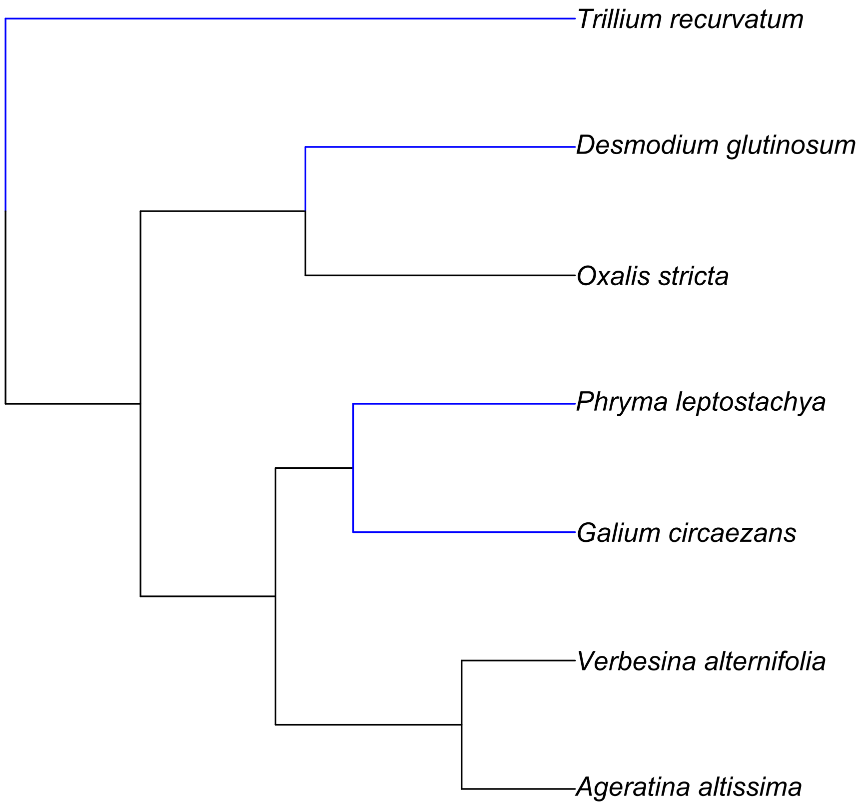
Figure A2.6. Species' deviations from neutral sampling effects. Depiction of the relationship between species abundance and deviations from the null model, standardized from -1 to 1, of all 10 sites from Hawai'i (A-C), Florida (D-F), and Missouri (G-J), United States. For each location (i.e., U.S. state), sites are presented in numerical order, as shown in Table 2.1. All sites show a negative rank correlation between species abundance in the uninvaded community and the magnitude of deviation from abundance in the invaded community expected from a sampling effect, revealing that commoner species tended to deviate more negatively from expected abundances than rarer species.



APPENDIX 3

Supplementary text and figures for Chapter 3

Figure A3.1. Dendrogram representing the taxonomic relationships among the species we monitored in the demographic experiment (see Table 3.1). Blue lines indicate locally rare species and black lines indicate locally common species. Relationships were calculated with PHYLOMATIC v3 (http://phylodiversity.net/phylomatic/), which uses a megatree database constructed from published phylogenies (Phylomatic tree v R20120829) to infer species relationships.



APPENDIX 4

Supplementary text and figures for Chapter 4

Figure A4.1. Dendrogram representing the taxonomic relationships among the species used in the shade greenhouse experiment. Blue lines indicate locally rare species and black lines indicate locally common species (see Table 4.1). Relationships were calculated with PHYLOMATIC v3 (http://phylodiversity.net/phylomatic/), which uses a megatree database constructed from published phylogenies (Phylomatic tree v R20120829) to infer species relationships.