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To the Graduate Council:

I am submitting herewith a dissertation written by Sara Elizabeth Kuebbing entitled "Impacts and Implications of Co-occurring Invasive Plant Species." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Daniel Simberloff, Major Professor

We have read this dissertation and recommend its acceptance:

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Impacts and Implications of Co-occurring Invasive Plant Species

**A Dissertation Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville**

**Sara Elizabeth Kuebbing
May 2014**

DEDICATION

To Josh.

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ABSTRACT

The anthropogenic spread of species is a potent form of global change that impacts the population dynamics of native species, the composition of native communities, and the functioning of ecosystems. As the reorganization of species around the globe continues unabated, there is an increasing likelihood that habitats will contain co-occurring invaders. In this dissertation, I emphasize the need to study co-occurring invasive plants by juxtaposing the relative occurrence of multiple versus single invasive plants in important conservation habitats to the relative occurrence of published studies that consider the impacts of single versus multiple invasive plants. I found that over two-thirds of conservation habitats are multiply invaded while less than one-third of studies consider the impacts of co-occurring invaders and only 6% of studies focused on invasive plant interactions. To address this conservation-research mismatch, I use an observational study of the above- and belowground impacts of two co-occurring invasive woody plants among plots containing both shrubs, each species singly, or lacking both species. I found that subdominant invasive plant richness in plots with both invaders was twice as high as in plots with either invader singly and that β [beta]-glucosidase activity, a carbon-degrading extracellular soil enzyme, was three times greater than in control plots. These findings indicate that co-occurring invaders can have additive and non-additive effects compared to when they are found singly. Next, using a greenhouse experiment, I asked how interactions within native and nonnative plant communities affected their response to species gains and losses. I constructed phylogenetically paired native and nonnative plant communities that varied in species richness and measured above- and belowground productivity and seedling establishment of woody species. I found that native and nonnative plant communities differed in their overall biomass allocation patterns, the mechanisms driving community response to species losses, and the receptivity of communities to species gains. Overall, my work implies that the impacts of co-occurring invasive plant species are not necessarily predictable based upon single-invader impacts or interactions of closely related native species.

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INTRODUCTION

A Global Reorganization of Species

Both historically and currently, humans are responsible for the dramatic reorganization of species around the globe. Sometimes species are intentionally deposited into new ranges for agriculture, forestry, horticulture, or aesthetics (Crosby 1986, Mack *et al.* 2000, Reichard & White 2001, Lockwood *et al.* 2007). Other species are moved unintentionally, as hitchhikers on plants, animals, produce, packaging crates and material, or transportation vessels (Mack 2003, Lockwood *et al.* 2007). These species that have been transported by humans across fundamental geographic barriers are considered “nonnative” to their new range (Richardson *et al.* 2011). Not all nonnative species are able to survive after relocation and some nonnative species do not establish in their nonnative range due to disease, low population densities, or unfavorable climates (Zenni and Nuñez, 2013). The nonnative species that survive and form naturalized, self-sustaining populations in their nonnative range are termed “alien,” “exotic,” or “nonnative” species. A subset of these nonnative species will not only persist in the new environment but rapidly expand in population density and range, many times great distances from the parental population, to become what ecologists have termed “invasive species” (Richardson *et al.* 2011).

The movement of species from native to nonnative ranges has led to inevitable and irreversible changes in nearly every ecosystem and region of the globe (Mooney and Hobbs 2000). Invader impacts are numerous and range from the ecological to evolutionary to economic (Vilà *et al.* 2011, Simberloff *et al.* 2013, Pyšek *et al.* 2012). Invader impacts have been outlined as occurring at five levels—individual, genetic, population, community, and ecosystem—and have been documented, to various degrees, for each level and across taxa (Parker *et al.* 1999). Invasive species have been implicated as a leading cause of extinction (Clavero and García-Berthou 2005), drivers of major shifts in ecosystem functioning (Vitousek *et al.* 1987, Ehrenfeld 2010, Nuñez *et al.* 2010, Simberloff 2011), and a vast economic drain (Pimentel *et al.* 2005).

Co-occurring Invasive Plant Species

The movement of invasive species, both aquatic and terrestrial, is linked with global trade activity and volume (Mack 2003) and, thus, the number of species introduced to new regions of the globe is increasing (Ruiz and Carlton 2003, Perrings *et al.* 2010). An obvious consequence of this continued flow of species is that there are few regions of the globe that do not contain nonnative species (Mooney and Hobbs 2000) and many regions and habitats are comprised of a notable proportion of nonnative species (Lockwood *et al.* 2001, Pyšek and Richardson 2006, Montserrat *et al.* 2007, Chytrý *et al.* 2008a, Chytrý *et al.* 2008b). The actual or relative number of nonnative species coexisting within a habitat is termed its “level of invasion” (Chytrý *et al.* 2008a) and habitats vary greatly in the average level of invasion (Chytrý *et al.* 2008b; Catford *et al.* 2012).

Habitats with high levels of invasion necessarily contain multiple invasive species and thus it is pertinent for studies to address the interactions and impacts of co-occurring invaders. Currently, there is limited research on this topic. Of the 29 leading invasion biology hypotheses, only one, invasional meltdown, explicitly considers the implications of interactions among two or more nonnative species (Catford *et al.*, 2009). The invasional meltdown hypothesis emphasizes the potential significance of positive nonnative interactions, suggesting that facilitation between nonnative species can increase the expansion of populations or the per capita effect of each species (Simberloff & Von Holle, 1999). A classic example of facilitation between two invasive species is the spread of the nitrogen-fixing plant *Morella faya* (previously *Myrica faya*) into nitrogen-limited, young volcanic sites on the Hawaiian islands. *Morella faya* increased available nitrogen levels in the soils, thus providing a more nutrient-rich environment for other invasive species (Vitousek *et al.* 1987).

The consequences and significance of co-occurring invaders is not wholly absent from the invasion literature, though it has yet to be comprehensively synthesized since the notion of “invasional meltdowns” emerged (Simberloff, 2006). For example, many authors have introduced terminology relating to the oft-noted phenomenon that the decline in one nonnative species population leads to a rapid increase of another

nonnative plant, which indicates competitive interactions among nonnative plants may be common. This phenomenon has earned many titles including: “invasion treadmill” (Thomas & Reid, 2007), “secondary invasion” (Pearson & Ortega, 2009), and “surprise effects” (Caut *et al.*, 2009). Other authors have coined terms to describe differences in the competitive ability of co-occurring invaders, including “strong” (Ortega & Pearson, 2005) and “dominant” (MacDougall & Turkington, 2005) nonnative plants. Likewise, the term “invasional interference” is the proposed antithesis to “invasional meltdown”, where the performance of an nonnative species is reduced when it co-occurs with another invader, thus reducing their overall impact when they co-occur (Yang *et al.*, 2011; Rauschert & Shea, 2012). Though this terminology is dispersed throughout the literature and no single term or set of terms has yet to gain traction, these authors all underline the importance of studying co-occurring nonnative species.

Dissertation Outline

My dissertation is focused on understanding the community and ecosystem consequences of co-occurring invasive plant species. I use observational and greenhouse manipulations in forested and old-field plant communities to address how invasive plants interact and how these interactions might influence invader impacts.

In Chapter 1, I reviewed the published literature and a comprehensive conservation management database (The Nature Conservancy’s Conservation Projects) to juxtapose how common co-occurring invasive plants are found in conservation habitats to how often academic studies on invasive plant impacts focus on single versus multiple invasive plants. I found that only one-third of studies mentioned co-occurring invaders and only 6% of all studies analyzed invader interactions, while over two-thirds of conservation habitats were multiply invaded. This chapter emphasizes the applied importance of studying the impacts and interactions of co-occurring invasive plant species.

In Chapter 2, I used a field observation experiment to investigate differences in the aboveground and belowground impacts of two invasive woody shrubs, *Ligustrum sinense* (Chinese privet) and *Lonicera maackii* (bush honeysuckle), among plots containing both shrubs, each species singly, or lacking both species. I found that

subdominant invasive plant richness in plots with both woody invaders was twice as high as in plots with either invader singly and that β -glucosidase activity, a carbon-degrading extracellular soil enzyme, was three times greater than in control plots. These findings indicate that co-occurring invaders can have additive and non-additive effects compared to when they are found singly.

In Chapter 3, using a greenhouse experiment, I asked how interactions within native and nonnative plant communities affected their response to species gains and losses. I constructed phylogenetically paired native and nonnative plant communities that varied in species richness and resource availability and measured above- and belowground productivity and community invasibility by woody species. I found that native and nonnative plant communities differed in their overall biomass allocation strategies, the mechanisms driving community response to species losses, and the receptivity of communities to species gains. This work implies that these phylogenetically similar native and nonnative species do not have similar interactions, and that differences in interactions lead to difference in ecosystem impacts of co-occurring nonnative plant species.

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**CHAPTER I: CURRENT MISMATCH BETWEEN RESEARCH AND
CONSERVATION EFFORTS: THE NEED TO STUDY CO-OCCURRING
INVASIVE PLANT SPECIES**

A version of this chapter was originally published by Sara E. Kuebbing, Martin A. Nuñez, and Daniel Simberloff:

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SEK conducted the survey, analyzed the data, and wrote the first draft of the manuscript. DS and MAN contributed substantially to survey and manuscript revisions.

Abstract

Though biological invasion studies have proliferated in recent decades, a consistent emphasis remains on the study of single-species invasions. Here, we juxtapose the number of invasive plants reported as co-occurring within conservation habitats in one of the most comprehensive global conservation management databases (The Nature Conservancy's Conservation Projects) with the number of published studies that address impacts of co-occurring invasive plants. We reviewed 86 conservation projects and 153 peer-reviewed publications and found that only one-third of studies mentioned co-occurring invaders, although over two-thirds of habitats were multiply invaded, indicating researchers are more likely to study single invaders, even though conservation managers are more often faced with multiple invaders in a given habitat. Of those studies focused on multiple invasives, the majority did not attempt to differentiate impacts caused by species when found alone or with other invaders and instead either treated co-occurring invaders together as a single, undifferentiated group or compared impacts between invasive plant monocultures. Less than 6% of all studies analyzed invader interactions. The high prevalence of co-occurring invasive plants should encourage more research on multiple invaders, which may better inform prioritization of which species to manage. Specifically, we suggest research on how effects of multiple invaders differ from those of single invaders, what types of interactions (facilitative, competitive, neutral) are most commonly found between invaders, and what effects interactions might have on the overall impact (additive or non-additive) of the individual invader. Though we acknowledge the challenge of studying multiple invaders, there is a critical need to address these questions to make invasion research more relevant to conservation programs.

Introduction

Biological invasion research has burgeoned in the last few decades (Gurevitch et al., 2011; MacIsaac et al., 2011; Simberloff, 2011a), in part owing to growing recognition of negative ecological and economic impacts of invasive species (Mack et al., 2000; Pyšek and Richardson, 2010; Simberloff et al., 2013) and the shrinking of regions of the globe that remain substantially unaffected by invaders (Mooney and Hobbs, 2000).

Historically, the focus of much invasion research has been on factors that characterize impacts of invasive species in their non-native ranges, with a strong emphasis on single-species invasions (Davis, 2006; Simberloff, 2011a).

Some of the best-studied invasive taxa are plants (Parker et al., 1999). This focus on plants has advanced our understanding of many facets of invasion biology. We now have better trait-based models to predict which exotic plant species might become invasive (Rejmánek and Richardson, 1996; Ordonez et al., 2010; Castro-Díez et al., 2011), an improved sense of potential factors that may influence community susceptibility to invasion (Levine and D'Antonio, 1999; Davis et al., 2000; Fridley et al., 2007; Drenovsky et al., 2008, 2012; Simberloff, 2009), better understanding of which mechanisms may produce larger invasion impacts (Levine et al., 2003), and a rich catalogue of individual invader impacts that include those driving major shifts in ecosystem functioning (Ehrenfeld, 2010; Vitousek et al., 1987; Zavaleta, 2000) and draining national economies (Olson, 2006; Vilà et al., 2010; van Wilgen et al., 2002).

Like much of the invasion literature in general, most invasive plant research considers only single invasive species and ignores the presence of co-occurring invaders. The effects of singleton plant invaders on native communities and ecosystems can be wide-ranging. Invasive plants can disrupt pollinator visitation rates and seed set of native species by exploiting pollinator visits (Brown et al., 2002) or by creating shaded, unfavorable habitats for pollinators (McKinney and Goodell, 2010). Other invasive plants are allelopathic, disrupting mutualistic relationships and decreasing native plant growth rates (Stinson et al., 2006). Many invasive plants can affect nutrient cycling through changes in litter quality or root exudates (Ehrenfeld, 2010; Liao et al., 2008) or affect timing and intensity of natural fire regimes (Brooks et al., 2004;

D'Antonio and Vitousek, 1992). Sometimes invasive plants modify a habitat's structural components (Simberloff, 2011b), which can affect predation rates on native species (Schmidt and Whelan, 1999) or change food resource availability (Gosper, 2004).

Because the total number of species' introductions trends upward (Perrings et al., 2010; Ruiz and Carlton, 2003), the probability that multiple invasive species will co-occur in the same habitat should also be increasing, which would indicate a need to shift studies to include these co-occurring invaders. Furthermore, many invasion publications are couched in terms of providing helpful management information for mitigation of invader impacts. These studies may be less useful if the scenario they study—single invaders—is uncommon or the impacts of multiple invaders are non-additive.

While we have much evidence that single invaders can have notable impacts, we have limited knowledge of the effects of multiple co-existing invaders on communities and ecosystems. Broadly, impacts of co-occurring invasive species could be additive (i.e., the sum of the impacts of each invader individually) or non-additive, and this relationship might direct management of species when they co-occur. If the overall impact of multiple invaders is additive, then it might be easy to extrapolate from previous single-invader impact studies to predict what will happen when invaders co-occur. Non-additive impacts, however, will be less predictable because the presence of a second invasive plant might magnify (Simberloff, 2006; Simberloff and Von Holle, 1999) or mitigate the overall impact on the community.

Several previous publications have drawn attention to the need to focus research on understanding non-additive outcomes when multiple invasive species are present, primarily focused on mutualistic interactions among invaders (Crosby, 1986; Richardson et al., 2000). Simberloff and Von Holle (1999) coined the term “invasional meltdown,” which described how positive interactions among invaders would result when co-occurring invaders benefit from each others' presence, which might lead to an increase in magnitude of the invaders' impacts or an increase in the probability of their survival. These ideas have propagated research on multiple invasions, much of this focused on

co-occurring animal invasions and cases in which introduced animals interact with introduced plants (Green et al., 2011; Olesen et al., 2002).

Here we juxtapose data on how commonly co-occurring plant invaders are found within conservation habitats with data on how often invader impact studies address multiple invaders. We define invasive non-native species as those species transported by humans across fundamental biogeographical barriers that sustain self-replacing populations and have the potential to spread over long-distances in the novel non-native range (*sensu* Richardson et al., 2011). We focus on invasive non-native species because they tend to appear in higher abundances and densities than non-invasive non-natives and therefore are more likely to cause considerable impacts. We focus on conservation habitats because these properties are considered valuable sites in need of conservation, they are currently managed to reduce invasive plant species when these are present, and they represent a wide variety of habitat types. Finally, we review studies that address impacts of multiple invaders and identify research gaps that may hinder our understanding about biological invasions, especially when multiple invasive plant species co-occur.

Materials and Methods

To address questions concerning the likelihood of encountering multiple plant invaders in conservation habitats we used the Conservation Project Database (ConPro), which contains conservation projects from over 30 countries in 5 continents (see TNC, 2011 for a complete listing of projects by country) and is compiled and curated by The Nature Conservancy (TNC), one of the largest international conservation organizations. ConPro is one of the most complete listings of conservation projects worldwide and contains over 1100 international conservation projects managed by TNC and their partner organizations (TNC, 2007, 2011). Although not all countries are included in this database and some regions have more representation than others (e.g., the Americas have more projects than Asia), it has been successfully used as a source of information in other projects concerning broad conservation questions such as ours because it provides a large sample of conservation efforts that use the same methods for ranking and describing projects (Goldman et al., 2008; McDonald et al., 2009). For each project

listed in ConPro, TNC project leaders specified conservation targets (e.g., Ecological System, Single Species, or Species Assemblages) and threats to those targets (e.g., “Pollution”, “Climate Change & Severe Weather”, “Natural System Modification”, or “Invasive & Other Problematic Species & Genes”). Single projects in the database may contain multiple entries that vary in habitat type, conservation target, and/or threat. Conservation targets and threats were categorized by an IUCN-CMP threat classification scheme (Salafsky et al., 2008; TNC, 2007).

We extracted all entries from the database that listed invasive species as a conservation threat. Beginning with over 4500 entries, because invasive species are by far the most commonly listed threat (J. Fisher, personal communication), we refined this list to 1700 entries that met the following criteria: (1) conservation threats that specified invasive non-native terrestrial plant species (i.e., excluding invasive animals or aquatic plants), and (2) conservation targets that specified habitat-based target types (i.e., plant species assemblages or ecological systems). We further refined this list to contain only entries that specified the invasive plant species of concern ($N = 137$). These restrictions insured that we counted only “invasive plant threats” that co-occurred within the same habitat. To obtain more detailed information on database listings, we queried an additional 106 public project managers (in English and their mother tongues) for more specific data concerning which particular invasive plant(s) threatened listed conservation targets and if those species were found adjacent to one another (n.b., the ConPro database comprises public entries, which can be reviewed online (TNC, 2011), and more sensitive private projects whose details are not available online). A second question provided additional confirmation that managers were listing co-occurring invasive plant species. We received answers from 43 (41%) of project leaders. This survey increased the dataset to 311 entries, detailing 86 conservation projects, for which we could identify the habitat type and specific plant invader(s) of concern. Once we refined the subset of entries, we identified the number of invasive species for each threat listing. Number of invasive species was scored from 1 to 5 species and entries with more than 5 invasives listed were combined into a 6+ category.

The ConPro database aims to collect information on conservation projects globally and reports these projects in a systematic fashion. Because this database collects information on projects from developing and developed nations, there may be inherent biases stemming from organizational and managerial differences between cultures (Nuñez and Pauchard, 2010). Understanding this limitation, we argue that the ConPro database provides us with the unique opportunity to systematically survey habitats globally. Finally, ConPro is not an exhaustive list of all nonnative species within a conservation project, but instead a list of species considered “threats” to listed conservation targets. We can therefore be confident that our analysis of listed invasive plant threats represents only those nonnative, invasive plant species that conservation practitioners consider of management concern.

To assess how often plant invasion impact studies considered more than one invasive species, we queried the database Web of Science (v. 5.2 Thomson Reuters 2011) for all published articles in the past 5 years (2006–2011) using the search terms from Simberloff and Von Holle’s (1999) previous literature search on invader–invader interactions: ‘species AND inva* OR introduced OR alien OR exotic OR non-native OR non-indigenous’. We used these search terms because they have been used in previous invasion literature reviews as reliable terms for locating published material on non-native species research. However, because the number of invasive-related articles has increased nearly 5-fold in the past decade (Simberloff and Von Holle (1999) found over 5000 articles with these search terms; we found over 27,000), we added the additional search terms ‘AND plant AND impact’ to mimic the results from the previous search on invasion in natural habitats and to filter some articles that were likely to be irrelevant. This reduced the database size to 1692 articles. Again, following the protocol of Simberloff and Von Holle (1999), we then selected the database articles published in the 12 journals that had the highest total number of invader publications. One journal, *Biological Invasions*, had triple the amount of articles of each of the other top 11 journals. Each of the remaining journals (*Biological Conservation*, *Biological Control*, *Diversity and Distributions*, *Ecological Applications*, *Ecology*, *Forest Ecology and Management*, *Journal of Applied Ecology*, *Journal of Ecology*, *Oecologia*, *Plant*

Ecology, and Restoration Ecology) had at least double the number of articles of any other single journal within the database. This literature search produced an incomplete sample of publications on the impact of invasive plants. Nevertheless, because our aim was to assess how commonly plant invasion impact studies address multiple invasive plants, we believe this survey is an appropriate sample of ecological studies for our question. We examined 562 articles from these 12 journals and found 153 articles that specifically considered plant invasion impacts that included observation and experimental studies in field or greenhouse settings. From these articles, we assessed the number of plant invaders the authors studied and recorded the species, habitat types where the study took place, and whether the authors considered invader–invader interactions. We acknowledge that this literature search has limitations. For example, relevant papers may be published in other journals or the grey literature, or our keywords may not be ideal to capture all the research on this topic (Fazey et al., 2005). However, we believe this search allows an adequate assessment of current scientific work on invasive species and speaks towards our goal of assessing the relative publication rates of research on single and multiple invaders.

To compare the results obtained from the managers in the ConPro database and what is published in the literature on the topic, we compared the distribution of observed values with the distribution of expected values with a G-test, an alternative to Pearson's chi-square test that is appropriate for observational studies that do not assign observations a priori to each category (i.e., a Model I design; Gotelli and Ellison, 2004). For our purposes, we compared the distribution of single versus multiple invasive plant impact studies in the published literature to the distribution of single versus multiple invasive plant reports in the ConPro database.

Results

An overwhelming 69% (N = 214) of entries from the ConPro database were concerned with more than one invasive plant species in a single habitat (Fig. 1.1). For multiple invasions, the reported number of invasive species per habitat ranged from 2 to 12 with a median of 3, and the mean number of invasive species was 4.27 ± 2.44 SD. Looking within those entries concerned only with single-species invaders (31% of the total; N =

97), we see that 47% (N = 42) of the listed invaders were grasses. The graminoid giant reed (*Phragmites australis*) (N = 12) and cheatgrass (*Bromus tectorum*) (N = 12) were especially likely to be cited as solo invaders. When we sorted entries by habitat type, forest and wetland habitats tended to have multiple species of concern (>75% of entries were for multiple invasions), while littoral communities were more likely to report only a single problematic invader (>75% of entries were for single invasions). We should interpret these habitat susceptibility patterns cautiously because the conservation projects are not a random or stratified sample of natural habitat types and may reflect a bias towards some ecosystems, but they support previous findings that there is great variability in invasibility across habitat types. Invasions in the literature.

Of the 153 published articles we analyzed that studied plant invasion impacts, only 31.4% (N = 48) considered more than one plant species in their studies (Fig. 1.1). These results contrast with what we found in conservation areas. The number of species studied in surveyed publications with multiple invaders ranged from 2 to 14 with a median of 3; the mean number of invasive species was 3.98 ± 3.02 SD. The G-test detected significant differences between observations of single and multiple invaders in the literature and analogous reports in the ConPro database ($G = 115.343$, $p < 0.0001$), showing that the published literature is significantly more likely to consist of studies on single invaders while conservation managers are more likely to report multiple invaders of concern.

Over three-fourths (N = 39) of the published articles that focused on multiple species did not specifically address how impacts between single and multiple invasive plants might differ. One large subset (33.3%; N = 16) of multiple-invader studies compared how monospecific stands of different invasive plants affected particular response variables (such as native plant diversity or soil nutrient properties). Another subset (47.9%; N = 23) acknowledged the presence of multiple invasive species within a study system and manipulated the invasive community as an entire unit or homogeneous group (i.e., plots with all invasive plants or plots with no invasive plants). These two types of studies will inform our understanding of multiple invader impacts only if impacts are additive. The remainder of the multiple invasive species publications

(19%, N = 9, constituting only 6% of the total studies) explicitly tested for interactions between co-occurring invasive plant species. One reported a facilitative interaction, three reported neutral interactions, and five reported competitive interactions (Table I.1).

Across all invasion-impact studies, focus was heavily on invasive plants found in forest (25%, N = 39) and grassland (23%, N = 36) habitats. Forest invasion studies were primarily focused on single invasive species (82%, N = 32), whereas grassland studies were almost evenly split between those on single (52%, N = 16) and multiple (48%, N = 20) invaders.

Discussion

Evident mismatch between invasion research and conservation management

These results show that when invasive plants are present in conservation habitats, it is more common to find multiple, rather than single, species covered by conservation projects. This pattern contrasts with current research activity, which focuses primarily on effects of single species. Invasion biologists have begun to address issues surrounding multiple invaders in terms of ‘levels of invasion’; for example, documenting the wide variability in invasion level (Chytrý et al., 2008a) and quantifying consistent metrics for measuring invasion level in terms of abundance, evenness, and richness of invasives (Catford et al., 2012). However, while studies indicate that some habitats have high levels of invasion, we still have limited knowledge of the effects of multiple co-existing invaders on communities and ecosystems. We suggest that the prevalence of co-occurring invasive plant species should encourage more multiple-species plant invasion studies that address three interrelated, but distinct, questions. Below we outline these three avenues of future research and how they might better inform management practices.

Are multiple plant invader impacts additive or non-additive?

Distinguishing between additive and non-additive impacts of invaders will be important for management of sites with multiple invaders. For example, two common forest invaders in the eastern United States are garlic mustard (*Alliaria petiolata*) and

Japanese stiltgrass (*Microstegium vimineum*). Both species are reported to reduce native herbaceous species biomass when found alone (Flory and Clay, 2010; Rodgers et al., 2008). However, in forests where both species co-occur (Fig. I.2) we do not know the species' combined impacts on understory plants. If multiple invader impacts are additive, their overall impact should be predictable—the sum of their individual impacts—and a manager can more easily extrapolate from single-invader impact studies to predict how management will change the co-occurring invaders' overall impact. If *A. petiolata* and *M. vimineum* have additive impacts, treatment of only one species should allow a fraction of the understory plant community to recover, based upon the impact of either species singly. The majority of multiple invader studies we reviewed either compared impacts between monocultures of multiple invasive species or lumped all non-native species together in one group (Fig. I.1). If invader impacts are additive, then these comparative and total removal experiments will help in predicting what to expect when species' co-occur.

Multiple invasive species may also have non-additive impacts, and thus the impact of multiple invaders may be greater or less than the impact of either invader in isolation and cannot be predicted based on the impact of each species in isolation. For example, it is possible that *A. petiolata*, an invader whose biomass is greatest in the early spring and summer, and *M. vimineum*, an invader whose biomass is greatest in the late fall, will cause a non-additive decrease in native ground cover because their greatest impacts do not overlap temporally and we might see a greater decrease of the understory plant community. Managers currently have no tools to assess how adding or removing an invader will impact the native community or ecosystem when impacts are non-additive (Zavaleta et al., 2001), and only studies that compare single and multiple invasion scenarios will allow sound prediction of the overall impact of co-occurring invaders (for example, Rauschert and Shea, 2012).

What types of interactions are most common among invasive plants?

Based upon the invader interaction studies we found, we outline the three broad types of interactions we might expect to see when invasive plants co-occur, how these

interactions fit into contemporary invasion theory, and possible management recommendations these interactions would suggest (Table I.1).

Facilitative interactions

Facilitative interactions arise when one invader promotes the invasion or increases the fitness of the other. One scenario could be a case of “invasional meltdown,” in which the presence of multiple invasive species increases the probability of survival and spread over that of any single invader (Simberloff and Von Holle, 1999). In our search we found only a single study that indicated the growth of an invasive plant was increased when it was growing near other invasive plants (Cushman et al., 2011). Other studies have shown plant invaders can create more favorable environments for the establishment of new invaders through soil nutrient modification (Fisher et al., 2006; Vitousek et al., 1987) or nurse plant effects (Tecco et al., 2007).

If facilitative interactions lead to non-additive impacts, this could indicate an important prioritization consideration for invasive plant management. A central question in predicting invasions is whether non-native species act as “drivers” or “passengers” of community change (MacDougall and Turkington, 2005). As drivers, invaders are hypothesized to enter intact and undisturbed habitats and cause notable effects on native species. As passengers, invaders enter degraded habitats that have already lost native diversity and thus are not the direct cause of diversity declines. However, if habitats contain multiple invasive species then this question widens to what role do previous invaders play in facilitating further invasion? Scenarios of ecosystem “hijacking” could occur in which an invader enters a community as a “passenger” but subsequently modifies the community, “driving” future invasions. Ecosystem “hijacking” may have important conservation implications. Such a phenomenon would suggest that if managers can reduce disturbance and prevent the first invader from entering a community, then future invasions may not occur.

Competitive interactions

Competitive interactions comprised the majority of invader-invader interaction studies we reviewed (Callaway et al., 2006; Jäger et al., 2009; Pfeifer-Meister et al., 2008; Rudgers and Orr, 2009; Schmidt et al., 2008). Other studies show that some invasive

plants can restrict the growth of other invasive plants through competition for light, space, or other limiting resources (Belote and Weltzin, 2006; Rice and Nagy, 2000; Tecco et al., 2007) and that interactions with co-occurring native species can moderate this competition (Metlen, 2010). Competition among non-natives may help explain the observed pattern of decline of some populations (Simberloff and Gibbons, 2004) when one invasive species replaces another (Jäger et al., 2009; Morrison et al., 2007). This apparent natural succession may not be due to the suggested transient nature of biological invasions (Davis et al., 2001) but rather to specific invader–invader interactions.

If interactions between invasive plants are commonly competitive, this information could be critical for decisions of how and when to manage for invasive populations. Competitive interactions might be particularly relevant in habitats that have a numerically dominant ‘strong’ invader and fewer individuals of ‘weak’ invaders (Ortega and Pearson, 2005). Management strategies in these instances may choose to focus on the more abundant invader, but if this is competitively suppressing other invasives, management of only the ‘strong’ invaders may result in a release of secondary invaders, or acceleration of “invasion succession” to a different invasive plant (Loo et al., 2009; Ortega and Pearson, 2010). Thus, if the removal of one species leads to the re-invasion of a site by another invader, management schemes would need to incorporate this possibility and adequately prepare for secondary invasions (Ruscoe et al., 2011). Likewise, if the impact of the primary invader is deemed less harmful than the future impacts of a suppressed invader, managers with limited resources might decide to forgo management of the former plant population until enough resources are available to treat both populations.

Neutral interactions

Though competitive and facilitative interactions among plant invaders have been documented, we cannot assume there will always be strong interactions between co-occurring invaders. A last possible scenario is that interactions among invaders are neutral or weak; we found this situation in three examples (Cushman and Gaffney, 2010; Milton et al., 2007; Shaben and Myers, 2010). However, interactions might differ

between life stages of the plant (Tecco et al., 2006, 2007), based on presence of native species (Metlen, 2010), or under changing environmental contexts (Besaw et al., 2011).

How do invader interactions affect the overall impact of a species?

We currently have limited knowledge on how overall impacts of multiple invaders differ from those of single invaders, which seems a critical lacuna in light of the evidence that co-occurring invaders are common. Understanding differences in impact and management between multiple and single invasions will arise, in part, through better understanding of interactions between invaders. It is necessary to remember, however, that the direction of invader–invader interactions may not lead to an obvious overall impact on the native community. For example, even when species compete by having different but substantial negative effects on the native community, they may have still more detrimental effects together than in isolation, since low-density species can still exert significant effects (Peltzer et al., 2009). Building a larger body of case studies on co-occurring invasive plant species would be prudent, because our limited results restrict our ability to suggest whether any of these scenarios is a rule or an exception, whether invasive plants might tend to interact in certain directions, and how temporal or spatial variability of invasions might moderate interactions.

How researchers and managers can adapt to multiple invader scenarios

Though we acknowledge the challenges to studying multiple invaders, especially in field settings, we feel there is a critical need to begin addressing this issue. The many cited studies in this manuscript provide an excellent framework for applicable methods, including observational, field manipulation, or greenhouse experiments on how to address these questions. Observational studies can confirm if certain patterns of co-occurrence among invaders exist and experimental research can begin to decipher mechanisms of interactions. The large body of research on single-invader impacts has allowed researchers to use meta-analytic techniques to compare impacts of invaders on single species, communities, and ecosystem processes (Liao et al., 2008; Vilà et al., 2011), but we seem to lack a comprehensive set of studies on cases of multiple invasions for similar analyses.

Though there is less research on the impacts and interactions of multiple invasive species, managers should adapt management plans to encompass co-occurring invaders; probably many are already doing so. Because limiting resources typically constrain management budgets, managers must decide which habitats to target and, under multiple invasion scenarios, which species within these habitats they should manage. One recommendation that could arise from this study is that if the costs associated with managing additional invasive species are low (e.g., both invasives respond to the same treatment, such as co-occurring woody shrubs; Fig. 1.2), managers should target all invasive species. Where this is feasible, management strategies should avoid treating only the ‘strong’ invaders, because as mentioned above, removal of dominant invaders may lead to the release of secondary invaders or propel “invasion succession”. If limited resources prevent managers from targeting multiple species, then specific knowledge of the impacts and interaction of co-occurring species would be essential to prioritizing management, but unfortunately this is likely to be context-specific for the habitat type and co-occurring species at that location. However, if information on the particular invasive species is not available (either in the published literature or through management networks), then managers could conduct trial removal experiments in which they treat smaller areas to assess how management of single invasive species is likely to affect outcomes when multiple species are present. Alternatively, gathering information on the effect of single-species removal in comparable habitats could provide precious information on the management of multiple invaders.

Conclusions

Overall, our data show a disconnect between what is occurring in many conservation habitats and what is typically published in the invasion biology literature. This suggests that application of current invasion theory and research for conservation purposes might be pertinent only for practitioners dealing with single invader scenarios, or where the co-occurring invasive species have non-interactive additive effects. The divergence between research and on-the-ground needs has been recognized for many areas of invasion biology, where scientific research rarely translates into useable management

practices (Hulme, 2003; Papeş et al., 2011). This issue mirrors, but is distinct from, the acknowledged “knowing-doing” gap in conservation (Knight et al., 2008) and invasion (Esler et al., 2010) research. Mismatches between research and conservation reality—a “not-knowing-doing” gap—might be just as significant a hindrance to effective conservation. This insight has important implications for how we currently study plant invasions and, potentially more importantly, how relevant scientific results may be for those managing invasive plant populations.

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Appendix

Table I.1. Three potential outcomes of interactions of co-occurring invasive plants, where they fit into current invasion biology paradigms, and published examples of each.

Scenario	Facilitative	Neutral	Competitive
	Invasive plants exacerbate the impact of the other invasive plants	Invasive plant species do not interact or have weak, inconsequential interactions with each other	Invasive plant species reduce the impact (via reducing fitness or population density) of other invasive species
Examples of theoretical framework	<i>Invasional meltdown</i> (Simberloff, 2006; Simberloff and Von Holle, 1999)	Standard invasion hypotheses including <i>propagule pressure</i> (Simberloff, 2009), <i>enemy release</i> (Keane and Crawley, 2002), <i>evolution of increased competitive ability</i> (EICA) (Blossey and Nötzold, 1995), or <i>fluctuating resources</i> (Davis et al., 2000) which assume the characteristics of the invading plant or invaded ecosystem trump all other biotic interactions	Non-typical cases of <i>biotic resistance</i> (Elton, 1958) where existing invasive plant(s), as part of the local community, resist invasion. When <i>novel weapons</i> (Callaway and Aschehoug, 2000) of one plant invader may negatively affect another plant invader that is native to a different region from the first
Possible management strategies and goals	Keep invasive plant richness low. Identify the species that promote other plant invasions and target them for management	Do not need to make special management recommendations. Invasive plant populations can be treated individually, with no presumed effect on populations of other invasive species	Removing one invasive plant may trigger the invasion of another, relatively rare, invader. If certain invasive plants prevent establishment or decrease fitness of other invaders, managers may choose to allow those populations to persist and focus on other invasive issues. Need to identify which of the co-occurring invasive species have the most negative effects on the other invaders but the least effects on the target native community

Table I.I. Continued

Scenario	Facilitative	Neutral	Competitive
Published examples from our literature search	(1) Invasive grass, <i>Ehrharta calycina</i> , grows more frequently in association with invasive shrub, <i>Carpobrotus edulis</i> and invasive grass <i>Ammophila arenaria</i> (and native <i>Baccharis pilularis</i>); proposed mechanism is invader released from herbivory when growing in close proximity to these other invaders (Cushman et al., 2011)	(1) Two common riparian invaders, <i>Arundo donax</i> and <i>Vinca major</i> , decrease native plant community richness, abundance and seedling performance when found in monoculture or in mixture patches (Cushman and Gaffney, 2010) (2) The canopy of the invasive tree <i>Prosopis</i> spp. was no more likely to harbor exotic fleshy-fruited species than the native tree <i>Acacia tortilis</i> in a South African savanna. Instead, distance from host/source plant was most important in determining exotic plant presence (Milton et al., 2007) (3) In a greenhouse competition experiment, the invasive shrub <i>Cytisus scoparius</i> did not impact the growth of the invasive grass <i>Dactylis glomerata</i> (Shaben and Myers, 2010)	(1) The invasive grass <i>Avena barbata</i> reduced biomass of <i>Centaurea solstitialis</i> when grown together in a greenhouse competition experiment. Likewise, <i>A. barbata</i> biomass decreased when <i>C. solstitialis</i> leaves were clipped (Callaway et al., 2006) (2) The spread of the shrub invader <i>Cinchona pubescens</i> on Santa Cruz Island, Galapagos was negatively correlated with the presences of the invasive herb <i>Stachys agraria</i> ; when <i>C. pubescens</i> populations decreased, the two invaders <i>S. agraria</i> and invasive shrub <i>Psidium guajava</i> cover increased (Jäger et al., 2009) (3) In a greenhouse competition experiment the invasive grass <i>Lolium multiflorum</i> decreased biomass of the invasive grass <i>Schedonorus arundinaceus</i> across moisture and nutrient treatments (Pfeifer-Meister et al., 2008) (4) The invasive tree <i>Ailanthus altissima</i> and shrub <i>Elaeagnus umbellata</i> lost biomass when grown in pots conditioned by the invasive grass <i>Lolium arundinaceum</i> and its symbiotic endophyte <i>Neotyphodium coenophialum</i> (Rudgers and Orr, 2009) (5) Two invasive old world bluestem grasses, <i>Bothriochloa bladhii</i> and <i>B. ischaemum</i> , inhibit the growth of the other when grown as “neighbors” in a controlled field experiment (Schmidt et al., 2008)

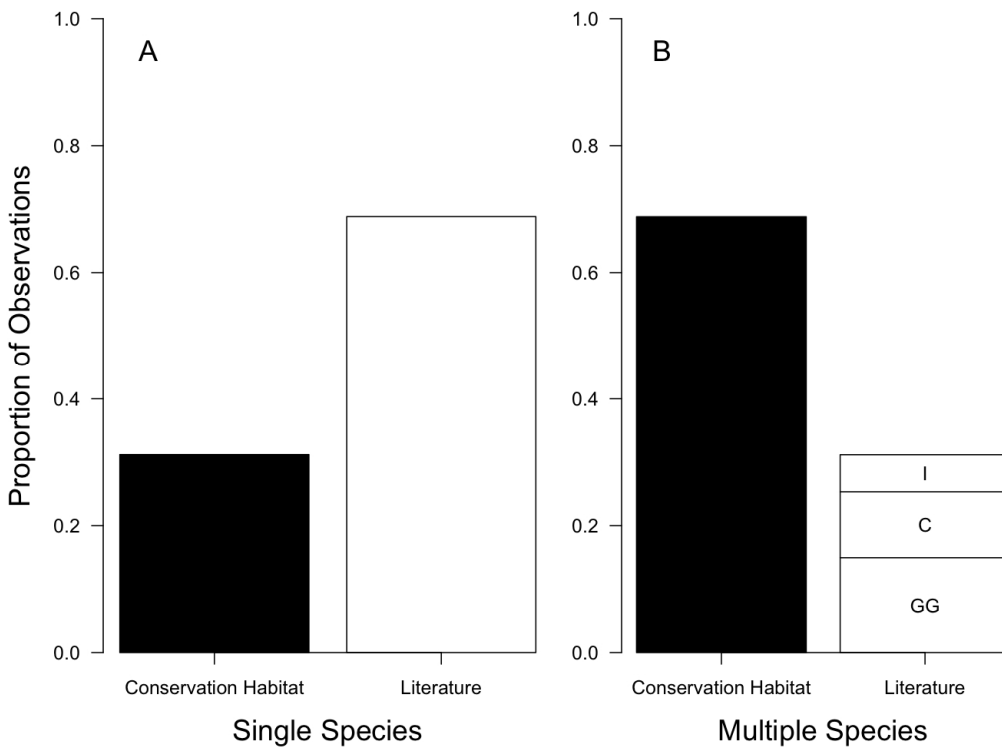


Figure I.1 The proportion of times single (A) or multiple (B) invasive plants were of concern within conservation habitats and in the published literature.

Habitat data are frequency counts when invasive plant species were listed as a conservation threat for 86 projects listed in The Nature Conservancy's Conservation Projects database. Literature data are frequency counts of 153 published studies from 2006 to 2011 that dealt with the impacts of invasive plant species in their invaded range. Of those studies that reported on the impacts of multiple invasive species, less than 6% explicitly tested for impacts of invader–invader interactions (I). The majority of multiple invader studies either compared the impacts among multiple invasive plants [e.g., Rodewald et al. (2010) compared nesting success of Northern Cardinals (*Cardinalis cardinalis*) between two invasive woody shrubs, *Rosa multiflora* and *Lonicera maackii*; (C)] or considered the invasive plant community as a grand group, studying plots with and without invasive species [e.g., Corbin and D'Antonio (2010) compared the competitive ability of a group of exotic perennial grasses to a group of native perennial grasses; (GG)].

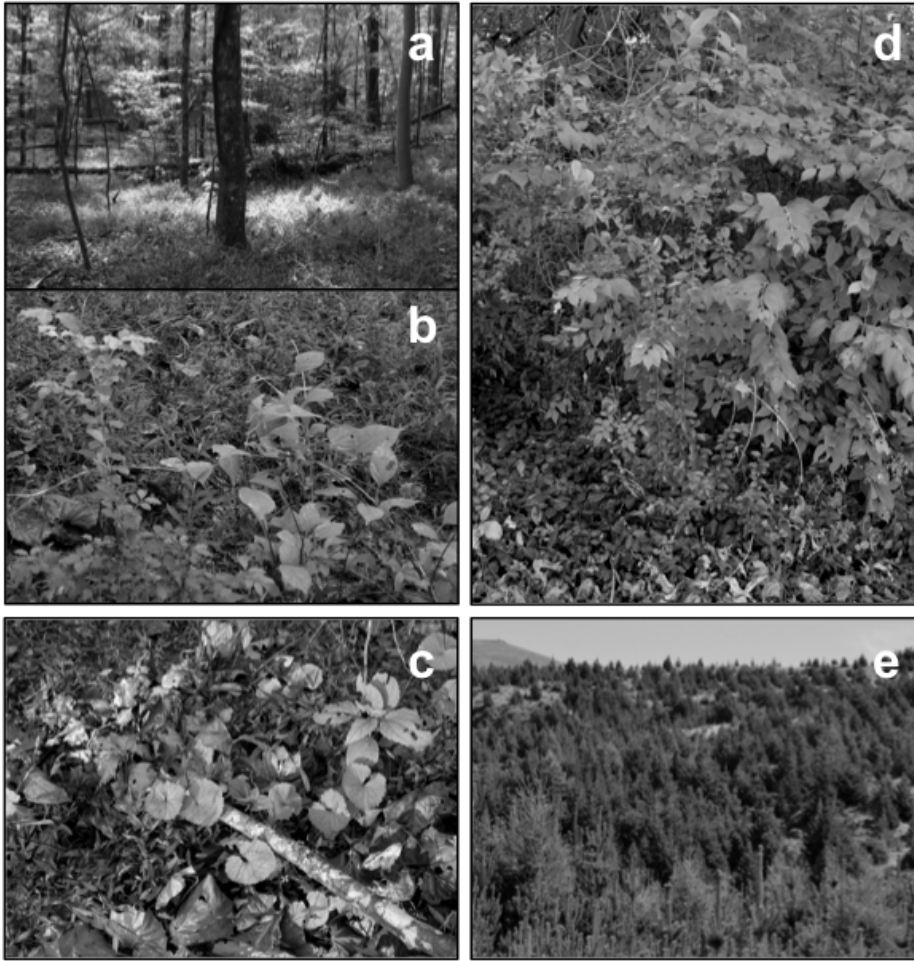


Figure I.2 The presence of co-occurring invasive plant species is increasing, creating a variety of multiple invasion scenarios.

Examples include a southeastern United States forest understory containing “strong” invader Japanese stiltgrass (*Microstegium vimineum*) (a), and “weak” invaders Chinese privet (*Ligustrum sinense*) and Asiatic bittersweet (*Celastrus orbiculatus*) (b); southeastern forest with herbaceous invader garlic mustard (*Alliaria petiolata*) and annual grass Japanese stiltgrass (*Microstegium vimineum*) (c); southeastern forest with co-dominant woody shrub invaders Chinese privet (*Ligustrum sinense*) and bush honeysuckle (*Lonicera maackii*), and woody vine wintercreeper (*Euonymus fortunei*) (d); and invasive trees *Pinus contorta* and *Larix decidua* in New Zealand (e). Photos by Sara Kuebbing (a–d) and Martin Nuñez (e).

CHAPTER II: TWO CO-OCCURRING WOODY SHURBS ALTER SOIL PROPERTIES AND PROMOTE SUBDOMINANT INVASIVE SPECIES

A version of this chapter was originally published by Sara E. Kuebbing, Aimée T. Classen, and Daniel Simberloff:

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SEK designed and conducted the experiment, analyzed the data, and wrote the first draft of the manuscript. ATC provided assistance with soil analysis, and ATC and DS contributed substantially to manuscript revisions.

Abstract

Though co-occurrence of invasive plant species is common, few studies have compared the community and ecosystem impacts of invaders when they occur alone and when they co-occur. Prioritization of invasive species management efforts requires sufficient knowledge of impacts – both among individual invasive species and among different sets of co-occurring invaders – to target resources towards management of sites expected to undergo the largest change. Here, we observed differences in above- and belowground impacts of two invasive woody shrubs, *Lonicera maackii* and *Ligustrum sinense*, among plots containing both shrubs (mixed), each species singly or lacking both species (control). We found additive and non-additive effects of these co-occurring invasives on plant communities and soil processes. Mixed plots contained two times more subdominant invasive plant species than *L. maackii* or *L. sinense* plots. Compared to control plots, mixed plots had three times the potential activity of α -glucosidase, a carbon-degrading extracellular soil enzyme. *L. maackii* plots and mixed plots had less acidic soils, while *L. sinense* plots had higher soil moisture than control plot soils. Differences in soil properties among plots explained plant and ground-dwelling arthropod community composition as well as the potential microbial function in soils. Our study highlights the importance of explicitly studying the impacts of co-occurring invasive plant species singly and together. Though *L. maackii* and *L. sinense* have similar effects on ecosystem structure and function when growing alone, our data show that two functionally similar invaders can have non-additive impacts on ecosystems. These results suggest that sites with both species should be prioritized for invasive plant management over sites containing only one of these species. Furthermore, this

study provides a valuable template for future studies exploring how and when invasion by co-occurring species alters above- and belowground function in ecosystems with different traits.

Introduction

An ecosystem's level of invasion is the actual or relative number of non-native invasive species coexisting within a habitat (Chytrý et al. 2008a). Habitats vary greatly in their level of invasion (Chytrý et al. 2008b; Catford et al. 2012) owing to habitat characteristics such as distance from propagule sources or the competitive ability of the species within the habitat. Though some habitats have high levels of invasion, a disproportionate amount of research has focused on understanding the effects of single rather than multiple invaders (Kuebbing, Nuñez & Simberloff 2013). The impacts of co-occurring invaders are likely to vary by species, ecosystem and the specific properties measured. Similarly, the impacts of co-occurring invaders are likely to differ from those of single-species invasions. For example, for eight non-native grassland species, the change in relative aboveground biomass when the species were grown in monoculture and mixture plots varied through time and by species (Isbell & Wilsey 2011). In the first year of growth, the four non-native grasses underyielded, the two forbs overyielded, and the two legumes showed no change when grown with other non-natives. Through time, the species that consistently underyielded were likely to be lost from mixture plots. Here, the differential response of non-native species when found singly versus together provides important management information, suggesting that prioritization could initially focus on species that overyield in mixture.

Habitats that exhibit high levels of invasion will contain multiple interacting non-native and native species. While the impacts of co-occurring invasives are not well documented, there is ample evidence that single invaders have notable impacts, particularly on native plant communities (Vilà et al. 2011; Simberloff et al. 2013). Invasive plants can competitively exclude native species owing to increased aboveground biomass production (Vilà et al. 2011), increased shading caused by extended leaf phenology (Fridley 2012) or alteration of ecosystem structure (Simberloff 2011). When invasive plants decrease space, light and resource availability in a

community, the abundance and fitness of native populations and the diversity of entire communities decline (Vilà et al. 2011).

Modification of plant communities by invaders can link to changes in belowground communities and vice versa (Pyšek & Richardson 2010; Vilà et al. 2011; Simberloff et al. 2013), because plant and soil communities are connected by nutrient flows between above- and belowground systems (Wardle et al. 2004). Invasive plants can affect soil processes directly by changing soil nutrient cycles or by altering the quality and quantity of nutrient inputs (Ehrenfeld 2010) or indirectly by changing microbial communities' structure or function (Kourtev, Ehrenfeld & Haggblom 2003). For example, *Alliaria petiolata* (M. Bieb.) Cavara and Grande secretes secondary allelopathic compounds that decrease the abundance and diversity of arbuscular mycorrhizal fungi, which reduces the growth of native plants that depend on these beneficial soil organisms (Stinson et al. 2006). This feedback potentially explains *A. petiolata*'s competitive dominance in its non-native range (Lankau & Strauss 2011). In instances such as this, the belowground effect of an invasive plant manifests in aboveground native plant communities. Again, though there is much evidence of invaders altering above- or belowground communities singly, we have much less documentation of how co-occurrence of invaders might change these impacts (but see Ehrenfeld & Scott 2001).

Here, we use an observational study to ask how the occurrence of one or two invasive woody shrub species changes the above- and belowground impacts in deciduous forests of the southeastern USA. Linking above- and belowground effects of invasion will help to inform management decisions by directing management towards aboveground biomass removal or soil remediation efforts (Kardol & Wardle 2010). Likewise, a better understanding of the impacts of invasives on resident communities and ecosystems is the first step in any invasive management plan (Buckley 2008), and ranking impacts of single invasive species is useful for prioritization of where to expend limited resources (Parker et al. 1999). When habitats contain multiple invaders, it becomes necessary to understand how the impacts differ when non-native species co-occur. As level of invasion increases, the combined impacts of co-occurring invaders

can decrease, stay the same, increase linearly (additively) or increase nonlinearly (non-additively). Interactions among the invaders may lead to a variety of responses, such as when positive interactions among invaders lead to a non-additive increase in impacts (i.e. invasional meltdown, Simberloff & Von Holle 1999). Though true invasional meltdown examples are uncommon (Simberloff 2006), cases of non-additive impacts should rank highest in prioritization of management efforts because of the acceleration of impacts when the invaders co-occur.

Two ubiquitous and invasive woody shrubs in southeastern forests are Chinese privet *Ligustrum sinense* Lour. and Amur bush honeysuckle *Lonicera maackii* (Rupr.) Herder. The rapid invasion of *L. maackii* across the southeastern USA at the end of the 20th century (Luken & Thieret 1996) included encroachment into forests previously invaded by *L. sinense*. Although most studies focus on the impacts of each shrub singly, forests now contain a mosaic of areas where each shrub is found alone and where they co-occur. How these species interact in the non-native range is unknown, but they are functionally similar species (i.e. understory woody shrubs) that have similar impacts when they occur singly.

The presence of each shrub correlates with decreased native plant diversity (Hutchinson & Vankat 1997; Collier, Vankat & Hughes 2002), reduced plant growth (Miller & Gorchoff 2004; Greene & Blossey 2011) and decreased insect abundance (Goodell, McKinney & Lin 2010; Ulyshen, Horn & Hanula 2010). Additionally, their presence altered soil nutrient availability and decomposition rates (Mitchell, Lockaby & Brantley 2011; Poulette & Arthur 2012; Trammell et al. 2012). Previous work on interactions among co-occurring invasive plants suggests that functionally dissimilar species, such as those that can or cannot fix nitrogen, might be more likely to have non-additive impacts (Vitousek & Walker 1989). This hypothesis implies that non-additive effects of functionally similar species might be uncommon and thus best ignored by managers. In fact, previous findings in areas invaded by one or the other of our focal species indicate that co-invasion by both species will be additive or neutral relative to one-shrub areas because they are both woody shrubs. However, these assumptions

have never been tested. We hypothesize that even seemingly functionally similar invasive plants can interact and have non-additive effects.

Materials and Methods

We surveyed naturally occurring stands of *Lonicera maackii* and *Ligustrum sinense* in three forests near Knoxville, Tennessee, USA: Ijams Nature Center (35°57'19.29"N, 83°51'56.3"W), which is a 70-ha nature park managed for pedestrian-only recreation; IC King (35°53'58.88"N, 83°56'41.65"W), which is a 49-ha recreation site managed for mountain biking and hiking; and Forks of the River Wildlife Management Area (35°57'13.04"N, 83°51'3"W), which is a 134-ha natural area managed for biking, hiking, and hunting. Hunting restrictions prevented our access to this site during plant and arthropod sampling times; thus, we present only soil data from this site. All sites are hardwood forests, dominated by ash *Fraxinus* spp., oak *Quercus* spp., maple *Acer* spp. and beech *Fagus grandifolia*, and there are no current forest management plans.

Ligustrum sinense is a semi-deciduous shrub whose native range covers much of China, Vietnam and Laos (Nesom 2009). First introduced to the USA in 1852 (Dirr 2009), *L. sinense* occurs in 18 states (EDDMapS 2012). *Lonicera maackii* is a deciduous shrub native to central and northeastern China, Korea and Japan. The first North American record of *L. maackii* was in Ottawa, Canada, in 1896 (Luken & Thieret 1996). *Lonicera maackii* occurs in 29 states (EDDMapS 2012).

Within each site, we located three blocks that contained four circular 6-m diameter (c. 113 m²) plots. Each plot was defined by one of the following vegetation types: *L. sinense* only, *L. maackii* only, *L. maackii* and *L. sinense* co-occurring, or *L. maackii* and *L. sinense* (control plot) for a total of 36 plots (3 sites x 3 blocks x 4 treatments). The 'invaded' treatments had > 75% foliar cover of the respective vegetation type. To determine percentage canopy openness and leaf area index (LAI), we analyzed hemispherical photographs taken in the plot center with a fisheye lens mounted on a 1-m tripod with Gap Light Analyzer software (Frazer, Canham & Lertzman 1999). All photographs were taken on cloudless days in late July between 0630 h and 0830 h.

We sampled plant communities at Ijams and IC King in late May of 2010 when herbaceous cover was highest. Within each plot, we counted all plants in four haphazardly placed, non-overlapping 0.5-m² quadrats, noting the identity, abundance (number of stems) and percentage cover of all species present. We sampled ground-dwelling arthropods with dug-in pitfall traps at Ijams and IC King. We set three traps per plot, the first placed at the plot's center (directly under the center plant) and the subsequent traps ~ 1 m apart in a line. Each trap consisted of a 266-mL plastic cup filled with a soap and water mixture (~ 1 drop liquid soap per liter of water to relax surface tension) with a styrofoam plate secured above to prevent rain from overflowing the traps. We trapped arthropods for 48 h on 15–17 September 2010 and identified all individuals to morphospecies.

We measured the potential activity of three extracellular enzymes, soil pH, and gravimetric water content. We analyzed enzymes important in soil carbon (α -glucosidase), nitrogen (α -N-acetylglucosaminidase [nagase]) and phosphorus (phosphatase) cycling (Sinsabaugh & Follstad Shah 2012). On 13 October 2010, we sieved (2-mm mesh size) and homogenized four 10-cm mineral soil cores (5.08 cm diameter) collected within 1 m of each plot center. Soil pH was calculated from 10-g slurries of field-moist soil and 20 mL of deionized water with a pH conductivity meter (Denver Instruments Model 220, New York, USA). Soil moisture content was calculated as the percentage difference in weight after 20 g of field-moist samples was placed in a drying oven at 105 °C for 48 h. Enzyme activity was assayed by mixing 1 g of field-moist soil with 125 mL of a 50 mmol L⁻¹ sodium acetate buffer and stirring the mixture in a stir plate for 2 min. We measured enzyme activity on 96-well plates that were divided into blank controls, reference standards and negative controls, replicating each eight times (see Saiya-Cork, Sinsabaugh & Zak 2002). We incubated α -glucosidase plates for 2 h and nagase and phosphatase plates for 0.5 h and then measured fluorometric activity using a Modulus fluorometer (Turner Biosystems, California) at an excitation of 365 nm and an emission of 450 nm. After corrections, we report potential enzyme activity as nmol h⁻¹ g⁻¹.

We used mixed-effect nested ANOVAS to test for the effects of invasive plants (*L. maackii*, *L. sinense*, mixture, or control) and habitat variation (block and site) on soil pH, soil moisture, canopy openness, LAI, potential soil enzyme activity (α -glycosidase, β -glucosidase and phosphatase), as well as plant and arthropod abundance, richness and diversity (Shannon's diversity index). The main effect of invasive plant cover type was modeled as a fixed factor nested within block and site, which were modeled as random factors. We calculated F-ratios and estimated variance components according to Quinn & Keough (2002). Transformations were necessary to meet the normality assumption of ANOVA; β -glycosidase activity, arthropod abundance, arthropod diversity and plant abundance were log-transformed, and α -glucosidase activity and LAI were square-root-transformed.

We used unconstrained (PERMANOVA and non-metric multidimensional scaling) and constrained (redundancy analysis) multivariate analyses to describe differences in plant and arthropod community composition and potential soil microbial function. Unconstrained multivariate techniques are useful for examining broad patterns, whereas constrained ordinations allow tests for relationships between explanatory and response variables (Borcard, Gillet & Legendre 2011). For all multivariate analyses, we created presence/absence matrices with plots as rows and species as columns. *Lonicera maackii* and *L. sinense* individuals were excluded from the plant matrix because we wanted to test the influence of their presence on the remainder of the resident community. We combined our enzyme activity measurements into a single matrix to assess total microbial function. Potential activity of extracellular enzymes can be used as an indicator of the nutrient demand of microbial organisms and thus as a proxy for potential microbial function in soils (Sinsabaugh & Follstad Shah 2012).

To detect patterns in community composition among vegetation types and blocks, we used two-way permutational multivariate analysis of variance, which is a more robust test than traditional multivariate analysis of variance (PERMANOVA; Anderson 2001). For each PERMANOVA, we calculated Bray–Curtis similarity matrices on the log-transformed community matrix. We treated 'blocks' as random factors and 'invasive plant vegetation type' as a fixed factor, and we calculated pseudo-F and *P*-

values from 9999 permutations of the original data with type III sum of squares. Owing to software limitations, we were unable to include the nested 'site' factor in this analysis.

We used unconstrained redundancy analysis (RDA) to test for the environmental variables correlated with changes in community composition (Legendre & Gallagher 2001). We created Hellinger-transformed plot-by-species community matrices using plant cover, arthropod abundance, and potential soil enzyme activity data. The full environmental matrix included the variables percentage canopy openness, LAI, soil moisture, soil pH and density of *L. maackii* or *L. sinense* stems (see Table II.2). To select the most significant variables for each RDA, we used the `ordistep` function (R `vegan` package, v. 2.15.1), and the most significant environmental variables were then included in the final model, excluding collinear variables [i.e. variables with a variance inflation factor (VIF) >10, Legendre & Gallagher 2001]. We tested for significance of the full RDA model with the `anova.cca` function (R `vegan` package, v. 2.15.1), which is an ANOVA-like test using 10,000 step permutations. All analyses were performed in R software program (R Core Team 2013).

Results

We found an additive effect of co-occurring invasive shrubs on subdominant invasive plant richness. Subdominant invasive species richness was twice as high in mixed plots (4.00 ± 0.73 SE) compared to *L. maackii* or *L. sinense* plots (2.00 ± 0.37 SE and 2.00 ± 0.40 SE, respectively; Table II.3 and Fig. II.3).

Other invasive plants sampled included *Ailanthus altissima* (Mill.) Swingle, *Albizia julibrissin* Durazz., *Celastrus orbiculatus* Thunb., *Dioscorea oppositifolia* L., *Glechoma hederacea* L., *Hedera helix* L., *Lonicera japonica* Thunb., and *Vinca minor* L.

The presence or absence of *L. maackii* and *L. sinense* was associated with different soil properties. Mixed plots had triple the potential β -glycosidase extracellular enzyme activity (103 ± 34 nmol h⁻¹ g⁻¹; mean \pm SE) compared to control plots (35 ± 11 nmol h⁻¹ g⁻¹), a marginally significant difference ($p < 0.1$; Fig. II.4.a). *L. sinense* plots had 30% higher gravimetric water content (0.31 ± 0.02 SE) than control plots (0.22 ± 0.02 SE; Fig. II.4.e). Soils in control plots were more acidic (5.81 ± 0.30 SE) than those in *L.*

maackii plots (6.34 ± 0.2 SE) and mixed plots (6.33 ± 0.27 SE; Fig. II.4.d). We did not find significant variation in nagsase or phosphatase potential activity among plots that differed in the presence or absence of *L. maackii* or *L. sinense* (Fig. II.4.b,c).

We found that blocks and sites also explained variation in many forest features, including plant community composition (total cover, total richness and native richness) ground-dwelling arthropod abundance, soil properties (nagsase or phosphatase potential activity) and canopy properties (canopy openness and LAI; Table II.3).

Overall community composition was less similar among blocks than among plots that varied in the presence or absence of *L. maackii* or *L. sinense*. Plant community composition varied significantly by block (Fig. II.5.a; PERMANOVA pseudo- $F_{5,15} = 4.09$, $P = 0.0001$), but not by vegetation type (Fig. II.5.a; PERMANOVA pseudo- $F_{3,15} = 1.37$, $P = 0.10$; Table II.4). Ground-dwelling arthropod community composition varied significantly by block (Fig. II.5.d; PERMANOVA pseudo- $F_{5,15} = 2.81$, $P = 0.0001$), but not vegetation type (Fig. II.5.d; PERMANOVA pseudo- $F_{3,15} = 1.30$, $P = 0.08$; Table II.5). Finally, potential soil microbial function varied significantly by block (Fig. II.5.g; PERMANOVA pseudo- $F_{8,24} = 4.44$, $P = 0.001$), but not by vegetation type (Fig. II.5.h; PERMANOVA pseudo- $F_{3,24} = 2.02$, $P = 0.13$; Table II.6).

We used constrained multivariate analysis to define which plot properties were the most important in describing differences in above- and belowground community composition and function. Soil pH and LAI were selected as the most important environmental predictors of plant community composition (Table II.7 and Fig. II.5.c). The two RDA axes explained ~19% of the variation (axis 1, 11.3%, $P < 0.001$; axis 2, 7.4% $P = 0.019$). Soil pH, LAI and *L. sinense* density were the best predictors for arthropod community composition, and these variables explained 19% of the variation in community composition (Table II.7, Fig. II.5.f; axis 1, 7.1%, $P = 0.002$; axis 2, 6.7% $P = 0.018$; axis 3, 5.5%, $P = 0.270$). Together, soil moisture, soil pH, and *L. maackii* density explained 35% of the variation in potential soil microbial function (Table II.7, Fig. II.5.i; axis 1, 19.8%, $P = 0.009$; axis 2, 15.3% $P = 0.028$; axis 3, < 0.001%, $P = 0.990$).

Discussion

We found that when two functionally similar invasive plants co-occur, their combined community and ecosystem impacts were not always equal to the sum of the impacts of each individual invader. This suggests that scientists and managers cannot use studies on single invasive species to infer impacts when invaders co-occur. We show that the co-occurring invasive woody shrubs, *Lonicera maackii* and *Ligustrum sinense*, had neutral, additive and non-additive effects on various attributes of resident communities and ecosystems when they grew separately and together. Importantly, both shrubs either singly or in mixture were associated with differences in soil properties, indicating these shrubs can have more subtle impacts on forest soils and that even with the removal of the species from invaded forests, soil legacies might persist (Ehrenfeld 2010; Simberloff et al. 2013). Likewise, plots with both shrubs contained more subdominant invasive plant species than other plots, indicating that removal of these two dominant invaders might lead to re-invasion of the area by subdominant invaders at the site (Hulme & Bremner 2006; Cox & Allen 2008; Pearson, Ortega & Columbus 2009). Whether this is a common occurrence in other ecosystems or for other co-occurring invasive species is currently unknown and an area for further work. A comprehensive understanding of invader impacts across habitats that may vary in level of invasion would provide an informed foundation for developing hypotheses regarding the impacts of non-native communities as well as better predictive tools for the types of invasive plant combinations that are most likely to have the greatest impacts.

Increasing non-additive impacts should be a concern for invasive species managers who would like to restore native ecosystem function. In our study, mixed plots had three times higher potential activity of α -glucosidase (Fig. II.4.a), an enzyme that breaks down cellulose, compared to control plot soils. High carbon-degrading enzyme activity suggests high decomposition rates, which could be caused by high-quality invasive plant leaf litter stimulating microbial activity (Sinsabaugh & Follstad Shah 2012). Invaded sites often have higher leaf decomposition rates (Ehrenfeld 2010), and leaf litter from *L. maackii* and *L. sinense* is higher in quality (i.e. lower leaf C : N) and decomposes faster than native woody species' litter (Blair & Stowasser 2009; Mitchell,

Lockaby & Brantley 2011; Arthur et al. 2012). Though we did not study decomposition, our results suggest that adding leaf litter from these two invasive plants is different than adding litter from one of them alone, resulting in a non-additive impact of co-occurring invasive plant litter. An invader-induced change in nutrient cycling may drive invader dominance and decrease native plant abundance and diversity (Kourtev, Ehrenfeld & Haggblom 2003).

Though we did not find a difference in the native plant community between control and invaded plots (Table II.2, Fig. II.4.b), we did see an increase in subdominant invasive plant richness in mixed plots. Sites with more than one invasive species are susceptible to reinvasion if management includes only the removal of dominant invaders and not subdominant invaders (Hulme & Bremner 2006). Thus, the presence of subdominant invasive plants is a management concern. The additive effect of *L. maackii* and *L. sinense* on invasive plant richness (Table II.3, Fig. II.3.a) suggests that the likelihood of re-invasion is higher in areas with both invaders because there are twice as many invasive species present to take their place. Contrary to our findings, richness of invasive and native species was equally low in riparian plots that contained the herbaceous vine *Vinca major* L., the grass *Arundo donax* L. or both invasive species relative to plots where both invaders were absent (Cushman & Gaffney 2010). While studies across ecosystems are few, these two contrasting results indicate that additive and non-additive effects of invasive species might depend on the invaded ecosystem, the species involved and functional differences between the co-occurring invaders.

The presence of each invasive shrub was related to differences in soil properties. Soil moisture differences between *L. sinense* and control plots suggest that *L. sinense* performance is higher in moist microsites, which is in accord with observations that the species is particularly invasive in riparian areas (Merriam 2003; Miller 2010). Soils in control plots were more acidic than soils in *L. maackii* plots and mixture plots (Fig. II.4.d). Other forest invaders, including *L. maackii*, affect the pH of soils when they invade (Ehrenfeld & Scott 2001; Schradin & Cipollini 2012), which suggests that *L. maackii* might be changing soil properties rather than selecting less acidic sites.

It is important to note that we consistently found a strong signal of variation among blocks and sites in canopy and soil properties, plant community structure, and plant and arthropod community composition (Table II.3, Fig. II.5.a,d,g). Small-scale habitat heterogeneity such as this is common in forested ecosystems (Chávez & Macdonald 2010; Douda et al. 2012), especially younger secondary forests such as the ones we sampled (Moora et al. 2007). We found that small-scale (block) environmental heterogeneity affected the community structure and spatial distribution of plants, as in other forest studies (Chávez & Macdonald 2010; Douda et al. 2012). The variation in enzyme activity among blocks could be due to the variation in soil pH, the most important driver of enzyme activity globally (Sinsabaugh & Follstad Shah 2012). Interestingly, we did not find an effect of block or site on arthropod diversity, although habitat heterogeneity is an important predictor of arthropod diversity (Tews et al. 2004; Báldi 2008), particularly microhabitat heterogeneity in forested systems (Ziesche & Roth 2008). We may have failed to detect variation in arthropod community owing to our single-sampling period or because our plots did not vary in percentage shrub cover or vertical structure complexity, which have the largest effect on forest arthropod diversity (González-Megías, Gómez & Sánchez-Piñero 2007; Janssen, Fortin & Hébert 2009). Finally, the presence of subdominant invasive species in mixed plots may contribute to the variation we found in other plot properties (Peltzer et al. 2009), although our observational design precludes our disentangling these effects.

Environmental variation in abiotic site properties such as soil nutrients and soil moisture can moderate the impact of invasive species (Pyšek et al. 2012), as we found in our redundancy analysis. The impacts of invaders on soil nutrient pools can be dampened or magnified by variation in soil nutrient availability or soil texture (Scharfy et al. 2009). Soil pH and LAI varied among blocks and were selected as significant variables in redundancy analysis, explaining ~19% of the variation in plant and arthropod community composition (Table II.4, Fig. II.5.c, f); this result is similar to other findings (Barbier, Gosselin & Balandier 2008; Chávez & Macdonald 2010; Douda et al. 2012). However, our redundancy analysis detected direct and indirect influences of invasive shrubs on plant and arthropod communities as well, despite strong

microhabitat variation. The density of *L. sinense* stems helped explain compositional differences in arthropod communities (Table II.3, Fig. II.5.f). Removal of dense monotypic stands of *L. sinense* can increase beetle diversity compared to untreated or uninvaded sites, indicating *L. sinense* stem density is important for ground-dwelling arthropod fauna (Ulyshen, Horn & Hanula 2010). Soil pH was an important predictor in all of our redundancy analyses (Table II.3). Higher soil pH was associated with *L. maackii*, indicating that the potential effect of the shrub on soil properties could indirectly affect forest community composition.

Interestingly, we found that *L. maackii* and *L. sinense* had greater effects on belowground soil properties than on aboveground plant or arthropod communities. Effects of invaders on soils can feed back to aboveground communities, particularly invaders that might change ecosystem carbon cycling. The invasive grass *Microstegium vimineum* (Trin.) A. Camus increases carbon fixation and shunts more carbon into belowground communities, affecting above- and belowground food webs (Bradford et al. 2012). We found that when the invasive shrubs co-occur, there was a threefold increase in carbon-degrading enzyme activity. This belowground change could have long-term consequences for aboveground communities.

Though we found no difference among plant communities in invaded plots, previous studies show that *L. maackii* and *L. sinense* are associated with decreased native plant abundance or diversity (Hutchinson & Vankat 1997; Collier, Vankat & Hughes 2002; Hartman & McCarthy 2008; Hanula, Horn & Taylor 2009; Greene & Blossey 2011). Thus, impacts of invasive plants can vary in their frequency and reliability across ecosystems (Hulme et al. 2013). Other studies typically compared forested sites across a larger spatial scale, such as forested stands with and without *L. sinense* (Hanula, Horn & Taylor 2009) or sites that varied in level of invasion (Hutchinson & Vankat 1997; Hartman & McCarthy 2008; Greene & Blossey 2011; but see Collier, Vankat & Hughes 2002). Our comparison of plots at a smaller spatial scale suggests that environmental variation may be more important at this scale for determining plant community composition.

Currently, few studies test how the influence of co-occurring invaders differs from that of single invaders (but see Cushman & Gaffney 2010), making comprehensive recommendations for management of co-occurring invaders difficult. As the level of invasion increases within habitats, managers are faced with two scenarios. First, they must choose specific sites to manage, which may vary in level of invasion. Second, managers must choose which invaders to manage within any given habitat. We suggest that managers of sites with *L. maackii* or *L. sinense* initially prioritize sites containing both species because they cause non-additive impacts, but that these same sites should be monitored for potential re-invasion by subdominant invaders. As we expand our knowledge of how impacts of co-occurring invaders differ from those of single invaders across different ecosystems and invasive species combinations, we will build a larger body of research that will enable us to develop better hypotheses for predicting the impacts of co-occurring invasive plants.

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Appendix

Table II.2. The full suite of environmental variables used in unconstrained redundancy analysis

Abbreviations are as follows: percentage canopy openness (CO), leaf area index (LAI), soil moisture (gravimetric water content: GWC), soil pH (pH), and density of invasive plant stems (*Lonicera maackii* or *Ligustrum sinense*). Plant and arthropod communities were sampled only at the two sites IC King (IC) and Ijams (IJ), thus environmental variables from only these two sites were used in RDA analysis.

Site	Block	Veg	CO	LAI	GWC	pH	<i>L. maackii</i> density	<i>L. sinense</i> density
IC	1	control	12.63	2.2	0.10	5.86	0	0
IC	1	<i>L. maackii</i>	14.47	2.23	0.30	6.53	3	0
IC	1	mixture	14.91	1.96	0.43	6.78	1	0.75
IC	1	<i>L. sinense</i>	10.82	2.39	0.41	6.61	0	1.25
IC	2	control	8.66	2.67	0.20	5.59	0.25	0.5
IC	2	<i>L. maackii</i>	9.01	2.76	0.23	5.94	2	2.25
IC	2	mixture	20.2	1.82	0.23	5.43	0.25	2.5
IC	2	<i>L. sinense</i>	11.56	2.49	0.34	5.13	0	5.25
IC	3	control	9.08	2.78	0.11	4.98	0	0
IC	3	<i>L. maackii</i>	13.13	2.14	0.27	6.67	0.25	1.5
IC	3	mixture	11.3	2.33	0.21	6.64	0.25	0.5
IC	3	<i>L. sinense</i>	13.09	2.08	0.40	6.32	0	7.5
IJ	4	control	8.06	2.59	0.30	6.07	0	0
IJ	4	<i>L. maackii</i>	10.65	2.85	0.29	6.07	0.25	0
IJ	4	mixture	12.59	2.39	0.29	5.29	0	2.5
IJ	4	<i>L. sinense</i>	10.98	2.33	0.22	5.05	0	2.5
IJ	5	control	9.31	3.01	0.28	6.71	0	0
IJ	5	<i>L. maackii</i>	4.51	3.69	0.26	7.02	0.5	0
IJ	5	mixture	4.7	3.51	0.30	7.27	0.25	0.75
IJ	5	<i>L. sinense</i>	5.16	3.39	0.26	6.48	0	0.75
IJ	6	control	19.8	1.59	0.27	7.37	0	0
IJ	6	<i>L. maackii</i>	14.17	2.22	0.36	7.28	0.25	0
IJ	6	mixture	11.04	2.36	0.27	7.43	0.75	1.25
IJ	6	<i>L. sinense</i>	10	2.5	0.29	7.46	0	1.25

Table II.3. Plots dominated by two invasive shrubs, *Lonicera maackii* and *Ligustrum sinense*, were associated with variation in the number of subdominant invasives present, potential activity of carbon-degrading soil enzyme β -glucosidase, soil pH, and soil moisture.

Nested ANOVA accounted for strong variation among plots containing each invader singly, plots with both species or control plots lacking either shrub. Plots were blocked within sites. Percentage (%) values represent estimates of variance components for each model error term, and bold *P*-values are significant at $P < 0.1$.

Dependent Variable	Invasive Shrub (Block [Site])			Block (Site)			Site		
	%	F	<i>P</i>	%	F	<i>P</i>	%	F	<i>P</i>
<i>Plant Community</i>									
total cover	0.0	0.27 _{3,15}	0.85	22.3	7.39 _{4,3}	0.07	0.5	1.90 _{1,4}	0.24
total richness	4.3	2.10 _{3,15}	0.14	0.0	0.94 _{4,3}	0.54	2.8	5.32 _{1,4}	0.08
native richness	0.8	1.19 _{3,15}	0.35	0.0	0.75 _{4,3}	0.62	2.8	10.39 _{1,4}	0.03
non-native richness	9.6	4.11 _{3,15}	0.03	16.3	1.32 _{4,3}	0.43	0.0	0.003 _{1,4}	0.96
diversity	4.6	2.18 _{3,15}	0.13	1.7	1.05 _{4,3}	0.50	0.2	1.27 _{1,4}	0.32
<i>Arthropod Community</i>									
abundance	1.1	1.61 _{3,15}	0.23	55.3	5.73 _{4,3}	0.09	0.0	0.26 _{1,4}	0.63
richness	0.6	1.16 _{3,15}	0.36	12.4	1.74 _{4,3}	0.34	0.0	0.07 _{1,4}	0.80
diversity	2.5	1.62 _{3,15}	0.23	0.0	0.52 _{4,3}	0.73	0.0	0.57 _{1,4}	0.49
<i>Soil Properties</i>									
β -glucosidase	6.8	3.05 _{3,18}	0.06	0.4	1.01 _{4,3}	0.52	0.2	1.25 _{2,4}	0.38
nagase	0.0	0.44 _{3,18}	0.72	40.3	11.6 _{4,3}	0.04	0.0	0.41 _{2,4}	0.69
phosphatase	0.2	1.11 _{3,24}	0.37	50.4	8.37 _{6,3}	0.05	0.0	0.45 _{2,6}	0.66
pH	3.5	3.28 _{3,24}	0.04	46.5	3.29 _{6,3}	0.18	0.4	1.26 _{2,6}	0.35
gravimetric water content	6.0	3.06 _{3,24}	0.05	0.0	0.24 _{6,3}	0.93	0.0	0.33 _{2,6}	0.73
<i>Plot Properties</i>									
canopy openness	0.0	0.56 _{3,24}	0.65	25.0	5.77 _{6,3}	0.09	0.0	0.59 _{2,6}	0.58
leaf area index	0.2	1.13 _{3,24}	0.36	41.9	6.12	0.08	0.0	0.79 _{2,6}	0.49

Table II.4. Plant species identified in 0.5 m² plots containing *Ligustrum sinense* (Chinese privet), *Lonicera maackii* (bush honeysuckle), both species together, or control plots where both shrubs were absent.

Family	Species	Growth Habit
Aceraceae	<i>Acer negundo</i> L.	W
	<i>Acer rubrum</i> L.	W
	<i>Acer saccharum</i> Marsh.	W
Anacardiaceae	<i>Toxicodendron radicans</i> L. Kuntze	W
Apiaceae	<i>Cryptotaenia canadensis</i> (L.) DC.	H
Apocynaceae	<i>Vinca minor</i> L.	H
Araceae	<i>Arisaema quinatum</i> (L.) Schott	H
	<i>Arisaema triphyllum</i> (L.) Schott	H
Araliaceae	<i>Hedera helix</i> L.	H
Asteraceae	<i>Aster</i> spp. 2 *	H
	<i>Aster</i> spp. 3 *	H
	<i>Smallanthus uvedalius</i> (L.) Mack. Ex Small	H
	<i>Symphyotrichum novae-angliae</i>	H
Balsaminaceae	<i>Impatiens capensis</i> Meerb.	H
Berberidaceae	<i>Podophyllum peltatum</i> L.	H
Betulaceae	<i>Carpinus caroliniana</i> Walter	W
Betulaceae	<i>Ostrya virginiana</i> (Mill.) K. Koch	W
Bignoniaceae	<i>Bignonia capreolata</i> L.	H
Brassicaceae	<i>Cardamine</i> *	H
Caprifoliaceae	<i>Lonicera japonica</i> Thunb.	W
	<i>Lonicera maackii</i> (Rupr.) Herder	W
Celastraceae	<i>Celastrus orbiculatus</i> Thunb.	W
	<i>Euonymus americana</i> L.	W
Cornaceae	<i>Cornus florida</i> L.	W
Dennstaedtiaceae	<i>Pteridium aquilinum</i> (L.) Kuhn	H
Dioscoreaceae	<i>Dioscorea villosa</i> L.	H
Dryopteridaceae	<i>Polystichum acrostichoides</i> (Michx.) Schott	H
Fabaceae	<i>Albizia julibrissin</i> Durazz.	W
	<i>Apios Americana</i> Medik.	H
	<i>Cercis canadensis</i> L.	W
	<i>Gleditsia triacanthos</i> L.	W
Fagaceae	<i>Fagus grandifolia</i> Ehrh.	W
	<i>Quercus prinus</i> L.	W
	<i>Quercus rubra</i> L.	W

Growth habits defined as G = graminoid, H = herbaceous, W = woody. The * indicates identification was to morphospecies, owing to the lack of floral or other identifying features.

Table II.4. Continued.

Family	Species	Growth Habit
Fumariaceae	<i>Dicentra eximia</i> (Ker Gawl.) Torr.	H
Geraniaceae	<i>Geranium maculatum</i> L.	H
Hamamelidaceae	<i>Liquidambar styraciflua</i> L.	W
Hippocastanaceae	<i>Aesculus</i> spp. *	W
Juglandaceae	<i>Carya</i> spp. *	W
Lamiaceae	<i>Glechoma hederacea</i> L.	W
Lauraceae	<i>Lindera benzoin</i> (L.) Blume	W
Lilaceae	<i>Trillium</i> spp. *	H
	<i>Maianthemum racemosa</i> (L.) Link	H
	<i>Polygonatum biflorum</i> (Walter) Elliot	H
	<i>Trillium luteum</i> (Muhl.) Harbison	H
	<i>Uvularia perfoliata</i> L.	H
Magnoliaceae	<i>Liriodendron tulipifera</i> L.	W
Menispermaceae	<i>Cocculus carolinus</i> (L.) DC.	H
Oleaceae	<i>Fraxinus Americana</i> L.	W
	<i>Fraxinus quadrangulata</i> Michx.	W
	<i>Ligustrum sinense</i> Lour.	W
Phytolaccaceae	<i>Phytolacca Americana</i> L.	H
Plantaginaceae	<i>Plantago</i> spp. *	H
Poaceae	<i>Microstegium vimineum</i> (Trin) A. Camus	G
Poaceae	Grass spp. 1 *	G
Poaceae	Grass spp. 2 *	G
Ranunculaceae	<i>Anemonella thalictroides</i> (L.) Eames & B. Boivin	W
	<i>Clematis virginiana</i> L.	W
Rosaceae	<i>Fragaria virginiana</i> Duschesne	H
	<i>Prunus serotina</i> Ehrh.	W
	<i>Prunus</i> spp. *	W
Rubiaceae	<i>Galium aparine</i> L.	H
	<i>Galium</i> spp. *	H
Saxifragaceae	<i>Parnassia asarifolia</i> Vent.	H
Simaroubaceae	<i>Ailanthus altissima</i> (Mill.) Swingle	W
Smilacaceae	<i>Smilax tamnoides</i> L.	W
		H
Urticaceae	<i>Boehmeria cylindrical</i> (L.) Sw.	
Violaceae	<i>Viola</i> spp. *	H
Vitaceae	<i>Parthenocissus quinquefolia</i> (L.) Planch.	W
Vitaceae	<i>Vitis rotundifolia</i> Michx.	W

Growth habits defined as G = graminoid, H = herbaceous, W = woody. The * indicates identification was to morphospecies, owing to the lack of floral or other identifying features.

Table II.5. Ground-dwelling arthropod morphospecies collected in pitfall traps in plots containing *Ligustrum sinense* (Chinese privet), *Lonicera maackii* (bush honeysuckle), both species together, or control plots where both shrubs were absent.

Taxonomy		Morphospecies
Subphylum Chelicerata		
Class Arachnida		
	Order Acari	Acari1 Ixodida1 Ixodida2 Ixodida3 Orbatida1 Orbatida2 Trombidiformes: Trombiculidae: <i>Trombicula</i> spp.
	Order Araneae	Aglenidae: <i>Tenuiphantes</i> spp. Aglenidae1 Dictynidae1 Dysederidae1 Linyphiidae1 Linyphiidae2 Lycosidae1 Lycosidae2 Lycosidae3 Lycosidae4 Mimetidae1 Miturgidae1 Miturgidae2 Miturgidae3 Mygalomorphae1 Oonopidae1 Salticidae1 Salticidae2 Thomisidae1 Thomisidae2
	Order Opiliones	Cladonchiidae1 Opiliones1 Opiliones2 Opiliones3
	Order Pseudoscorpiones	Chthoniidae: Chtonius: <i>Ephippiochthonius tetrachelatus</i>
Subphylum Crustacea		
Class Malacostraca		
	Order Isopoda	Isopoda1

Table II.5. Continued.

Taxonomy	Morphospecies
	Oniscidae1
	Oniscidae2
	Oniscidae3
	Oniscidae4
Subphylum Atelocerata	
Class Chilopoda	
Order Lithobiomorpha	Lithobiomorpha1
Order Scholopendromorpha	Scholopendromorpha1
Order Scutigeromorpha	Scutigeridae1
Class Diploda	
Order Chordeumatida	Chordeumatida1
Order Polydesmida	Nearctodesmidae
	Polydesmida1
Order Polyxendia	Polyxenidae: <i>Polyxenux</i> spp.
Order Spirobolida	<i>Trigoniulus</i> spp.
Order Spirosterptida	Cambalidae1
Class Hexapoda	
Order Blattodea	Blattelidae1
Order Coleoptera	Carabidae: <i>Galerita</i> spp.
	Carabidae1
	Carabidae2
	Curculionidae: <i>Otiorhynchus</i> spp.
	Lampyridae larvae
	Nitidulidae1
	Nitidulidae2
	Sphaeritidae1
	Staphylinidae1
	Staphylinidae2
	Staphylinidae3
	Staphylinidae4
	Staphylinidae5
	Unidentified larvae1
	Unidentified larvae2
	Unidentified larvae3
	Unidentified larvae4
	Unidentified larvae5
Order Collembola	Entomobryidae1
	Entomobryidae2
	Entomobryidae: <i>Homidia sauteria</i>
	Entomobryidae: <i>Lepidocyrtus paradoxus</i>

Table II.5. Continued.

Taxonomy	Morphospecies
	Entomobryidae: <i>Pseudosinella</i> spp.
	Hypogastruridae1
	Hypogastruridae2
	Hypogastruridae: <i>Ceratophysella</i> spp.
	Isotomidae1
	Isotomidae: <i>Desoria</i> spp.
	Neoneuridae: <i>Pseudocoruides</i> spp.
	Sminthuridae1
	Sminthuridae: <i>Sminthurus</i> spp.1
	Sminthuridae: <i>Sminthurus</i> spp.2
	Tomoceridae: <i>Pogonognathellus</i> spp.
	Tomoceridae: <i>Thomosorus</i> spp.
Order Diptera	Cediomyiidae1
	Cediomyiidae2
	Cediomyiidae3
	Chironomidae1
	Culicidae larvae1
	Culicidae pupae1
	Culicidae pupae2
	Culicidae pupae3
	Diptera1
	Dolichopodidae1
	Dolichopodidae2
	Empididae1
	Phoridae: <i>Apocephalus</i> spp.1
	Phoridae: <i>Apocephalus</i> spp.2
	Phoridae: <i>Apocephalus</i> spp.3
	Phoridae: <i>Phalacrotophora</i> spp.1
	Psychodidae1
Order Hemiptera	Aetalionidae1
	Aphididae1
	Aphididae2
	Aphididae3
	Aphididae4
	Cercopidae1
	Cicadellidae1
	Derbidae1
Order Hymenoptera	Derbidae2
	Bethylidae1
	Chalcidoidea: Braconidae

Table II.5. Continued.

Taxonomy	Morphospecies
	Chalcidoidea: Ceraphronidae
	Chalcidoidea: Eupelmidae1
	Chalcidoidea: Mymarida1
	Chalcidoidea: Mymarida2
	Chalcidoidea: Mymarida3
	Chalcidoidea: Mymaridae1
	Chalcidoidea: Mymaridae2
	Chalcidoidea: Mymaridae3
	Chalcidoidea: Mymaridae4
	Chalcidoidea: Scelonidae
	Chalcidoidea: Trichogrammatidae1
	Chalcidoidea: Trichogrammatidae2
	Chalcidoidea1
	Chalcidoidea2
	Chalcidoidea3
	Chalcidoidea4
	Formicidae: <i>Aphenogaster rudis</i>
	Formicidae: <i>Camponotus americanus</i>
	Formicidae: <i>Camponotus castaneus</i>
	Formicidae: <i>Camponotus decipiens</i>
	Formicidae: <i>Crematogaster lineolata</i>
	Formicidae: <i>Neivamyrmex opacithorax</i>
	Formicidae: <i>Nylanderia fasionensis</i>
	Formicidae: <i>Nylanderia vividula</i>
	Formicidae: <i>Ponera exotica</i>
	Formicidae: <i>Ponera pennsylvanica</i>
	Formicidae: <i>Preneopsis imparis</i>
	Formicidae: <i>Strumigenys</i> spp.
	Formicidae: <i>Lasius alienus</i>
	Ichneumonidae1
	Pompilidae1
	Pompilidae2
	Vespidae: <i>Vespula flavopilosa</i>
	Vespidae1
Order Lepidoptera	Lepidopteran larvae1
	Notodontidae: Phalerinae, <i>Datana contracta</i>
Order Microcrophia	Machilidae1
	Machilidae2
Order Orthoptera	Gryllidae: <i>Allonemobius socius</i>
	Gryllidae: <i>Gryllus</i> spp.

Table II.5. Continued.

Taxonomy	Morphospecies
	Gryllidae: <i>Velarifictorus micado</i>
	Rhaphidophoridae: <i>Ceuthophilus</i> spp.1
	Rhaphidophoridae: <i>Ceuthophilus</i> spp.2
Order Pauropoda	Pauropoda1
Order Philraptera	Philopteridae1
Order Pscoptera	Dasydemellidae1
	Pscoptera instar1
Order Thysanoptera	Thripidae1

Table II.6. Two-way PERMANOVA comparing how microhabitat (block) and presence of the invasive shrubs *Lonicera maackii* or *Ligustrum sinense* (plots with each invader singly, plots with both invaders, and control plots where neither shrub is present) affect composition of understory plants and ground-dwelling arthropods and potential soil function.

Potential soil function was assessed using potential activity of three extracellular soil enzyme assays (β -glycosidase, β -N-acetylglucosaminidase, and phosphatase). All PERMANOVA analyses were conducted on Bray-Curtis dissimilarity matrices of presence-absence (plant and arthropod) or normalized (potential soil function) site-by-species matrices. *P*-values are based on 9999 permutations of the data.

	df	SS	MS	pseudo-F	<i>P</i> (perm)
<i>Plant Community</i>					
Microhabitat (block)	5	3.73	0.75	4.09	0.0001
Dominant Vegetation	3	0.75	0.25	1.37	0.10
Residuals	15	2.74	0.18		
<i>Arthropod Community</i>					
Microhabitat (block)	5	1.98	0.4	2.11	0.0001
Dominant Vegetation	3	0.73	0.24	1.30	0.08
Residuals	15	2.81	0.19		
<i>Functional Soil Community</i>					
Microhabitat (block)	5	0.25	0.03	4.44	0.001
Dominant Vegetation	3	0.04	0.01	2.02	0.13
Residuals	15	0.17	0.01		

Table II.7 Soil pH, soil moisture, leaf area index (LAI), and number of invasive plant stems (*Lonicera maackii* or *Ligustrum sinense*) affect potential soil function and composition of understory plant and ground-dwelling arthropod communities.

All unconstrained redundancy analyses were conducted on Hellinger-transformed abundance matrices. *P*-values are based on 9999 permutations of the data, and asterisks (*) indicate significance levels: *** *P* < 0.001, ** *P* < 0.01, * *P* < 0.05.

Model	Variables	Constrained Variance	adjusted R ²	F _{perm}
Plant Community	Soil pH, LAI	0.19	0.11	2.42 ***
Arthropod Community	<i>Ligustrum</i> Stems, soil pH, LAI	0.19	0.09	1.77 ***
Potential Soil Function	<i>Lonicera</i> stems, soil pH, soil moisture	0.35	0.25	3.43 *

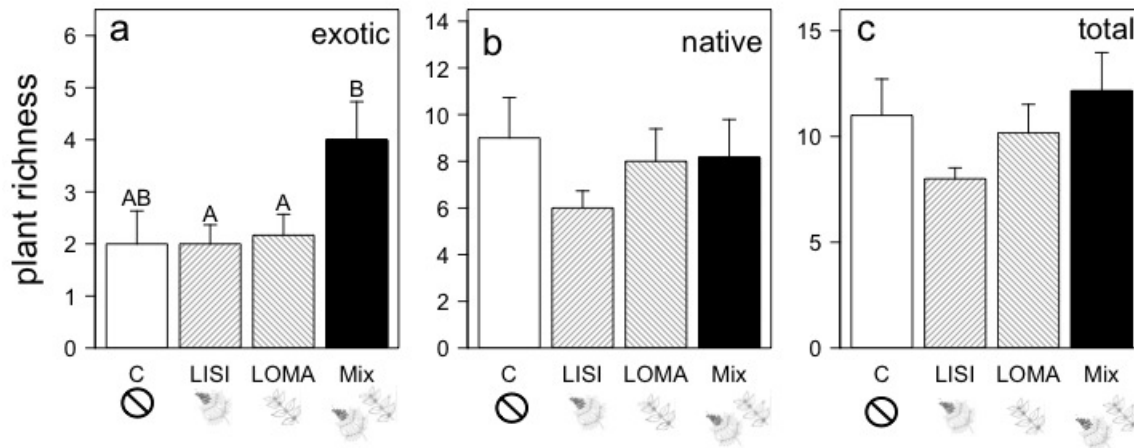


Figure II.3 Subdominant invasive plant richness (a) in plots containing two invasive shrubs (Mix) was double that of plots containing each shrub, *Ligustrum sinense* or *Lonicera maackii*, or control plots (C) where neither shrub was present. Plant richness of native species (b) and total richness (c) did not vary between plots.

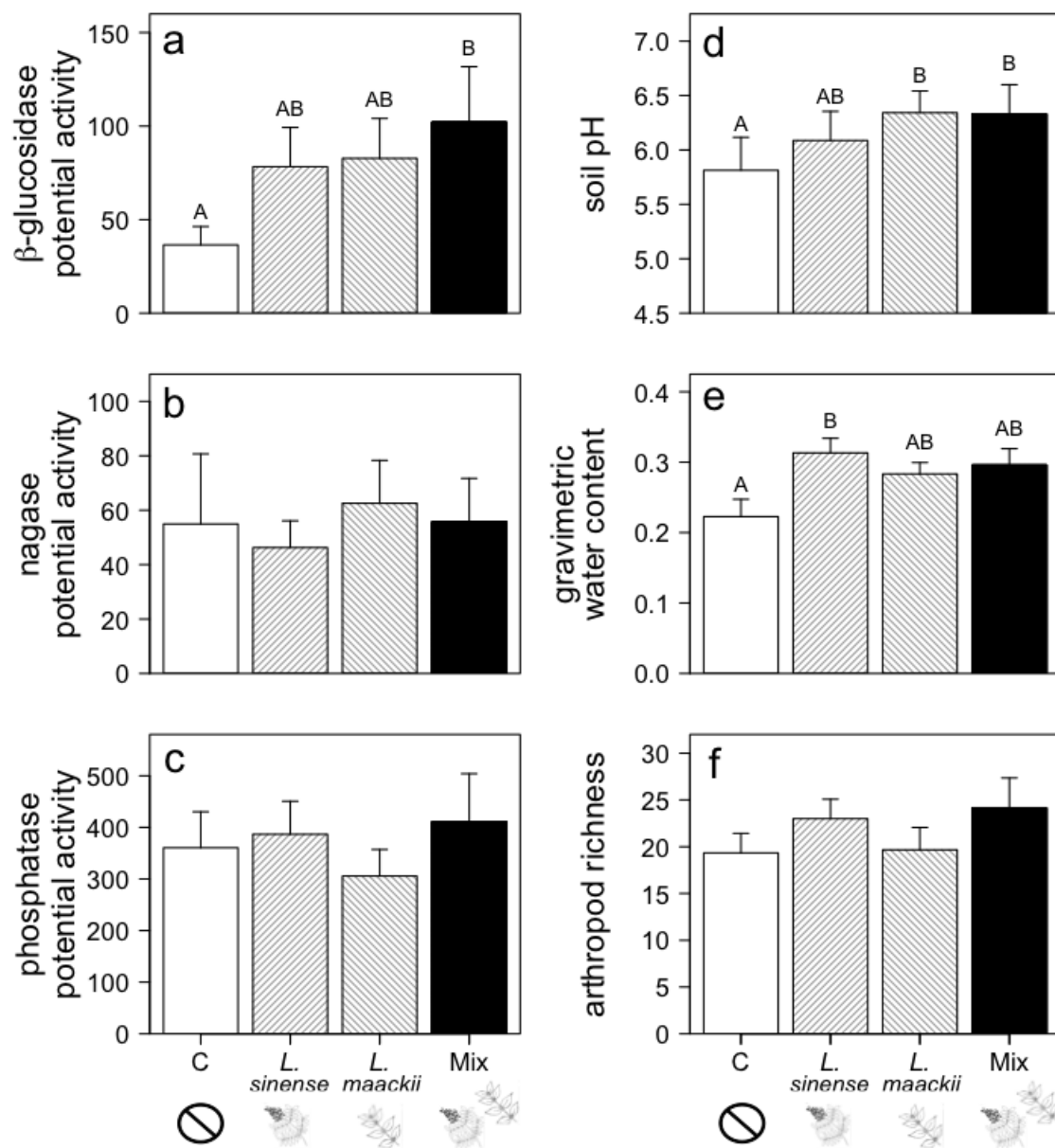


Figure II.4. Potential activity of the soil enzyme β -glucosidase (a), soil pH (d), and soil moisture (e) varied in plots that differed in the presence of zero (control plots: C), one (*Ligustrum sinense* or *Lonicera maackii* plots) or two (mixture plots: Mix) invasive woody shrub species. Potential activity of the soil enzymes nagase (b) and phosphatase (c) and arthropod richness (f) did not vary between plot types. Bars represent mean and standard error.

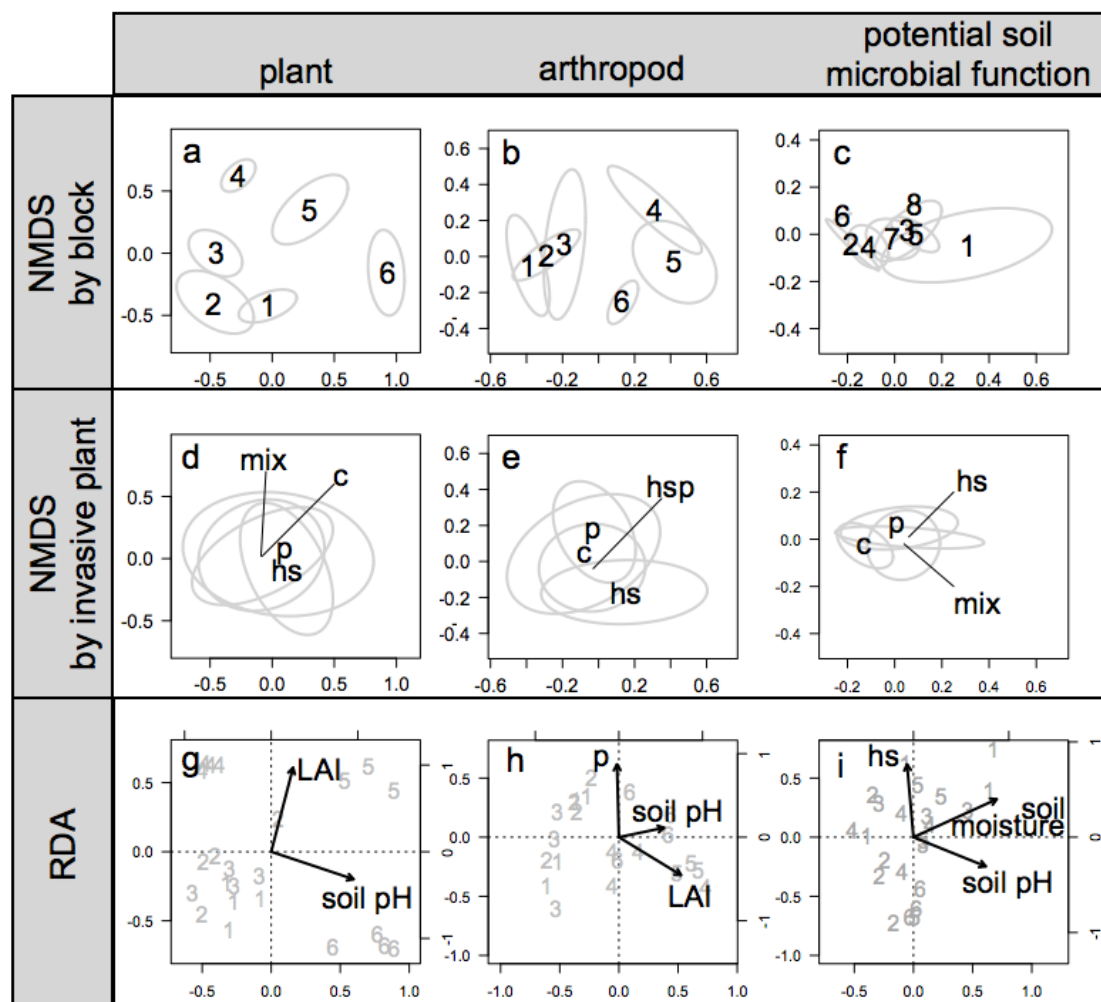


Figure II.5. Understory plant and ground-dwelling arthropod communities, as well as potential soil microbial function, showed more variation between blocked plots (a, b, c) than between plots that differed in the presence of zero (control plots, c), one (*Ligustrum sinense*, p or *Lonicera maackii*, hs) or two (mixture plots: m) invasive woody shrub species (d, e, f).

Unconstrained non-metric multidimensional scaled plots based on Bray-Curtis dissimilarity matrices for each taxon show centroids and 95% confidence limits based on standard deviation of individual points. All ordination stress values were < 0.2. Constrained redundancy analysis (g, h, i) depicts the most significant variables driving community composition for each taxon. Variables included in models included leaf area index (LAI), soil moisture, soil pH, and invasive plant average density (*L. sinense*, p; *L. maackii*, hs) across blocked plots (gray numbers).

CHAPTER III: NATIVE AND NONNATIVE PHYLOGENETICALLY PAIRED PLANT COMMUNITIES RESPOND DIFFERENTLY TO SPECIES GAINS AND LOSSES

Abstract

The loss and gain of species is altering community structure, associated species interactions, and ecosystem functions. Yet, we have limited information on whether the relationship between community structure and ecosystem function depends upon whether communities consist of native or nonnative species. That is, does the gain and loss of coevolved native species differ from the gain and loss of nonnative evolutionary naïve species? Here, we experimentally test how differences in community richness of phylogenetically paired native and nonnative plant communities affect community productivity and seedling establishment. Native and nonnative communities differed in overall biomass allocation patterns and the mechanism responsible for productivity differences—negative and positive selection effects in native and nonnative communities, respectively—was significantly and oppositely related to seedling establishment. These results indicate that different processes in native and nonnative communities influence the relationship between community structure and ecosystem function.

Introduction

Anthropogenic global change is leading to widespread changes in species distributions (Chen *et al.* 2011), altering community composition and associated species interactions (Hobbs *et al.* 2006; Wardle *et al.* 2011), and can affect a suite of ecosystem functions (Hooper *et al.* 2005; Wardle *et al.* 2011; Strayer 2012). The addition of novel species to communities is one of the most prevalent causes of species losses and gains (Pyšek *et al.* 2012), and the addition of single nonnative species can cause striking transformations in community composition and ecosystem function (Vilà *et al.* 2011; Pyšek *et al.* 2012; Strayer 2012).

Considering how a single invasive species alters ecosystems can be misleading because many ecosystems now consist of multiple invasive species (Chytrý *et al.* 2008; Catford *et al.* 2012; Strayer 2012; Kuebbing *et al.* 2013). How interactions among co-occurring nonnative species differ from those among co-occurring native species is understudied (Kuebbing *et al.* 2013), and there is little information on whether community and ecosystem responses to species gains and losses depend on the origin of the species within that community or whether communities consist of co-evolved native species or novel, evolutionarily naïve nonnative species.

A lack of coevolutionary history among co-occurring nonnative species could change the strength or nature of interactions relative to interactions among coevolved native species, ultimately modifying community and ecosystem responses to environmental change (Wilsey *et al.* 2009; Isbell & Wilsey 2011). Studies on how changes in species richness affect ecosystems, generally termed biodiversity-ecosystem function experiments, have found that community productivity is frequently positively related to the number of species or functional groups in the community (Fargione & Tilman 2005; Hooper *et al.* 2005), though the underlying mechanisms are the subject of much debate. Generally speaking, however, when a richness-productivity relationship is detected, the cause of this “net biodiversity effect” is attributed to one of two mechanisms: complementary use of resources between species that differ in their ability to access resources and/or facilitation between species (the diversity-productivity hypothesis; Tilman *et al.* 1996); or a statistical “sampling” or “selection” effect, in which

communities with more species are more likely to contain a highly productive species and thus more likely to overyield in mixture (the sampling effect hypothesis; Wardle 1999). Evidence supporting both hypotheses is widespread in studies of communities consisting of solely coevolved species (Loreau & Hector 2001; Hooper *et al.* 2005; Cardinale *et al.* 2007; Fargione *et al.* 2007). However, a single study of communities consisting entirely of nonnative species found that a productivity increase was due to a selection effect (Wilsey *et al.* 2009).

Differences between native and nonnative communities in productivity and associated mechanisms (i.e., complementarity or selection effects) can drive declines in community species richness and alter the direction of biodiversity-productivity relationships (Wilsey *et al.* 2009; Vilà *et al.* 2011). How these mechanisms might influence other community processes, like seedling establishment, has not been explored, although it is well established that differing mechanisms have different implications for long-term ecosystem processes and ecosystem stability (Loreau & Hector 2001). Additionally, while most biodiversity-ecosystem studies have focused solely on aboveground biomass, how that biomass is allocated between the above- and belowground components of ecosystems is also important for better assessments of total primary productivity in an ecosystem (Wilsey & Polley 2006; Bessler *et al.* 2009). However, surprisingly few studies consider differences in root to shoot ratios, which differ between native and nonnative plants (Wilsey & Polley 2006). Here, we use old-field ecosystems to test how phylogenetically paired native and nonnative plant communities respond to species losses and gains and ask how the two biodiversity mechanisms, selection effect and complementarity effect, are related to these responses. Old-field communities are model “novel ecosystems” that contain previously unseen combinations of coevolved native, coevolved nonnative, and evolutionarily naïve nonnative plant species (Hobbs *et al.* 2006; Cramer *et al.* 2008). Old fields are dominated by herbaceous and graminoid plants, but under minimal anthropogenic management (i.e., mowing or burning) these ecosystems would revert to wooded shrub or forested communities. We ask three inter-related questions:

- (1) How do species loss and gain affect above- and belowground biomass production in native and nonnative plant communities?
- (2) Is the mechanism (i.e., complementarity or selection effect) responsible for the “net biodiversity effect” similar in native and nonnative communities?
- (3) How do above- and belowground productivity and associated mechanisms affect woody seedling establishment in native and nonnative plant communities?

We show that while both native and nonnative communities had a positive diversity-productivity relationship, the biomass allocation patterns, seedling establishment patterns, and underlying mechanism differed between native and nonnative communities.

Materials and Methods

Potted plant communities

We used old-field ecosystems to test for differences in native and nonnative community response because they have been widely studied in tests on impacts of species gains and losses (Wilsey & Potvin 2000; Sanders *et al.* 2007; Wilsey *et al.* 2009), contain high native and nonnative species richness (Souza *et al.* 2011; Kuebbing *et al.* In Press), and are becoming more common ecosystems in the eastern United States as agricultural land abandonment continues (Cramer *et al.* 2008). We selected four phylogenetically paired native and nonnative plant species commonly found in old fields in East Tennessee that provide a robust, representative suite of native and nonnative species pairs for this particular ecosystem (Table III.8, “R” species; Wofford & Kral 1993; Souza *et al.* 2011). Some of the nonnative species overlapped in their native range, allowing us to consider the implications of coevolutionary origin (Table III.8). We selected species pairs based on the following three criteria: (1) species are locally common in old fields; (2) species had a closely related native/nonnative match at the family or genus level; and (3) we were able to obtain viable seeds.

We constructed plant communities that varied in species origin (native or nonnative) and species richness (1 to 4 species; Table III.8) in a nearly full factorial design. Owing to a limited number of seedlings of the native mint *Pycnanthemum virginianum* and the nonnative grass *Poa pratense*, we did not plant the following three-

species mixtures: *Lespedeza capitata*/*Sorghastrum nutans*/*Pycnanthemum virginianum* and *Lespedeza cuneata*/*Poa pratense*/*Leucanthemum vulgare*. All other possible species combinations within either the native or nonnative groups were replicated 20 times and each community contained 12 individual seedlings in a 3 × 4 grid with random species placement in mixed species pots. We planted a total of 560 pots (14 total species combinations × 2 community types × 20 replicates = 560 pots) and 6,720 individual plants.

We germinated seedlings in trays of twice-autoclaved sand (Quikrete Hardscapes Play Sand, item #212779) in growth chambers (12/12 h day/night photo regime, 18/22° C) and planted one-week-old seedlings in 2 L square pots (Belden Jumbo Senior Square pots, dim 13.34 cm by 16.51 cm, Belden Plastics, St. Paul Minnesota, USA). We staggered seed planting dates so that seedling emergence was within ±1 day for all seedlings. We collected seeds from local populations or purchased seeds from suppliers (Ernst Conservation Seed LP, Meadville Pennsylvania, USA; Roundstone Native Seed L.L.C, Upton, Kentucky, USA; Prairie Moon Nursery, Winona, Minnesota, USA; B and T World Seeds, Aigues Vives, France). To improve water filtration and permeability, we filled pots with a 1:1 volumetric ratio of autoclaved sand (Quikrete Hardscapes Play Sand, item #212779) and field soil, which we collected from the upper 15 cm of mineral soils from 5 fields in Oak Ridge National Environmental Research Park (35°54' 12" N, 84°20' 22" W), in Oak Ridge, Tennessee, USA. The soil classification is Captina silt loam with moderate-to-medium granular structure and medium internal drainage. Prior to 2002 the fields were managed for fescue production and now fields are maintained as old-field communities through regular mowing (Souza *et al.* 2011). We homogenized and sieved the soils (10mm) before mixing with sand.

After one week of planting, we replaced dead individuals, which we assume died from transplant stress. We unsystematically arranged pots on benches in a greenhouse at the University of Tennessee, Knoxville, Tennessee, USA and watered as necessary. At days 50 and 100, plants were fertilized with a 20-20-20 (N-P-K) water-soluble fertilizer (Southern Agricultural Insecticides, Inc., Palmetto, Florida, USA).

How do species loss and gain affect above- and belowground biomass production in native and nonnative plant communities?

After 112 days of growth, we randomly selected half of the pots (10 pots per treatment combination for 280 total pots) for biomass removal. Aboveground biomass was clipped, sorted, and dried in a forced-air oven at 60° C for 48 hours before weighing. To remove belowground coarse root biomass, we sieved soil from each pot through a 5 mm wire sieve. We did not separate root biomass by species in the mixed species pots because we were unable to distinguish individual roots visually. Roots were rinsed, dried at 60° C for ~72 hours, and weighed. The remaining soil from each pot was placed back into its respective pot for use as “biomass removal pots” (see below).

To test for differences in productivity between native and nonnative communities and across richness treatments, we used permutational ANOVAs with non-sequential sums of squares. Permutational tests are appropriate when data do not meet the assumptions of traditional parametric tests but still test the null hypothesis that imposed treatments (here, plant community origin and richness) have no effect on the response variables (Anderson 2001). In models of the community biomass response variables (aboveground, belowground, total, and above:belowground ratio) we tested for the main effects of origin (native or nonnative), richness (1 to 4 species), and composition (phylogenetic composition, e.g. “Fabaceae” or “Fabaceae-Poaceae” pair) and the interactions between origin and richness and origin and composition. The “composition” term accounts for the phylogenetic pairing of native and nonnative species while the origin × composition interaction tests how origin effects vary between paired native and nonnative communities (Wilsey *et al.* 2009).

Is the mechanism (i.e., complementarity or selection effect) responsible for the “net biodiversity effect” similar in native and nonnative communities?

We used the aboveground biomass data to calculate the net biodiversity effect (NBE) and its two additive components, the complementarity (CE) and selection effects (SE), which describe the overyielding behavior of species in mixture compared to monoculture (Loreau & Hector 2001). We calculated each component as follows: SE =

$N \times \text{cov}(\Delta RY, M)$ and $CE = N \times \overline{\Delta RY} \times \bar{M}$, where N is the species richness, ΔRY is the difference between the observed relative yield and the expected relative yield, M is a species' average monoculture biomass, and $\overline{\Delta RY}$ and \bar{M} are the mean change in relative yield and monoculture biomass for each species mixture (Loreau & Hector 2001). We analyzed the significance of the three biodiversity effects using permutational ANOVAs as described previously.

How do above- and belowground productivity and associated mechanisms affect woody seedling establishment in native and nonnative plant communities?

To test how native and nonnative plant communities respond to species gains, we added three seeds from six additional native and nonnative phylogenetically paired woody plant species (Table III.8, "SE" species) to all pots. We selected woody species that had phylogenetic pairs and are common early successional species found invading old fields in the southeastern USA. We compared seedling establishment and growth between pots with original plant biomass remaining (biomass presence pots) and pots with removed plant biomass (biomass removal pots, see above) in both monoculture and mixture pots. The inclusion of pots with soils from the previous experiment allowed us to test for soil legacy effects of plant communities.

After 100 days, we counted, clipped, and weighed the established seedlings. Overall, the native woody species had negligible seedling establishment (on average < 1 native woody seedling per pot) across all pot treatments and thus we compared variation in total number of seedlings established and average seedling biomass across pot treatments. Seedlings were dried in a convection oven at 60° C for 48 h before weighing.

We analyzed seedling establishment and growth data using the same methods as in the first experiment but included the additional fixed terms in the models: biomass removal (yes or no) and biomass removal \times origin interaction. Because selection and complementarity effects are known to influence the establishment of species in some communities (Fargione & Tilman 2005), we tested for relationships between these diversity effects and two seedling response variables, seedling number and average

seedling mass, with Pearson's correlation test (Wilsey *et al.* 2009). For all permutational ANOVAs we used the R package lmer (Wheeler 2010) and we performed all data analysis in R v.3.0.0 (R Development Core Team 2013).

Results

How do species loss and gain affect above- and belowground biomass production in native and nonnative plant communities?

Native and nonnative communities differed in their overall biomass allocation patterns. Nonnative communities had 52% higher ratios of aboveground to belowground biomass than native communities (nonnative: 3.3 ± 0.15 SE; native: 2.15 ± 0.20 SE; Table III.9). Across all potted communities, nonnative communities produced 27% more aboveground biomass and 29% less belowground biomass than did native communities (Fig. III.6.a, III.6.c, Table III.9, Table III.10). We found transgressive overyielding (when biomass in a mixture is greater than the most productive monoculture) for belowground biomass in native communities (Table III.11) but not in nonnative communities. The native community composed of the woody nitrogen fixing species *Lespedeza capitata* and the perennial grass *Sorghastrum nutans* had 18% more belowground biomass ($0.40 \text{ g cm}^{-2} \pm 0.04 \text{ g cm}^{-2}$ SE) than did the most productive native monoculture (*L. capitata*, $0.34 \text{ g cm}^{-2} \pm 0.03 \text{ g cm}^{-2}$ SE).

Both native and nonnative communities showed a positive diversity-productivity relationship for aboveground biomass production, but only native communities had a positive diversity-productivity relationship for belowground biomass production (significant origin \times richness interaction, Table III.9, Table III.10). Native communities with 4 species had 51% more above- and 67% more belowground biomass than monoculture native communities (Fig. III.6.b), whereas nonnative communities with 4 species had only 34% more above- biomass and 19% more belowground biomass than monoculture nonnative communities (Fig. III.6.d).

Community composition, which accounted for phylogenetic pairing of species within communities, always significantly predicted community response to species gains and losses (Table III.9 and Table III.10). The variation in above- and belowground biomass production in monoculture and mixture pots varied widely among species pairs

(Fig. III.7). The nitrogen-fixing Fabaceae species, *Lespedeza cuneata* (nonnative) and *L. capitata* (native), typified the differences in behavior of closely related native and nonnative species. While both species produced the highest monoculture biomass in terms of aboveground (*L. cuneata*, $0.79 \text{ g cm}^{-2} \pm 0.05 \text{ g cm}^{-2} \text{ SE}$; *L. capitata*, $0.52 \text{ g cm}^{-2} \pm 0.02 \text{ g cm}^{-2} \text{ SE}$; Table III.11) and belowground biomass (*L. cuneata*, $0.35 \text{ g cm}^{-2} \pm 0.02 \text{ g cm}^{-2} \text{ SE}$; *L. capitata*, $0.34 \text{ g cm}^{-2} \pm 0.03 \text{ g cm}^{-2} \text{ SE}$; Table III.11), they had opposite responses in mixed-species pots. Polyculture pots containing Fabaceae species (Fig. III.9) had greater differences in aboveground biomass between native and nonnative plant species than polyculture pots lacking Fabaceae species (Fig. III.9), which shows that the nonnative *Lespedeza* was primarily responsible for the overyielding behavior of nonnative plant communities in mixture and thus the positive selection and net biodiversity effect (Table III.12). The nonnative *Lespedeza* is the only nonnative species that does not overlap in its native range with the other nonnative plants used in this experiment. However, the native *Lespedeza*, presumably coevolved with its native plant counterparts, did not overyield in mixture. Instead the native grass *Sorghastrum nutans* and native herb *Achillea millefolium* did overyield in mixture, causing the negative selection effect in native plant communities.

Is the mechanism (i.e., complementarity or selection effect) responsible for the “net biodiversity effect” similar in native and nonnative communities?

Native and nonnative species differed in the sign and magnitude of the selection effect. On average native communities had a negative selection effect ($-0.22 \pm 0.09 \text{ SE}$) and nonnative communities had a positive selection effect ($0.37 \pm 0.09 \text{ SE}$), and these differed significantly by community origin ($P < 0.05$ for origin and origin \times richness; Table III.9 and Table III.10). This difference arose because native species with lower monoculture yields and nonnative species with higher monoculture yields tended to overyield in mixture (Table III.11 and Fig. III.8).

Native communities had slightly higher positive complementarity effects ($1.47 \pm 0.14 \text{ SE}$) than nonnative communities ($0.83 \pm 0.10 \text{ SE}$), but this difference was not significantly different. Both native and nonnative communities had positive net

biodiversity effect (native, 1.24 ± 0.12 SE; nonnative, 1.20 ± 0.14 SE) that did not differ across richness treatments or by community origin. The direction and magnitude of all biodiversity effects were similar across two-, three-, and four-species mixtures ($P > 0.05$ for richness terms; Table III.9).

How do above- and belowground productivity and associated mechanisms affect woody seedling establishment in native and nonnative plant communities?

Native and nonnative communities differed in seedling recruitment and growth in pots that contained intact plant communities ($P < 0.05$ community origin \times biomass removal; Fig. III.9, Table III.9). The number of seedlings was $\sim 61\%$ lower in nonnative pots with plants present than all other pot types ($P < 0.05$ community origin \times biomass removal; Fig. III.9, Table III.9). The average seedling biomass in biomass-present nonnative pots was 89% lower than that in biomass-removed nonnative pots and 46% lower than that in biomass-present native pots. We found no difference between pots that had biomass removed (soil only pots) versus pots with intact plant communities (plants + soil pots), indicating no significant soil legacy effect on woody seedling establishment in this experiment.

The average selection effect for a plant community was significantly related to woody seedling establishment and growth in native and nonnative plant communities, although the direction of this relationship differed by community origin. Increasingly positive selection effects were related to decreasing number of established seedlings and total seedling mass in nonnative plant communities (seedling number, $r = -0.69$, $P = 0.03$, seedling mass, $r = -0.57$, $P = 0.08$, Fig. III.10) but to an increasing number of established seedlings in native plant communities (seedling number, $r = 0.71$, $P = 0.02$, seedling mass, $r = 0.75$, $P = 0.01$, Fig. III.10).

Discussion

Native and nonnative communities did not have the same responses to species gains or losses in our experiment. Plant community productivity increased with species richness, but native and nonnative communities differed in the proportion of biomass allocated to roots and shoots and the diversity mechanism responsible for the total

increase. Differences between native and nonnative communities in productivity and the mechanism responsible for the positive biodiversity-productivity relationships affected woody seedling establishment. Nonnative communities had fewer established seedlings, and the total biomass of seedlings was lower, particularly in pots that had above- and belowground biomass removed. Importantly, the differences between native and nonnative plant community responses were mediated by the composition of the plant communities and by differences in the response of individual phylogenetically paired native and nonnative species; The most prominent differences between individual species were exhibited by the response of the two nitrogen-fixing plants, the native *Lespedeza capitata* and the nonnative *L. cuneata*.

Native plant communities diverged widely from nonnative plant communities in their biomass allocation strategy. Differences in yielding behavior between native and nonnative communities could affect ecosystem services, like long-term carbon storage (Tilman *et al.* 2006), that are affected by the amount of belowground biomass in the ecosystem. Native communities produced more belowground biomass than nonnative communities. Comparisons between native and nonnative species typically show that nonnatives produce more aboveground biomass than natives (Ehrenfeld 2010; Vilà *et al.* 2011). To our knowledge no research has extensively reviewed the differences between native and nonnative belowground biomass production or above- to belowground biomass ratios (i.e., root-to-shoot ratios), but studies of grassland species (Wilsey & Polley 2006) have found similar patterns to ours. Root-to-shoot ratios are affected by environmental conditions and constrained by plant phylogeny (Gedroc *et al.* 1996), both of which were controlled in our experiment, demonstrating that the origin of the species may cause this difference. For the species pairs we studied, the difference in belowground biomass between paired native and nonnative monoculture pots was near 0 and differences in belowground productivity were manifested in mixture pots (Fig. III.7). Additionally, we found transgressive overyielding, which is relatively uncommon, in belowground biomass for one native species pair (Hector *et al.* 2002).

Decreasing species richness caused a decrease in productivity in both native and nonnative communities, but the mechanisms responsible for these changes differed

by community origin. Native communities had negative selection effects and positive complementarity effects, suggesting that niche differentiation or facilitation between species may cause overyielding in mixture (Loreau & Hector 2001). However, nonnative communities had positive selection and complementarity effects, in part because the most productive nonnative species in monoculture, *Lespedeza cuneata*, overyielded in mixture more than the other, less productive, nonnative species. Our results support other studies that suggest positive selection effects are important mechanisms in nonnative communities based upon meta-analyses (Vilà *et al.* 2011) and experimental data (Wilsey *et al.* 2009). When positive selection effects are found in a community, the expectation is that the species responsible for the positive selection effect will competitively exclude the other species in that community (Wardle 2001), which fits our general understanding of how invasion by nonnative species can cause decreases in diversity over time (Wilsey *et al.* 2009; Vilà *et al.* 2011).

Although we had phylogenetically paired and functionally similar native and nonnative species, communities comprised of compositionally similar species did not necessarily respond similarly to one another. The magnitude of differences in productivity varied substantially between compositionally similar native and nonnative communities and some of these differences were due to differences in yielding behavior between phylogenetically paired species. The largest difference in individual species response was between the two most productive monoculture species: the nitrogen-fixing perennials *Lespedeza cuneata* (nonnative) and *L. capitata* (native). The nonnative *Lespedeza* overyielded in mixture, but the native *Lespedeza* did not, which influenced the positive selection effects in communities containing the nonnative *Lespedeza* and negative selection effects in communities containing the native *Lespedeza*.

Interestingly, the nonnative *Lespedeza* was the only one of the four nonnative plants used in the productivity-richness experiment that did not share an overlapping native range and therefore definitively does not have a shared coevolutionary history with the other nonnatives. While our experiment did not explicitly test for whether coevolution among nonnative species influences their interactions with one another, our results suggest that a lack of coevolution between co-occurring nonnative species (e.g., in this

experiment, *L. cuneata*) could cause divergence between compositionally similar native and nonnative communities (Thompson *et al.* 2001; Wilsey *et al.* 2009).

The average selection effect of a community was significantly related to the response of thaa plant community to species gains. Previous studies have found negative relationships between selection effects and community richness (Wilsey *et al.* 2009) and positive relationships between selection effects and community invasibility (Fargione & Tilman 2005). These results show that mechanisms responsible for altering plant community productivity owing to changing species richness can also be important for describing other plant community characteristics. Positive selection effects signal that productive monoculture species are overyielding in species mixture. Overyielding of the nonnative *Lespedeza* caused the positive selection effect in nonnative communities while the underyielding of the native *Lespedeza* influenced the negative selection effect in native communities. The opposite relationship in seedling establishment between native and nonnative communities could, therefore, be a response to the presence of *Lespedeza* in those pots. Nonnative *Lespedeza* is known to suppress woody seedling establishment through shading (Brandon *et al.* 2004), whereas native *Lespedeza* is associated with increased yielding of many grassland species (Hille Ris Lambers *et al.* 2004). The different impacts of the dominant congeneric legumes in our study align with previous studies finding differences in growth and impact of native and nonnative congeners (Morrison & Mauck 2007; Feng & Fu 2008; Burghardt & Tallamy 2013).

Our findings are driven by the differences in the yielding behavior between one species pair, native and nonnative *Lespedeza*; thus one might question whether our results are widely applicable to other plant communities. We think our results are pertinent to many invaded plant communities for two reasons. First, many plant communities contain two distinct categories of nonnative species: “dominant” or “strong” nonnatives, as determined by the relative biomass of the species within the community, such as our nonnative *Lespedeza*, and “subdominant” or “weak” nonnatives (Ortega & Pearson 2005; Peltzer *et al.* 2009). We argue that there is a high likelihood that any community containing a dominant nonnative species would overyield in mixture and cause a positive selection effect (Wilsey *et al.* 2009; Vilà *et al.* 2011), as in the behavior

of the nonnative *Lespedeza* in our communities. Second, we constrained our selection of nonnative species to those that had closely-related native species in old-field communities. This criterion excluded selection of 7 nonnative species, including four nonnatives recorded as having impacts on native plant communities in Tennessee (Tennessee Exotic Pest Plant Council 2009) that represented 6 unique plant families. Theory and experimental evidence indicate that nonnative species that are less related to native species will be more likely to invade and cause impacts (Strauss *et al.* 2006; Funk *et al.* 2008). This fact indicates that our experiment, which excluded these phylogenetically unrelated nonnatives, was a conservative test of the differences between native and nonnative communities.

Our work joins a growing body of evidence that species origin is a relevant biological trait when considering the ecological impact of a species (Simberloff *et al.* 2012; Burghardt & Tallamy 2013; Paolucci *et al.* 2013). Furthermore, the origin of species within a community should always be considered in studies examining links between biodiversity and ecosystem function (Wilsey *et al.* 2009; Isbell & Wilsey 2011). Proponents of ignoring species origin as a relevant biological characteristic argue that we should focus only on “problematic” species, based on their singular community impact. We nearly always found significant interactions between community origin and community composition, thus, our results suggest that origin is important for considering how groups of nonnative species interact with one another. Importantly, our results show that while some phylogenetically similar natives and nonnatives “behave” similarly in comparison, the presence of a “dominant” or non-coevolved nonnative can cause deviations in ecosystem function. Thus the consideration of species origin, and perhaps coevolutionary history of co-occurring nonnatives, is important if we are to understand and predict the ecosystem response of communities with new combinations of native and nonnative species owing to species gains and losses.

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Appendix

Table III.8 Fourteen phylogenetically paired old-field plant species used in a test of plant community response to species gain and losses.

Some nonnative species had native ranges that overlapped either in Europe and/or western Asia (as indicated by asterisks, *) or in eastern Asia (indicated by crosses, ‡). The first four species comprise the initial experimental treatment that manipulated plant community richness (R) and the final three species were added in a subsequent treatment testing woody seedling establishment (SE) within the initial experimental plant communities.

Family	Native Species	Nonnative Species	Experiment
Asteraceae	<i>Achillea millefolium</i> L.	<i>Leucanthemum vulgare</i> Lam. *	R
Fabaceae	<i>Lespedeza capitata</i> Michx. Hornem.	<i>Lespedeza cuneata</i> (Dum. Cours.) G. Don ‡	R
Lamiaceae	<i>Pycnanthemum virginianum</i> Schrad.	<i>Prunella vulgaris</i> L. var. <i>vulgaris</i> *	R
Poaceae	<i>Sorghastrum nutans</i> (L.) Nash	<i>Phleum pratense</i> L. *	R
Celastraceae	<i>Celastrus scandens</i> L.	<i>Celastrus orbiculatus</i> Thunb. ‡	SE
Caprifoliacea	<i>Sambucus nigra</i> L. ssp. <i>canadensis</i> (L.) R. Bolli	<i>Lonicera maackii</i> (Rupr.) Herder ‡	SE
Oleaceae	<i>Fraxinus americana</i> L.	<i>Ligustrum sinense</i> Lour. ‡	SE

Table III.9 P-values from permutational ANOVAs for tests of plant community response to species gains and losses.

Response variables included measures of plant productivity (AG = aboveground biomass, BG = belowground biomass, Total = above- and belowground biomass, AG:BG = aboveground:belowground biomass ratio), biodiversity effects (NBE = net biodiversity effects, SE = selection effect, CE = complementarity effect), and seedling establishment success (No. = number of seedlings established, mass = average seedling mass).

Treatment	Plant Community Biomass				Biodiversity Mechanisms			Seedling Establishment	
	AG	BG	Total	AG:BG	NBE	SE	CE	No.	mass
Origin (O)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.29	0.02	0.39	0.04	0.06
Richness (R)	0.26	0.007	0.07	0.04	0.76	0.25	0.19	1.0	1.0
Composition (C)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.02	< 0.0001	< 0.0001	< 0.001	< 0.001
O × R	< 0.0001	< 0.0001	< 0.0001	0.76	< 0.0001	< 0.0001	0.47	0.04	0.04
O × C	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.75	0.04	0.18
Resource Availability (RA)	---	---	---	---	---	---	---	< 0.0001	< 0.0001
O × RA	---	---	---	---	---	---	---	< 0.0001	0.02

Table III.10 Full ANOVA table from permutational ANOVAS testing the effects of community origin (native or nonnative), species richness (1 - 4 species), community composition (paired species combinations), the effects of origin on richness (origin × richness interaction) and origin on composition (origin × composition) on response variables.

Models for the response variables number of seedlings and seedling biomass included the main effect (resource availability) and its interaction with origin. Response variables were untransformed and *P*-values were generated with the ImPerm package (Wheeler 2010) in R using the arguments perm= "Exact" and seqs = FALSE (R Core Team 2013).

Aboveground biomass (g)				
Treatment	d.f.	S.S.	Iterations	Pr (Prob)
Origin	1	10.55	5000	< 0.0001
Richness	1	0.39	294	0.26
Composition	13	1134.74	5000	< 0.0001
Origin × richness	1	27.02	5000	< 0.0001
Origin × composition	11	183.62	5000	< 0.0001
Residuals	252	337.72		

Belowground biomass (g)				
Treatment	d.f.	S.S.	Iterations	Pr (Prob)
Origin	1	43.20	5000	< 0.0001
Richness	1	10.96	5000	0.007
Composition	13	402.94	5000	< 0.0001
Origin × richness	1	18.59	5000	< 0.0001
Origin × composition	11	66.62	5000	< 0.0001
Residuals	252	316.83		

Total biomass (g)				
Treatment	d.f.	S.S.	Iterations	Pr (Prob)
Origin	1	96.44	5000	< 0.0001
Richness	1	7.22	72	0.58
Composition	13	2773.81	5000	< 0.0001
Origin × richness	1	90.44	5000	< 0.0001
Origin × composition	11	381.57	5000	< 0.0001
Residuals	252	1030.35		

Table III.10. Continued.

Aboveground:belowground biomass ratio				
Treatment	d.f.	S.S.	Iterations	Pr (Prob)
Origin	1	23.58	5000	< 0.0001
Richness	1	8.11	2551	0.04
Composition	13	400.81	5000	< 0.0001
Origin × richness	1	2.12	51	0.76
Origin × composition	11	146.72	5000	< 0.0001
Residuals	252	666.53		

Net biodiversity effect				
Treatment	d.f.	S.S.	Iterations	Pr (Prob)
Origin	1	0.72	246	0.29
Richness	1	0.25	51	0.76
Composition	9	36.71	5000	0.02
Origin × richness	1	16.81	5000	< 0.0001
Origin × composition	7	42.06	5000	< 0.0001
Residuals	180	264.32		

Selection effect				
Treatment	d.f.	S.S.	Iterations	Pr (Prob)
Origin	1	3.05	5000	0.02
Richness	1	0.68	311	0.25
Composition	9	21.64	5000	< 0.0001
Origin × richness	1	14.04	5000	< 0.0001
Origin × composition	7	43.16	5000	< 0.0001
Residuals	180	102.15		

Complementarity effect				
Treatment	d.f.	S.S.	Iterations	Pr (Prob)
Origin	1	0.81	156	0.39
Richness	1	1.75	424	0.19
Composition	9	26.18	5000	< 0.0001
Origin × richness	1	0.13	115	0.47
Origin × composition	7	6.18	591	0.75
Residuals	180	262.68		

Table III.10. Continued.

Number of seedlings				
Treatment	d.f.	S.S.	Iterations	Pr (Prob)
Origin	1	13.76	2648	0.04
Richness	1	0.14	51	1
Resource Availability	1	213.19	5000	< 0.0001
Composition	14	111.69	5000	0.0004
Origin × richness	1	9.80	2602	0.04
Origin × composition	11	60.71	3284	0.04
Origin × resource availability	1	301.72	5000	< 0.0001
Residuals	529	2057.87		

Seedling biomass (g)				
Treatment	d.f.	S.S.	Iterations	Pr (Prob)
Origin	1	0.2	1649	0.06
Richness	1	0.02	51	1
Resource Availability	1	6.00	5000	< 0.0001
Composition	14	0.47	5000	0.0004
Origin × richness	1	0.05	2415	0.04
Origin × composition	11	0.18	5000	0.18
Origin × resource availability	1	0.11	5000	0.02
Residuals	529	6.68		

Table ill.11 Average above- and belowground biomass (means \pm se) for phylogenetically paired native and nonnative communities grown for 100 days in a greenhouse experiment.

Owing to seedling limitations the native FLP combinations and nonnative AFP pots were not planted. Bold and numbered (1) values represent the three most productive communities for each community origin type.

Species Pair	<u>Native Communities</u>		<u>Nonnative Communities</u>	
	Aboveground	Belowground	Aboveground	Belowground
A	2.26 \pm 0.16	0.39 \pm 0.07	2.24 \pm 0.09	0.50 \pm 0.05
F	6.89 \pm 0.32 (1)	4.47 \pm 0.38 (2)	10.57 \pm 0.63 (1)	4.67 \pm 0.25 (1)
L	1.12 \pm 0.08	1.02 \pm 0.13	3.08 \pm 0.15	0.79 \pm 0.09
P	3.69 \pm 0.46	3.47 \pm 0.42	2.94 \pm 0.19	1.57 \pm 0.36
AF	5.09 \pm 0.35	3.50 \pm 0.91	7.39 \pm 0.34	2.69 \pm 0.25
AL	2.64 \pm 0.20	0.88 \pm 0.11	3.13 \pm 0.16	1.06 \pm 0.27
AP	3.81 \pm 0.34	2.60 \pm 0.30	2.95 \pm 0.23	1.67 \pm 0.25
FL	5.42 \pm 0.43	3.12 \pm 0.34	8.63 \pm 0.37 (3)	3.81 \pm 0.23 (2)
FP	5.86 \pm 0.44 (2)	5.27 \pm 0.59 (1)	8.90 \pm 0.51 (2)	3.56 \pm 0.43 (3)
LP	4.47 \pm 0.31	4.12 \pm 0.63 (3)	3.15 \pm 0.22	1.56 \pm 0.13
AFL	4.87 \pm 0.22	2.39 \pm 0.28	7.39 \pm 0.76	2.27 \pm 0.17
ALP	3.81 \pm 0.32	2.91 \pm 0.30	3.19 \pm 0.23	0.91 \pm 0.17
AFP	5.74 \pm 0.35 (3)	3.79 \pm 0.36	na	na
FLP	na	na	7.48 \pm 0.38	2.78 \pm 0.22
AFLP	5.25 \pm 0.61	3.88 \pm 0.55	6.33 \pm 0.35	2.25 \pm 0.20

Letters represent shared family name for species pairs: Asteraceae (A); Fabaceae (F); Lamiaceae (L); Poaceae (P).

Table ill.12 Aboveground biomass (means \pm se) of 8 old-field species grown in monoculture and mixtures in potted plant communities. Change in relative yields (ΔRY_i) of each species was calculated as the difference between the species expected relative yield in mixture based upon monoculture biomass (M_i) and its observed relative yield in mixture.

Means were tested if they differed from zero with a Student's T-test and significant values are bold and asterisks represent *0.05, *0.01, ***<0.001

Species	Family	M_i	ΔRY_i
Native			
<i>A. millifolium</i>	Asteraceae	2.26 \pm 0.17	0.34 \pm 0.04 ***
<i>L. capitata</i>	Fabaceae	6.89 \pm 0.32	0.002 \pm 0.02
<i>P. virgatum</i>	Lamiaceae	1.12 \pm 0.08	0.02 \pm 0.03
<i>S. nutans</i>	Poaceae	3.69 \pm 0.46	0.32 \pm 0.03 ***
Nonnative			
<i>L. vulgare</i>	Asteraceae	2.24 \pm 0.09	0.23 \pm 0.03 ***
<i>L. cuneata</i>	Fabaceae	10.57 \pm 0.63	0.17 \pm 0.02 ***
<i>P. vulgaris</i>	Lamiaceae	3.08 \pm 0.15	-0.02 \pm 0.02
<i>P. pretense</i>	Poaceae	2.94 \pm 0.19	-0.07 \pm 0.02 **

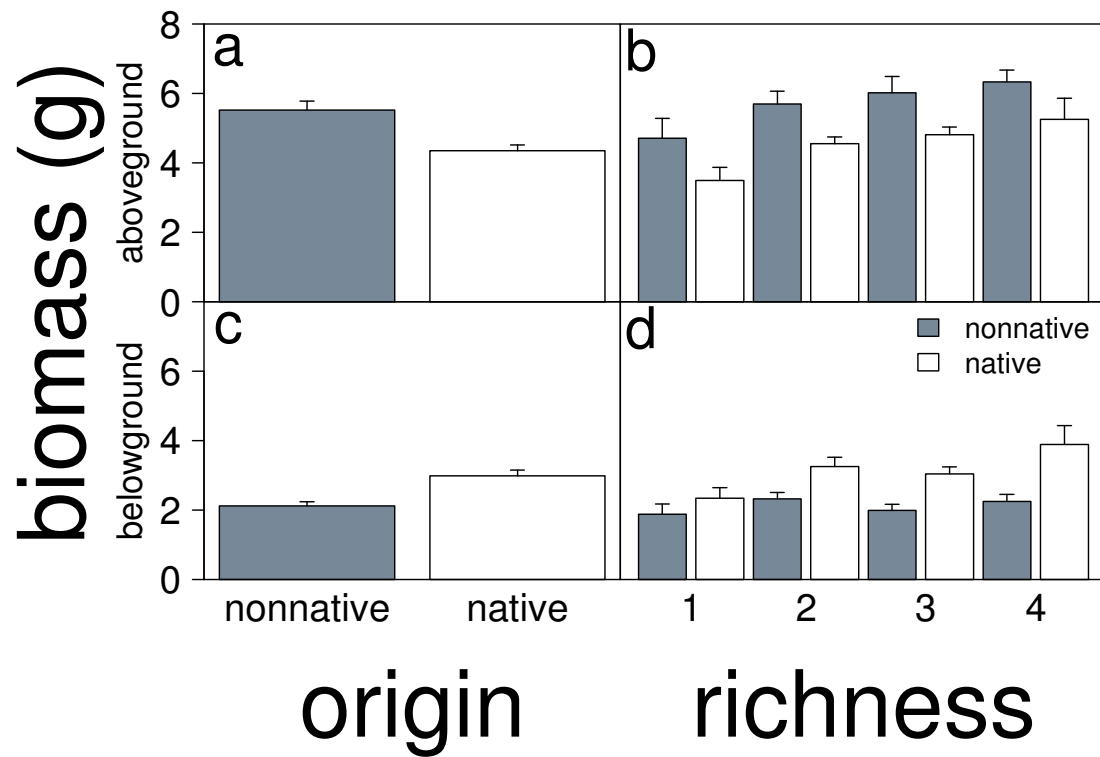


Figure III.6. Native and nonnative plant communities differed in their total aboveground (a) and belowground biomass production (c). These patterns were consistent across pot richness levels, where pots with higher plant species richness also had higher above- (b) and belowground (d) biomass.

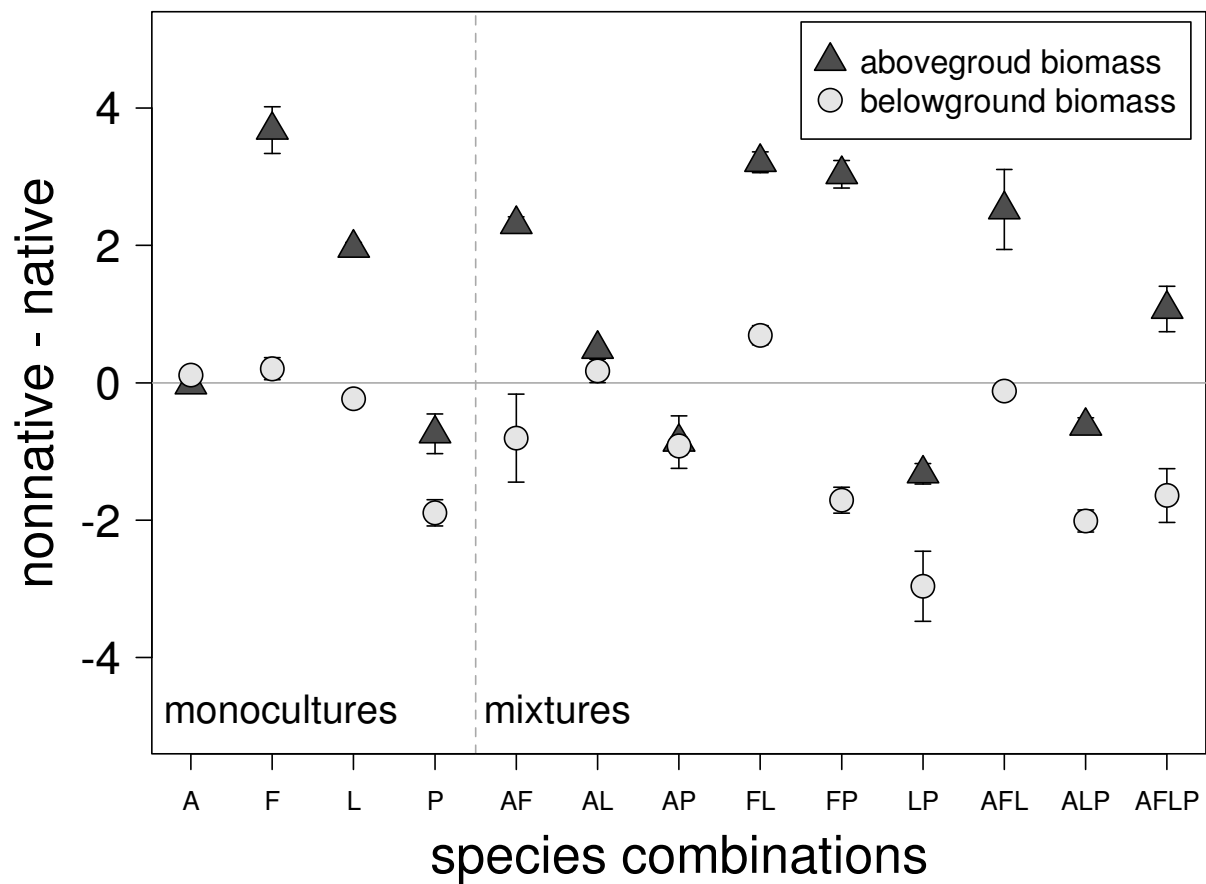


Figure III.7. Phylogenetically paired native and nonnative communities differed in the absolute differences between aboveground (triangles) and belowground (circles) biomass production after 100 days of growth in a greenhouse.

Points falling above the 0 line indicate that biomass was higher in nonnative communities than native communities and vice versa. Letters represent the following plant species families: Asteraceae (A), Fabaceae (F), Lamiaceae (L), and Poaceae (P).

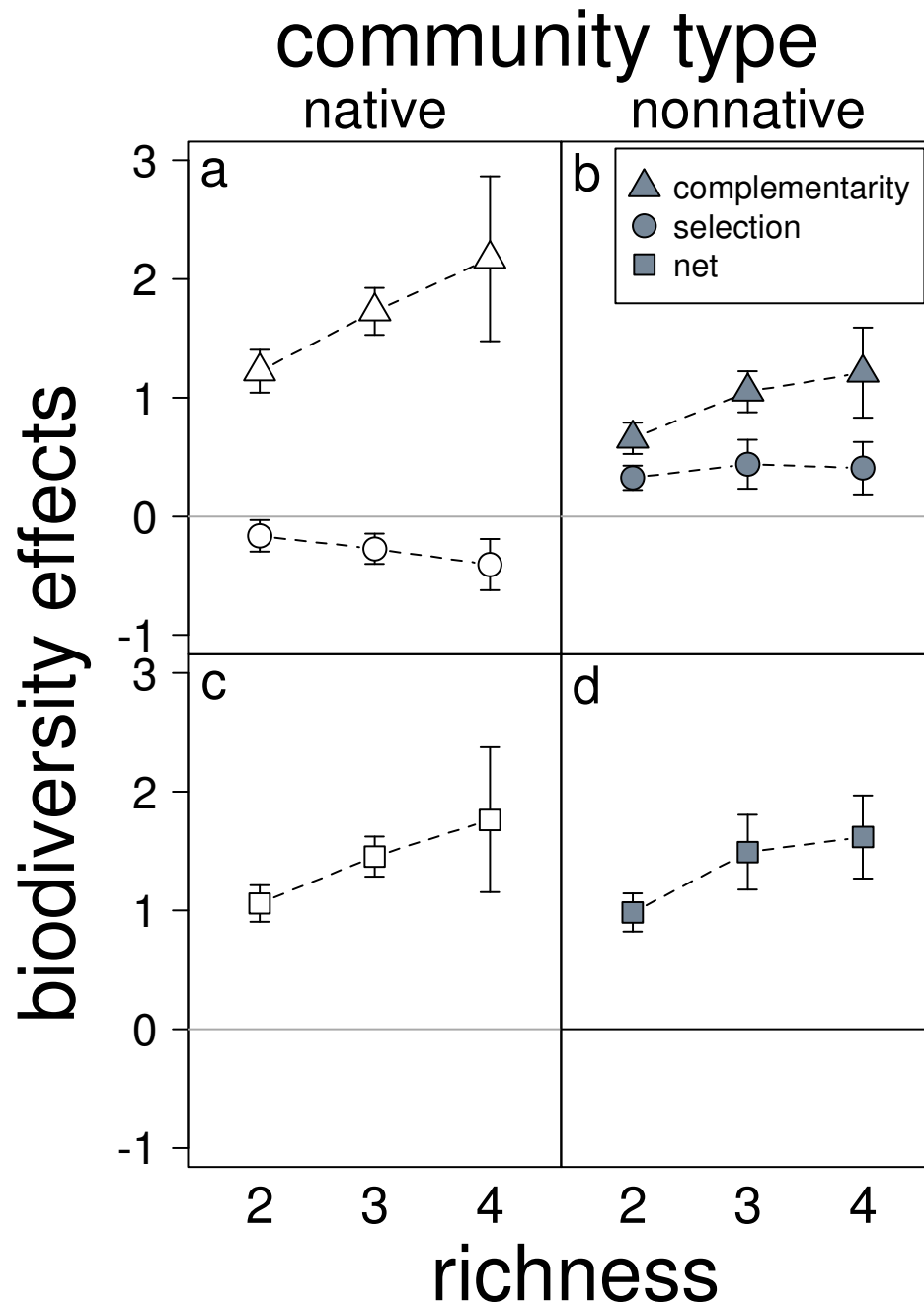


Figure III.8. Native and nonnative plant communities had similar positive net biodiversity effects, but this difference was explained by different mechanisms: negative selection and positive complementarity effects in native communities and positive selection and positive complementarity effects in nonnative communities.

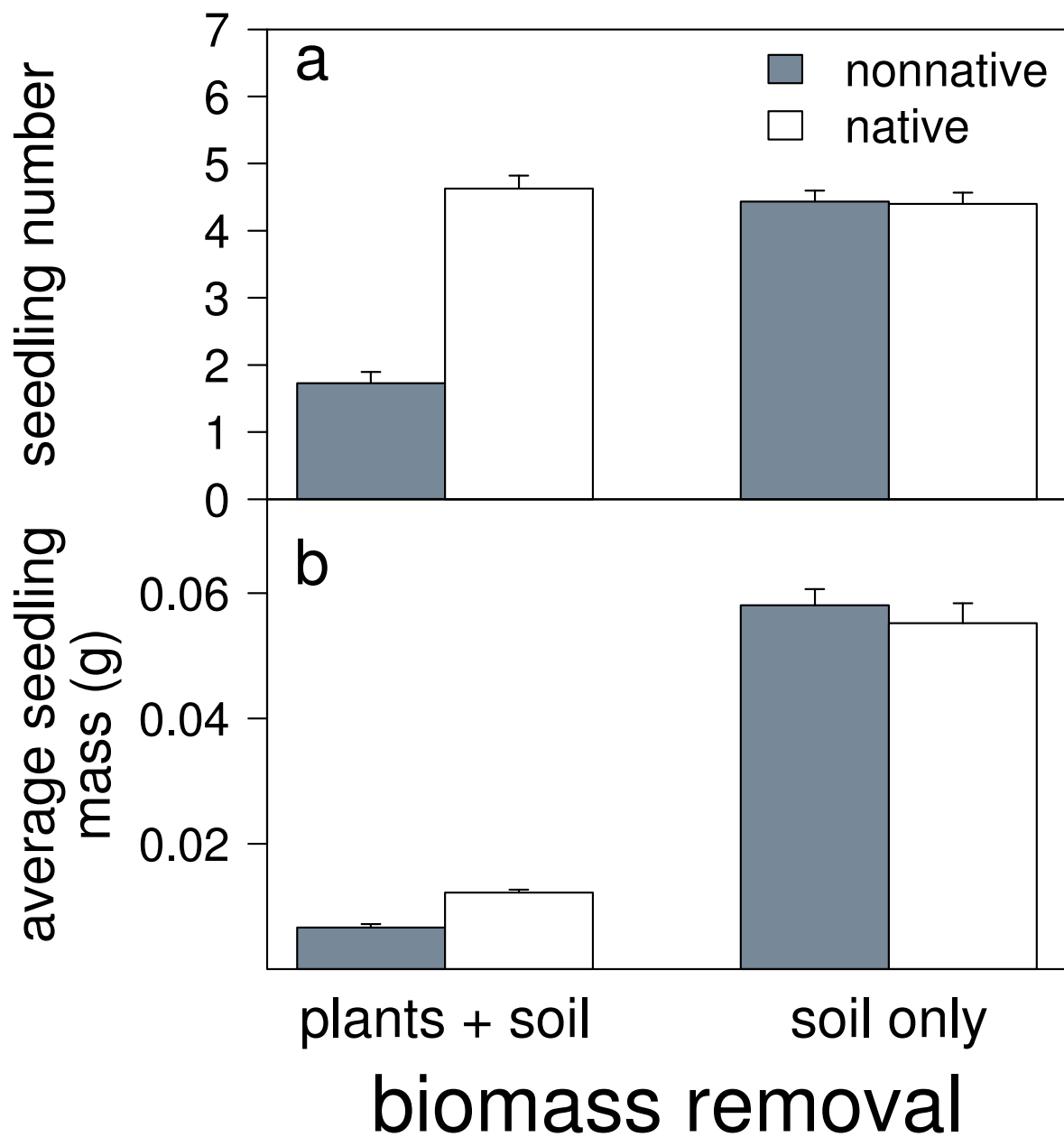


Figure III.9. Plant community origin and soil legacy effects altered the establishment (a) and average biomass (b) of introduced seedlings.

Soil legacy effect was tested by measuring seedling establishment success in pots where plant biomass had been removed (soil only) or remained intact (plants + soil)

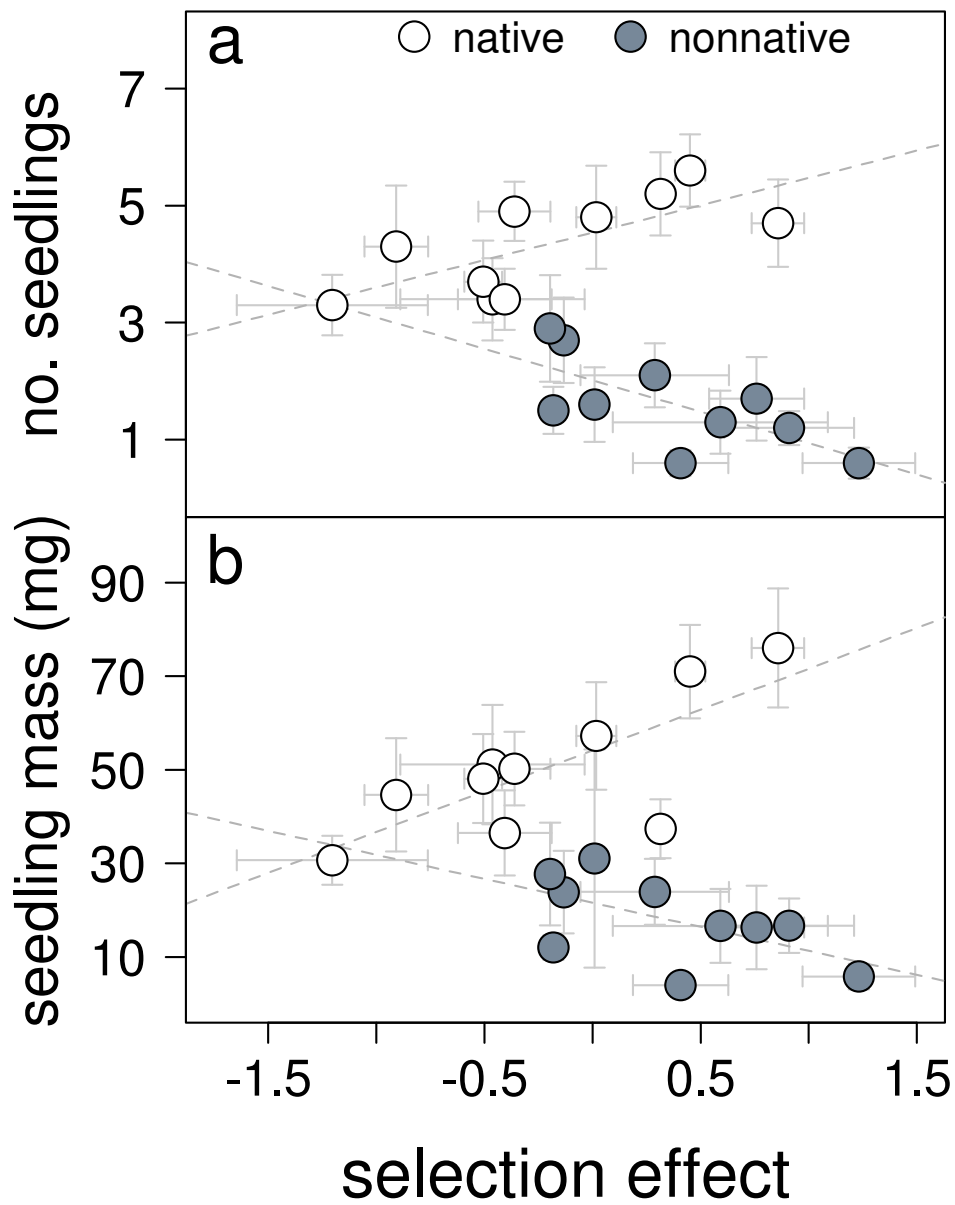


Figure III.10. Plant community selection effects were related to the number of plant seedlings established (a) and average seedling biomass(b) for native and nonnative plant communities, although the direction of the relationship differed by community type.

CONCLUSION AND FUTURE DIRECTIONS

My dissertation studied the community and ecosystem consequences of co-occurring invasive plant species. My work showed that co-occurring invasive plant species are very common in important conservation habitats, that two common woody invasive shrubs in the southeastern United States have additive and non-additive community and ecosystem impacts, and that interactions within native and nonnative plant communities are dissimilar, which leads to alterations in ecosystem impacts. Taken together, this research highlights the need for future studies to continue exploring the impacts of multiple invasive species and has generated the following questions:

1. As recommended in Chapter 1, more research on the interactions among invasive plants would be beneficial. An initial step could be a review of published research that has studied the interactions between invasive plants that addresses the relative frequency of positive, neutral, and negative interactions among invasive plants. Likewise, plant ecologists have proposed many hypotheses, such as the stress-gradient hypothesis or the productivity-gradient hypothesis, that suggest how plant interactions structures plant community dynamics. Future research could test these hypotheses using nonnative plant species.
2. As described in Chapter 1, there are a limited number of studies that address how the impacts of single invaders differ from multiple invaders and whether multiple plant invader impacts are additive or non-additive. Chapter 2 showed evidence of both additive and non-additive impacts between two functionally similar invasive plants.
 - a. We found an additive effect of the two woody shrubs on nonnative species richness, which suggests that the co-occurrence of these invasive plants promotes other nonnative species. This finding aligns with many reports that removal of 'dominant' invaders from an ecosystem leads to reinvasion of that ecosystem by 'subdominant' invaders. Future work should test for specific mechanisms that explain this pattern. Some proposed mechanisms are that nonnative plants have higher propagule pressure

than native plants in heavily invaded areas or that dominant nonnative plants can alter environmental traits that promote subdominant invaders.

- b. We found a non-additive effect of two woody shrubs on the potential activity of a carbon-degrading extracellular soil enzyme. This indicates that carbon cycling processes beneath the canopies of these two invaders differs, which could be a result of changes in the soil microbial community or the quality or quantity of plant litter into the soils. Further research could ask how co-occurring nonnative plants affect soil microbial communities and how these changes feedback to affect carbon and nutrient cycling in forests.
3. In Chapter 3, we found that closely related native and nonnative plant communities did not respond similarly to species loss and species gains, two ubiquitous forms of environmental change. Further studies could explore the response on native and nonnative plant communities to other environmental changes, such as increasing nitrogen deposition or anthropogenic disturbances.

VITA

Sara Elizabeth Kuebbing was born in Atlanta, Georgia and graduated from Henry W. Grady High School in May 2001. She attended the University of Delaware and graduated in January 2005 with a B.S. in Wildlife Ecology from the College of Agriculture and Natural Resources. From 2005—2009 Sara worked for a variety of conservation and scientific research organizations including The Nature Conservancy, The Lewis Creek Association, and the United States Geographical Survey. In August 2009, Sara enrolled as a graduate student in the Ecology and Evolutionary Biology Department at the University of Tennessee, Knoxville and completed her dissertation in May 2014.