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THE SPATIAL DISTRIBUTION OF INVASIVE PLANT PRESENCE, ABUNDANCE, AND IMPACT

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THE SPATIAL DISTRIBUTION OF INVASIVE PLANT PRESENCE, ABUNDANCE, AND
IMPACT

A Dissertation Presented

by

EVELYN M. BEAURY

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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Organismic and Evolutionary Biology

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DEDICATION

To diverse and healthy ecosystems, good friends, family, and my dogs.

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I would like to thank my committee, Jeff Corbin, Jack Finn, and Toni Lyn Morelli. Jeff, thank you for your kindness and composure. You helped me avoid imposter syndrome through some of the more difficult aspects of my dissertation and you encouraged me to take a chance on my new position, which I am thrilled about. Jack, thank you for your patience and good humor. Explaining complex statistics to someone with little to no background is not easy, and I appreciate all the time and effort you spent helping me figure everything out (and all the afternoon coffee breaks when we got stuck!). Toni Lyn, thank you for your ambition, energy, and enthusiasm. You inspire the go-getter scientist I hope to be someday.

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and I cannot thank you enough for the opportunity to work with you over the last few years (and hopefully more to come).

ABSTRACT

THE SPATIAL DISTRIBUTION OF INVASIVE PLANT PRESENCE, ABUNDANCE, AND IMPACT

FEBRUARY 2022

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Across the globe, native ecosystems are increasingly threatened by the spread and negative impacts of non-native, invasive plants. While many hypotheses explore what contributes to the damage caused by invasive species, few studies have tested these hypotheses at the macroscale. My dissertation addresses this knowledge gap by synthesizing thousands of vegetation surveys from ecosystems across the United States. I leverage existing, as well as explore new macroecological methods to deepen our understanding of the spatial ecology of plant invasions.

My dissertation also asks how effective management and policy has been at reducing plant invasions. The primary introduction pathway for invasive plants is the horticultural industry. Despite efforts to regulate horticultural trade, I found that 61% of U.S. invasive species were still marketed as garden plants. Consistently regulated invasive plants were sold less often, but many high-impact invaders were still available through plant trade. More policy efforts are needed to stop the spread of invasive plants.

A key take-home from my research is that the environmental conditions of recipient native communities play an important role in determining invasive plant success. For example, species-rich native plant communities were more resistant to invasive plant establishment. But once an invader reaches high abundance, high richness native communities were more susceptible to diversity loss. In areas with high anthropogenic effects, invasive plants were more likely to establish as well as have greater negative impacts on native plant communities. The effect of the

environment on invasive plant abundance differed by species. Some invasive plants reached high abundance in any environment where it was able to occur, whereas other invasive plants only reached high abundance in a subset of the habitats where they could occur. While some invasion processes may be species-specific, my research shows that at macroscales, top priority habitats for management should include species-rich native plant communities in high resource environments and communities facing high anthropogenic effects. These findings deepen our understanding of the spatial ecology of plant invasions.

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CHAPTER 1

INVADERS FOR SALE: THE ONGOING SPREAD OF INVASIVE SPECIES BY THE PLANT TRADE INDUSTRY

1.1 Abstract

The sale of ornamental nonnative plants is a primary pathway of invasive plant introduction into the US. As a result, many nonnative plants have been identified as noxious weeds by federal and state governments, or as problematic invasive plants by agencies and nonprofit organizations. However, it is unclear whether identifying a species as invasive has curtailed its sale as an ornamental. Using the Google search engine and a database of nursery catalogs, we found that 61% of 1285 plant species identified as invasive in the US remain available through the plant trade, including 50% of state-regulated species and 20% of federal noxious weeds. Vendors offering invasive plants were located in all lower 48 states. The widespread availability of invasive plants in the U.S. is likely a symptom of disjointed state regulations that fail to protect ecosystems and economies. Regional regulation coupled with outreach to growers and consumers is needed to reduce the ongoing propagation of invasive plants in the US.

1.2 Introduction

More than half of the world's flora has been introduced to novel regions for use in agriculture, medicine, and gardening (Mack & Erneberg 2002; Van Kleunen et al. 2018; Guo et al. 2019). The propagation of plants and plant products is a valuable component of economies from local to global scales (Hulme et al. 2018; Van Kleunen et al. 2018), but plant trade has unintended consequences. When relocated outside their native range, some ornamental plants escape cultivation, spread into natural areas, and become invasive, with potential negative impacts on the environment and human health (Van Kleunen et al. 2018). Nearly 40% of the

invasive plants now in the U.S. were originally introduced as ornamentals (Lehan et al. 2013), and these species affect nearly every ecosystem of the country and continue to expand into new areas (Allen & Bradley 2016).

Once discovered to be invasive, plant imports into the U.S. can be prohibited through border inspections (e.g., the U.S. Department of Agriculture Animal and Plant Health Inspection Service [APHIS] Plant Protection and Quarantine Program; Reichard & White 2001) or their sales can be regulated internally by government agencies at the federal and state levels (Beck et al. 2008; Hulme et al. 2018). Because management is costly, regulation is typically restricted to those invasive species with the most severe negative impacts (Beck et al. 2008). For example, the U.S. Federal Noxious Weed Act identifies 98 plant species and seven genera considered to be the greatest threats to U.S. natural resources; it is illegal to grow or sell these plants anywhere in the U.S. without a permit. Most states have similar regulatory lists intended to reduce the spread of high impact invasive plants, and there are a number of unregulated nonnative plants identified as invasive and managed by state and federal agencies or conservation organizations. These regulatory and nonregulatory lists combine to over a thousand species considered invasive in the U.S. (USDA PLANTS Database [<https://plants.usda.gov/home>], Invasive Plant Atlas [www.invasiveplantatlas.org]).

The purpose of regulatory and nonregulatory lists and the identity of listed species varies markedly across states (Beck et al. 2008; Quinn et al. 2013). Some regulatory lists focus on agricultural weeds (McCubbins et al. 2013), whereas others focus on ornamental species whose introduction could reasonably be prevented through nursery inspections (G Fish and D Cygan personal communication). Other regulatory lists include invasive plants likely to impact natural areas, in which the list is intended to prioritize species for management and prevent spread to new areas (M Renz personal communication). Unregulated invasive plants include species for which insufficient data exist to categorize them as invasive, species that have been reported as invasive

by local experts (e.g., by National Park Service ecologists), and species with high market value to the ornamental plant industry (Reichard & White 2001; Beck et al. 2008; Quinn et al. 2013).

Because plant invasions often span political boundaries (e.g., state borders), this piecemeal approach to regulation and management likely enables some invasive plants to remain on the market. For example, species identified as invasive and regulated in certain states can still legally be sold elsewhere (Reichard & White 2001; Hulme et al. 2018). It is therefore unlikely that horticulturists will abandon a species with high market value unless it is consistently regulated (Reichard & White 2001; Knight et al. 2011; Hulme et al. 2018). Moreover, inconsistent state lists make it difficult for plant traders and consumers to stay informed about which species are invasive (Reichard & White 2001; Burt et al. 2007). Popular ornamentals are often easy-to-grow yet hardy species that are resistant to pests and pathogens (Mack 2005; Van Kleunen et al. 2018; Guo et al. 2019). Because these traits are also associated with successful invaders (Van Kleunen et al. 2018), and given that there are over a thousand plant species considered invasive in the U.S., even well intentioned growers and consumers may continue to promote invasions (Dehnen-Schmutz et al. 2007).

It has been 20 years since the ornamental plant trade was first identified as a primary source of invasive plants in the U.S. (Reichard & White 2001). Following this discovery, numerous strategies to reduce ornamental invasions have been put forth, including increasing regulations (Lodge et al. 2006), creating “green lists” of native alternatives to invaders (Dehnen-Schmutz 2011), and voluntary initiatives encouraging growers to sell noninvasive plants (Burt et al. 2007; Hulme et al. 2018). Here, we examined how well these regulatory and ethical guidelines serve to limit the spread of invasive plants by identifying (1) the proportion of plants identified as invasive in the US that remain offered for sale as ornamentals, (2) the spatial extent of these sales across the lower 48 states, and (3) which sales co-occur with federal and state regulations.

1.3 Methods

We compiled a list of plants defined as invasive and/or noxious in the lower 48 U.S. Regulated species were identified by the USDA federal noxious weed list or by state invasive plant, noxious weed, and noxious seed laws. Unregulated species included additional species listed by the Invasive Plant Atlas. Collectively, these sources represent the pool of species considered harmful to US agriculture, natural resources, public health, or the environment (Beck et al. 2008). We excluded nonvascular species, taxa identified to genus only, and species invasive only in Hawaii or Alaska (although all federal noxious weeds were included).

We conducted a standardized search for opportunities to purchase all species (n = 1285) using Google and Plant Information Online (previously accessible via <https://plantinfo.umn.edu>). Plant Information Online is a University of Minnesota database that documents retail and wholesale nursery catalogs in the U.S. As of July 2021, the database is undergoing maintenance; please contact the University of Minnesota Horticultural Library for updates on access. Each species was searched for once between August 2017 and December 2019, and therefore results represent a static period in time. We considered a species to be available through the plant trade if it was offered for sale by at least one vendor.

Using Google, we searched for each species' scientific name (and synonymous scientific names listed by the USDA PLANTS Database using an "OR" statement) and common names followed by the key words "for sale", "plant for sale", and "seeds for sale" in separate searches. For each search string, we recorded offers for sale in the first three pages of Google results. We only recorded an offer for sale if the vendor was located within the lower 48 states and listed the full scientific name (species of the same genus often share common names). We distinguished between two types of vendors based on their websites: (1) commercial nurseries with a street address for a storefront or garden center where one can purchase plants and seeds (these vendors often sold online as well); and (2) e-commerce trade, where vendors or individuals offered plants or seeds online only and did not appear to have a storefront. For each vendor offering an invasive

plant, we recorded the name of the seller, their location if available, and for nurseries, whether or not the seller labeled the plant as problematic or restricted shipping the plant to certain states.

Using the Plant Information Online website, we searched for each species' scientific name and synonyms (this database did not allow searches by common name) and if a species was offered for sale, we recorded each seller's name and location. This database included nurseries with on-the-ground locations (i.e., no vendors were online only) and did not provide information whether the plant was labeled as problematic or could not be shipped. No information was found on the Plant Information Online website for 125 of the 1285 species.

Many invasive plants on our list were introduced into the U.S. accidentally (Lehan et al. 2013) and are therefore unlikely to be currently for sale or to have ever been for sale. To better assess whether invasive species originally introduced as ornamentals remain on the market, we compared our list to plants identified by Lehan et al. (2013) as having been introduced through the plant trade. We used R (v3.6.0) to generate summary statistics and ArcGIS (v10.6.1) to create map visualizations in a contiguous Albers equal-area conic projection.

1.4 Results

Of the 1285 plant taxa identified as invasive in the U.S., we found 778 (61%) available for purchase (Table 1.1). These species were offered by 1330 different vendors, resulting in more than 15,000 opportunities to purchase invasive plants across all lower 48 states (Figure 1.2). The majority of vendors were retail or wholesale nurseries ($n = 1081$, 81%) as opposed to e-commerce ($n = 249$, 19%); however, the greatest number of species for sale ($n = 281$) was on eBay, and other large online marketplaces were also common distributors (e.g., Amazon, Etsy, eCRATER). Few vendors labeled invasive species as problematic (4% of Google nursery sales) or identified restrictions on shipping species to certain states (16% of Google nursery sales). The number of vendors selling each species varied substantially but declined with the number of states regulating a species' movement (Figure 1.2).

1.4.1 Regulated plant sales

About half of the invasive plants on our lists (688 of the 1285) were regulated by one or more state governments or by the federal government, suggesting they are problematic enough to warrant regulation and management. Nonetheless, nearly 50% of these (n = 343) were offered for sale somewhere in the US (Table 1.1), amounting to 5539 opportunities to purchase regulated invasive plants from 916 vendors. The regulated species offered for sale by the most vendors included Chinese silvergrass (*Miscanthus sinensis*), available from 140 vendors in 37 states, including Connecticut, where it is regulated; common sunflower (*Helianthus annuus*), available from 122 vendors in 37 states, including Iowa, where it is regulated; butterflybush (*Buddleja davidii*), available from 109 vendors in 33 states, including Oregon, where it is regulated; and Japanese barberry (*Berberis thunbergii*), available from 109 vendors in 28 states, including Connecticut, Minnesota, and Wisconsin, where it is regulated.

Most instances in which vendors offered regulated plants (93%) occurred outside of states where species were regulated. However, we found 146 species offered for sale in the same state where their sale was regulated (Figure 1.1c). These species were available from 232 vendors, resulting in 382 unique opportunities to purchase invasive plants despite state regulations. This occurred in 34 states, most frequently in Wisconsin, Ohio, and Oregon. Japanese barberry (*B. thunbergii*, listed and available in Connecticut, Minnesota, and Wisconsin) and glossy buckthorn (*Frangula alnus*, listed and available in Connecticut, New York, Illinois, Minnesota, Ohio, and Wisconsin) were most frequently offered in states regulating their sale (Figure 1.3). We also documented 856 cases in which a species was offered for sale in a state directly neighboring another state where the species was regulated; this occurred for 221 regulated species across 447 vendors in 47 states, with North Dakota being the sole exception.

We found 20 of 98 (20%) federal noxious weeds offered for sale by 76 vendors, resulting in 81 opportunities to purchase noxious weeds in 30 states. Half of these cases were vendors selling a cultivar of the noxious weed cogongrass (*Imperata cylindrica*).

1.4.2 Unregulated plant sales

The remaining 597 species were identified as invasive by the Invasive Plant Atlas. We found 435 (73%) of these offered for sale by 1130 vendors distributed across all lower 48 states. The unregulated species offered most frequently included panicked hydrangea (*Hydrangea paniculata*) and Japanese maple (*Acer palmatum*).

1.4.3 Comparison to original introduction pathway and date

Lehan et al. (2013) reported introduction pathways for 916 of the species we searched; 434 of these species (47%) were deliberately introduced via pathways linked to plant trade: as forage crops, ornamentals, forestry plantings, turfgrass, and aquarium plants, or in wild seed mixes. Of these deliberately introduced species, 360 (83%) were still available for sale. Most were introduced in the 20th century, although the initial introduction of several ornamentals dates back to the 15th–16th centuries.

Table 1.1 Count and percentage of invasive plants available for purchase as ornamentals within the continental U.S.

List	Number of species searched	Number of species available for purchase	Percentage of species available for purchase
Regulated species*	688	343	50%
Unregulated species	597	435	73%
Imported ornamentals ⁺	434	360	83%
All species	1285	778	61%

*includes federal noxious weeds ($n = 98$, 20 found for sale); ⁺species originally introduced into the US as ornamentals.

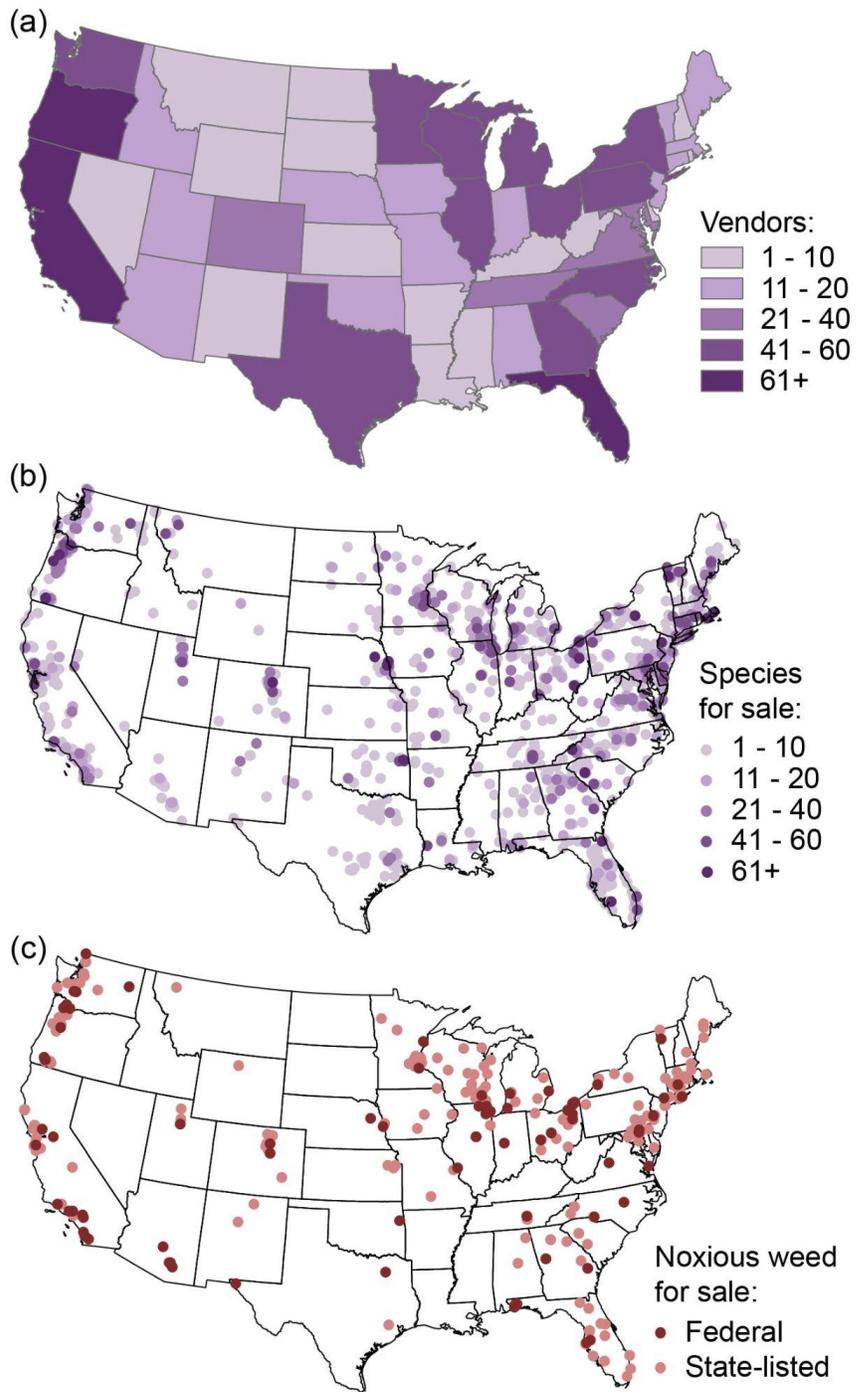


Figure 1.1 (a) The number of vendors offering invasive plants in each state. (b) The distribution of vendors offering invasive plants across the U.S.; colors correspond to the number of invasive species available for sale by that vendor. (c) Vendors offering invasive species for sale within states where their trade is subject to federal or state regulations.

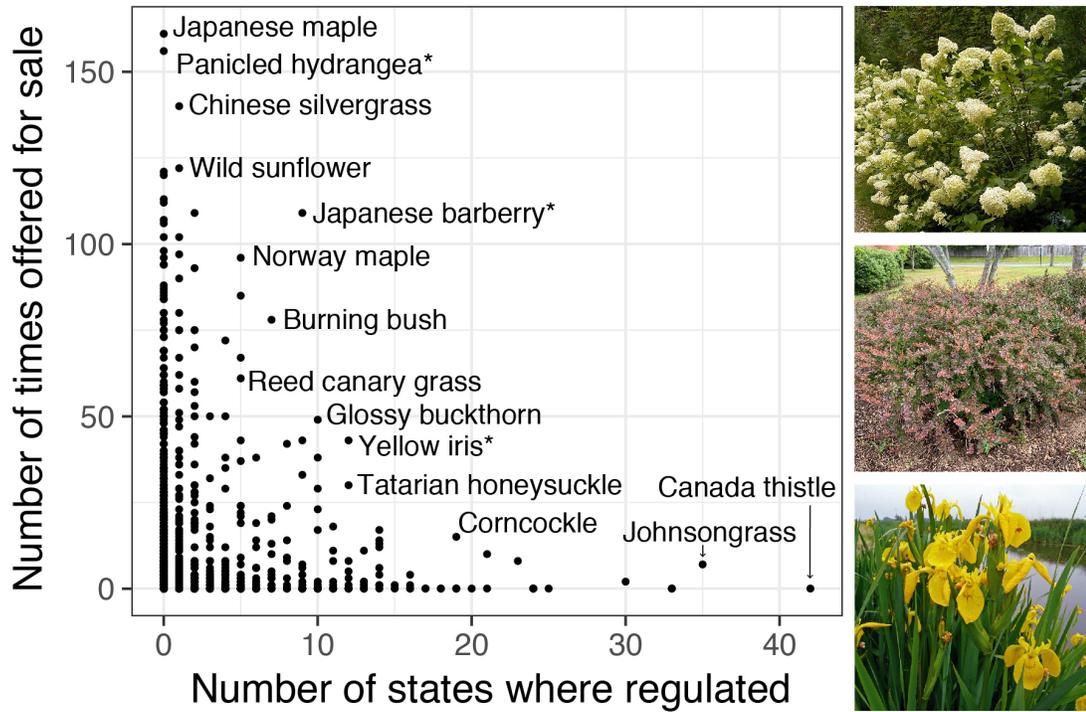


Figure 1.2 The number of vendors offering each species for sale versus the number of states in which the species was regulated. Asterisks indicate species pictured on the right. Top: panicked hydrangea (*Hydrangea paniculata*; photo by F Vincentz); middle: Japanese barberry (*Berberis thunbergii*; photo by E Beaury); bottom: yellow iris (*Iris pseudacorus*; photo by J Billinger).

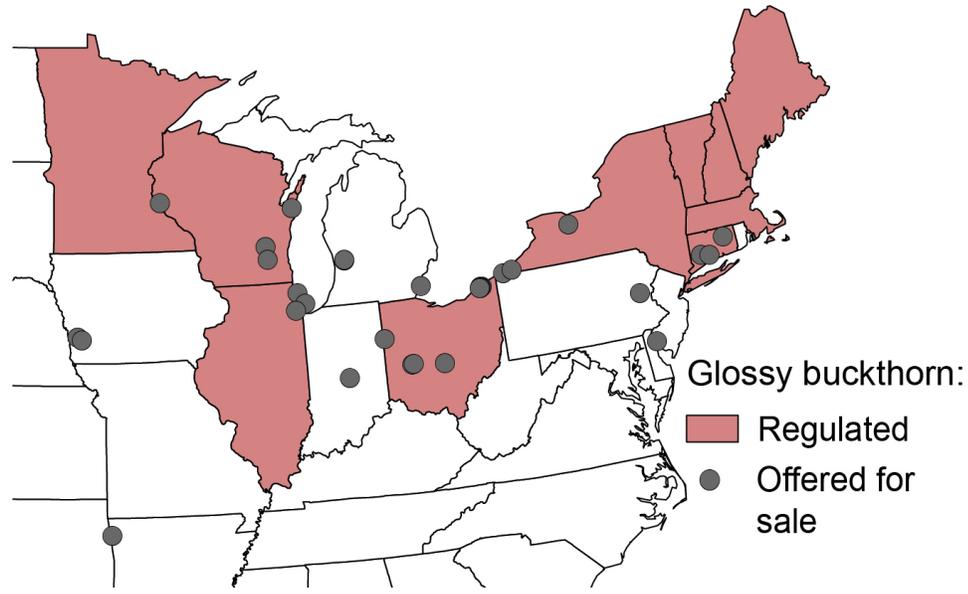


Figure 1.3 Locations of vendors selling glossy buckthorn (*Frangula alnus*) in the northeastern U.S., including within states where buckthorn is regulated.

1.5 Discussion

It has been known for decades that the sale of nonnative ornamental plants is the primary pathway through which invasive plants are introduced into the US (Reichard & White 2001; Mack & Erneberg 2002). Despite repeated calls for voluntary and regulatory change to the plant trade industry (Reichard & White 2001; Burt et al. 2007; Knight et al. 2011), imports of new exotic plants into the US continue to rise (Bradley et al. 2012; Seebens et al. 2017). We documented thousands of opportunities to purchase invasive plants in the U.S., including federal- and state-regulated species and ornamental plants that were identified as invasive decades ago. By quantifying the extent of access to invasive plants through the plant trade, our analysis shows that greater effort is needed to reduce the sale of invasive plants in the U.S.

All species included in our analysis were identified as invasive on regulatory or nonregulatory lists, but these species likely encompass a range of impacts, as well as market value to the plant trade. Although a consistent way to compare all species' invasiveness is lacking, states often select species for regulation following an assessment of negative impacts to

natural resources, agriculture, or the environment (Buerger et al. 2016), and therefore the number of states in which a species is regulated can serve as a proxy for its potential impacts (though many high-impact species remain unregulated). Similarly, although we did not record the costs of purchasing these plants, the number of different vendors offering a species for sale can inform how commonly a species is distributed, which can serve as a proxy for its market value.

Variation in the number of states where a species is regulated and the number of vendors offering it for sale (Figure 1.2) can serve as a framework for prioritizing species for regulation, including assessing the likelihood of phasing species out of cultivation given how popular they are as ornamentals. For example, Japanese maple and paniced hydrangea were offered by the most vendors, suggesting that these plants are popular with consumers and may be highly profitable for vendors. According to the Invasive Plant Atlas, both species have been observed growing outside of cultivation in the northeastern U.S., but neither is regulated in the U.S.; because their impacts may not be widespread, they could be considered low priority for management.

Species that are widely distributed as ornamentals and have well-documented negative impacts present a larger challenge for regulation (Knight et al. 2011). For instance, Japanese barberry is a popular ornamental shrub that was offered for sale by more than 100 vendors in 33 different states, including three states where it is regulated. This species, which has naturalized in more than half of the lower 48 U.S. states (Bargeron & Moorhead 2007), has the potential to form dense thickets, outcompete native species, and carry ticks that transmit Lyme disease (Williams et al. 2009). Barberry is regulated in nine states and could spread into the Northeast, Upper Midwest, and Pacific Northwest (Allen & Bradley 2016). For states in these regions, marketing native alternatives to barberry may be both profitable and environmentally friendly.

We found fewer vendors selling species that might be more likely to have widespread impacts considering their regulation in multiple states (Figure 1.2; Beck et al. 2008). These species included glossy buckthorn (regulated in ten states), common corncockle (*Agrostemma*

githago; 19 states), tatarian honeysuckle (*Lonicera tatarica*; 12 states), yellow iris (*Iris pseudacorus*; 12 states), and several others (Figure 1.2). Considering that these are considered to be problematic species in multiple states and that they were offered for sale by a smaller number of vendors, ending their sales more broadly across the U.S. should be a top priority for regulation and management. Special attention should be paid to species that were available for purchase in the same state where they are regulated; for instance, glossy buckthorn was frequently found for sale in states in which it is regulated, or in neighboring states (Figure 1.3). Although some of these sales may involve a sterile cultivar (which may not be fully sterile; Knight et al. 2011), inconsistent regulation of buckthorn provides opportunities for this species to continue to spread (Figure 1.3).

Across the U.S., disjunct regulations allow plants to be sold in states adjacent to where they are regulated, leading to high invasion risk in neighboring states with similar environments. In 47 of the lower 48 states, we found regulated species offered for sale in an adjacent state; this lack of regulatory consistency between adjacent states may result in invasive plants being introduced into new areas and creates barriers for growers to comply with guidelines. For example, horticulturists have reported difficulty accessing up-to-date lists of what is invasive in their area (Burt et al. 2007), which reduces the ability of nurseries to comply with regulations or participate in voluntary codes of conduct (Yue et al. 2011). However, local-scale studies have reported that when informed about the extent of invader impacts, both growers and consumers preferred native plants (Burt et al. 2007; Yue et al. 2011; Oele et al. 2015). More transparent and consistent lists of invasive plants can therefore improve guidance to the ornamental plant trade industry.

The development of regional lists of prohibited plants is one potential solution to facilitate the ornamental industry's awareness of regulations and states' capacity to reduce invasive plant spread (Lodge et al. 2006). The percentage of regulatory species available for purchase was lower than the percentage of unregulated species (Table 1.1), and most regulated

plants were offered for sale outside of states where they were prohibited. This suggests that regulations effectively reduce within-state invasive plant sales, and that suppliers and consumers are motivated to reduce ecological harm when provided direction from their state. However, inconsistent information, variation in regulations, and lack of enforcement allow invasive species to remain on the market (Reichard & White 2001). Consequently, expanding regulations to include regionally prohibited species may result in a more consistent and complete regulatory landscape. Several states have worked toward this under direction from the National Association of Invasive Plant Councils, which coordinates activities within and between state and regional invasive plant councils. At the national scale, we found vendors selling 20 of the 98 federally regulated species, but only three of these (*Imperata cylindrica*, *Prosopis velutina*, and *Rubus moluccanus*) were offered by more than five vendors across the U.S. In general, the percentage of federally regulated species that were available was much lower than that of state-or unregulated species (Table 1.1), suggesting that more direction at regional and national levels may result in fewer holes in the current approach to regulating invasive plants (Lodge et al. 2006).

The most concerning case of federal noxious weed sales was the widespread availability of cogongrass, which was offered by 33 vendors across 17 states. Cogongrass has been on the federal noxious weed list for more than a decade, and it is labeled as one of the International Union for Conservation of Nature's "world's most invasive plants", with negative impacts to native biodiversity, fire regimes, and nutrient cycling (Estrada and Flory 2015; Fusco et al. 2019). We often found offers of the "red baron" or "rubra" cultivar of cogongrass, which is exempt from regulation in some states because it has been described as a sterile, slow-growing cultivar. However, this cultivar has the potential to regain invasive tendencies (Cseke & Talley 2012) and similar escapes of "sterile" cultivars have been documented for other ornamental invaders, such as glossy buckthorn, burning bush (*Euonymus alatus*), and Japanese barberry (Knight et al. 2011). Continuing to plant cultivars for which sterility is uncertain has the potential to exacerbate active invasions.

In addition to risks associated with the sale of cultivars, the rise in e-commerce trade of invasive plants could seed future invasions, including in areas where conditions will become more suitable with climate change (Bradley et al. 2010). We observed very low rates of nurseries restricting plant shipments or labeling species as weedy or invasive. Plants available through large online marketplaces (such as eBay and Amazon) were often transient sales offered by individuals, which may make them more difficult to find and regulate (Humair et al. 2015). As a result, a single seller has the potential to ship plants to different regions of the U.S., including shipping plants that may be legally grown in their region but that are considered invasive elsewhere. For example, we documented more than a hundred vendors offering Chinese silvergrass for sale; although currently regulated only in Connecticut, this species is spreading rapidly throughout southern and Mid-Atlantic states (Bargeron & Moorhead 2007), with growing evidence that it outcompetes native species and exacerbates fires (Fusco et al. 2019). Considering its availability as an ornamental outside of its invaded range, there is high risk that Chinese silvergrass, and similarly distributed but unregulated species, will spread to new regions.

The ongoing sale of invasive ornamental plants documented here underscores the need for improved regulations and awareness of invasive species in the U.S. Potential solutions include increasing consistency in regulations, greater coordination among states at regional and national levels, and providing growers with transparent information to aid their efforts in reducing the spread of invasive plants. Although barriers to effective enforcement of federal and state regulations exist (e.g., lack of resources for regulation, high market value species; Knight et al. 2011), there are strong ecological and economic benefits to prohibiting the import of new exotic species that have the potential to become invasive (Keller et al. 2007) and to slowing the spread of species known to have negative impacts (Lodge et al. 2006).

CHAPTER 2

BIOTIC RESISTANCE TO INVASION IS UBIQUITOUS ACROSS ECOSYSTEMS OF THE UNITED STATES

2.1 Abstract

The biotic resistance hypothesis predicts that diverse native communities are more resistant to invasion. However, past studies vary in their support for this hypothesis due to an apparent contradiction between experimental studies, which support biotic resistance, and observational studies, which find that native and non-native species richness are positively related at broad scales (small-scale studies are more variable). Here, we present a novel analysis of the biotic resistance hypothesis using 24,456 observations of plant richness spanning four community types and seven ecoregions of the United States. Non-native plant occurrence was negatively related to native plant richness across all community types and ecoregions, although the strength of biotic resistance varied across different ecological, anthropogenic and climatic contexts. Our results strongly support the biotic resistance hypothesis, thus reconciling differences between experimental and observational studies and providing evidence for the shared benefits between invasive species management and native biodiversity conservation.

2.2 Introduction

In the past hundred years, the abundance and diversity of native species have dramatically declined across the globe (IPBES 2019). Along with climate change, land use and pollution, non-native species invasions have been cited as one of the leading drivers of the current biodiversity crisis (IPBES 2019). Not only are invasions driving biodiversity loss but, for decades, ecologists have hypothesised that one of the many consequences to biodiversity loss is a further increase in the establishment and spread of invasive species (Elton 1958; Fridley et al. 2007). The resulting biotic resistance hypothesis (also known as the diversity-invasibility relationship) predicts that species-rich native communities limit the niche space available to other

species, and thus more diverse communities have greater biotic resistance to incoming non-native species. Evidence in favor of this hypothesis would suggest that promoting native biodiversity is an effective strategy to limit non-native species establishment, ultimately reducing the number of invasions.

However, inconsistent support for the biotic resistance hypothesis raises the question as to whether efforts to target native biodiversity have any effect on non-native species invasions, particularly in plant communities (Fridley et al. 2007; Jeschke et al. 2012). Experimental studies provide substantial evidence that higher native species richness results in lower invasion (Levine et al. 2004; Fridley et al. 2007; Byun et al. 2013; Peng et al. 2019; Smith & Côté 2019).

Observational studies at the site level vary, but in the few observational studies that extend beyond a local scale to include multiple sites (e.g., Stohlgren et al. 2006; Iannone et al. 2016), all find that higher native richness relates to higher numbers of non-native species (Fridley et al. 2007; Peng et al. 2019; Smith & Côté 2019).

The lack of consensus among studies was previously thought to be an artefact of spatial scale: habitat quality and habitat heterogeneity drive diversity across broad spatial extents, whereas biotic interactions drive diversity within the smaller scale plant neighbourhood (Levine 2000; Shea & Chesson 2002; Davies et al. 2007; Sandel & Corbin 2010; Von Holle 2013). However, two recent meta-analyses suggest that the contradiction may be driven by differences in experimental vs. observational studies (Peng et al. 2019; Smith & Côté 2019). While observational studies have the power of describing variation across broad spatial extents, these studies have limited control over extrinsic environmental or anthropogenic variables that affect native and non-native plant richness (Rejmanek 2003; Nunez-Mir et al. 2017). These extrinsic variables are often controlled for in experiments, but may confound our understanding of biotic resistance in observational analyses. Thus, evidence in support of biotic resistance has been limited to manipulated systems confined to local scales, and we lack broad-scale evidence for biotic resistance across a diversity of habitats.

Despite inconsistent evidence for biotic resistance, natural resource managers have adopted the approach of conserving and restoring native plant diversity in hopes of reducing invasions (Funk et al. 2008; Nimmo et al. 2015; Guo et al. 2018). This strategy aims to prevent invasions during the establishment stage – before some non-native species spread (Blackburn et al. 2011) and eradication becomes less likely. Nonetheless, natural resource managers consistently report that they are losing ground against invasions (Beaury et al. 2019) and invasive plant management continues to absorb time and resources (Pimentel et al. 2005). As these invasions advance the global decline in native biodiversity (IPBES 2019), we must identify and validate resource-effective conservation and restoration strategies that limit the success of nonnative species during all stages of the invasion process.

Although past observational studies have not supported biotic resistance, new statistical techniques and the use of big data in ecology could alter those conclusions. An important component of broad-scale analysis (Iannone et al. 2016), and a potential flaw in past observational studies of biotic resistance (Rejmanek 2003; Nunez-Mir et al. 2017), are confounded interactions between species pools and other drivers of diversity. For example habitat characteristics correlated with species richness—such as resource availability, community type, or disturbance regime—affect the nature of the biotic resistance relationship (Stohlgren et al. 2006; Davies et al. 2007; Sandel & Corbin 2010; Von Holle 2013). Over large areas, heterogeneity in these factors may drive covariation between native and non-native richness even when biotic resistance is in effect (Levine 2000; Shea & Chesson 2002; Levine 2004). As large, standardized data sets become available and methods for analyzing these data advance, we have an opportunity to retest foundational ecological and invasion hypotheses underlying conservation decision-making (Guo et al. 2012; Nunez-Mir et al. 2017; Smith & Côté 2019).

To provide clarity to our understanding of biotic resistance, we used a novel statistical approach with 24,456 observational field surveys from the U.S. National Park Service to quantify

the relationship between native and non-native plant richness across ecosystems of the U.S. The National Park Service data are unique in that they were collected at a fine spatial grain (most plots $\leq 400 \text{ m}^2$), but span a vast spatial extent and a diversity of habitats. Using these data, we addressed the following questions: (1) Do more species-rich native plant communities reduce the probability of non-native occurrence?; and (2) How does the relationship between native and non-native richness vary with different drivers of species diversity such as (i) habitat, (ii) proximity to human activity and (iii) climate? We hypothesized that accounting for these multiple drivers of diversity would lead to a consistent negative relationship between native and non-native plant richness – thereby reconciling the contrasting findings that have thus far characterized broad-scale observational studies of biotic resistance.

2.3 Methods

2.3.1 Plant survey data

Plant survey data were obtained through the U.S. National Park Service (NPS) Vegetation Inventory Plot Data (Figure 2.1). Each park or monument ($n = 153$) was considered a site and was included in the analysis if located in the lower 48 states and if the vegetation sampling protocol followed the methods described in the U.S. Geological Survey's Field Methods for Vegetation Mapping (1994). Plot size varied from 25 m^2 to 5400 m^2 depending on community type (i.e., plots were larger in forests where sampling effort must be greater to capture species richness of larger growth forms), although most plots were 400 m^2 or smaller (Figure A3). Each plot ($n = 24,456$) included a list of all observed plant species, the dominant vegetation type and geolocation. We used the United States Department of Agriculture PLANTS Database to identify the origin of each plant species as either native or non-native to the continental U.S. (The PLANTS Database 2018). For each plot, we calculated native and non-native plant richness as the number of unique species of that respective

designation. Non-native richness serves as an estimate of the number of niches occupied by non-native species in a community.

2.3.2 Environmental characteristics

The number of non-native plants in a community depends on niche availability, which varies with habitat (Shea & Chesson 2002; Long et al. 2009). To analyze variation in biotic resistance between habitats, we included two measures of habitat for each plot: community type (e.g., forest, herbaceous), which describes the structure of the vegetation in each plot, and ecoregion (e.g., Eastern Temperate Forest, Great Plains), which describes the ecosystem characteristics specific to different regions of the U.S. The NPS categorized community type as one of the following: forest, woodland, shrubland or herbaceous (we excluded sparsely vegetated, disturbed or mixed community types due to uneven sampling across ecoregions). We used the Environmental Protection Agency's spatial layer of Level I Ecoregions (Omernik 1987) to assign each plot to one of seven ecoregions (Figure 2.1) based on its location. NPS sites often sampled across community types and in several cases spanned ecoregions.

Human activity and resulting landscape disturbance are primary sources of non-native propagules (Lonsdale 1999; Bartomeus et al. 2012) and cause periodic niche vacancies in plant communities (Shea & Chesson 2002; Brown & Peet 2003). These factors are thus likely to affect plot-level nonnative richness. To estimate each plot's proximity to human activity as a proxy for propagule pressure and disturbance, we used GIS to calculate the Euclidean distance between each plot and the nearest urban/developed or agricultural land. Land cover data were downloaded from the National Land Cover Database 2001 and 2011 spatial layers (Homer et al. 2012). We selected these years to straddle the time period over which the NPS sampled. We also measured the distance between each plot and the nearest road as an alternative measure of distance to human activity, but model comparison using Akaike Information Criterion (AIC)

showed that the model using distance to land cover types was a better fit than the model using distance to roads (Figure 5.1).

Finally, climate drives the distribution of both native (Lomolino et al. 2010) and non-native plant species (Sax 2001). To account for the effects of temperature on plant richness, we used GIS to assign each plot a USDA hardiness zone (PRISM Climate Group 2018). Hardiness zones divide the U.S. into regions based on average minimum winter temperature, which is commonly used to describe the climates within which plants are likely to successfully grow. Additional climatic variables were excluded to avoid collinearity (Appendix A).

2.3.3 Statistical approach

The data set included 12,359 plots with zero non-native species. To account for plots without non-native species, we used a zero-inflated model from the `glmmTMB` package in R (Zuur et al. 2009; Brooks et al. 2017). Total species richness varied from 1 to 163 species per plot. To account for variation in plot diversity, we used the binomial distribution (Zuur et al. 2013) to predict non-native species occurrence rather than non-native species richness.

This approach is different than previous analyses of plant richness data that more commonly use Poisson or negative binomial regression models to predict patterns in non-native richness. However, these models assume an unbounded upper limit to the number of ecological niches in a system (i.e., no competition for niche space), which is both unlikely to be true (Shea & Chesson 2002) and fails to control for variation in richness across ecosystems (Moore et al. 2001; Rejmanek 2003). For example, maximum species richness varies greatly between resource poor (e.g., desert) and resource rich ecosystems (e.g., forest), and thus ‘high’ native richness is relative to the community at hand. As native and non-native richness covary across habitats, studies may spuriously attribute this covariation to a lack of biotic resistance. In other words, resource abundant communities may have more native and non-native species because of

habitat quality, not because of a lack of biotic resistance (Levine 2000; Shea & Chesson 2002; Levine et al. 2004).

Using the binomial distribution, we assume that each community has a fixed number of available niches (trial size, estimated as total species richness per plot) and non-native species occupy a certain percentage of these niches (binomial probability, predicted as non-native species occurrence). This allows us to use the relative role of non-native species in a community to understand the likelihood of non-native occurrence and how this occurrence varies across ecosystems of different levels of diversity, vegetation structure, anthropogenic influence and climate. In other words, using the binomial distribution, we analysed the relationship between native and non-native richness in addition to, not in spite of, covarying habitat characteristics (i.e., biotic resistance may still occur in communities with high non-native richness, see Levine 2000 and Levine et al. 2004). Additional details are provided in Appendix A.

We included the following fixed effects: native richness, community type, ecoregion, distance to human activity as a proxy for propagule pressure and disturbance and hardiness zone as a measure of climate. Sites spanned a gradient of each of these variables, so we included site as a random effect to account for spatio-temporal autocorrelation between plots.

The two measures of habitat were included as additive effects and in an interaction with native richness (Appendix A). We compared fitted non-native richness across community types and ecoregions using a Tukey test for pairwise comparisons. To assess the relative effects of each variable, we used a Z score transformation so that all numeric variables (native richness, distance to human activity and hardiness zone) fell on the same scale. We used simulation to predict the binomial probability of non-native plant occurrence and uncertainty around this probability (Figure 5.1). All analyses were performed in R v. 3.5.1 (R Development Core Team 2018).

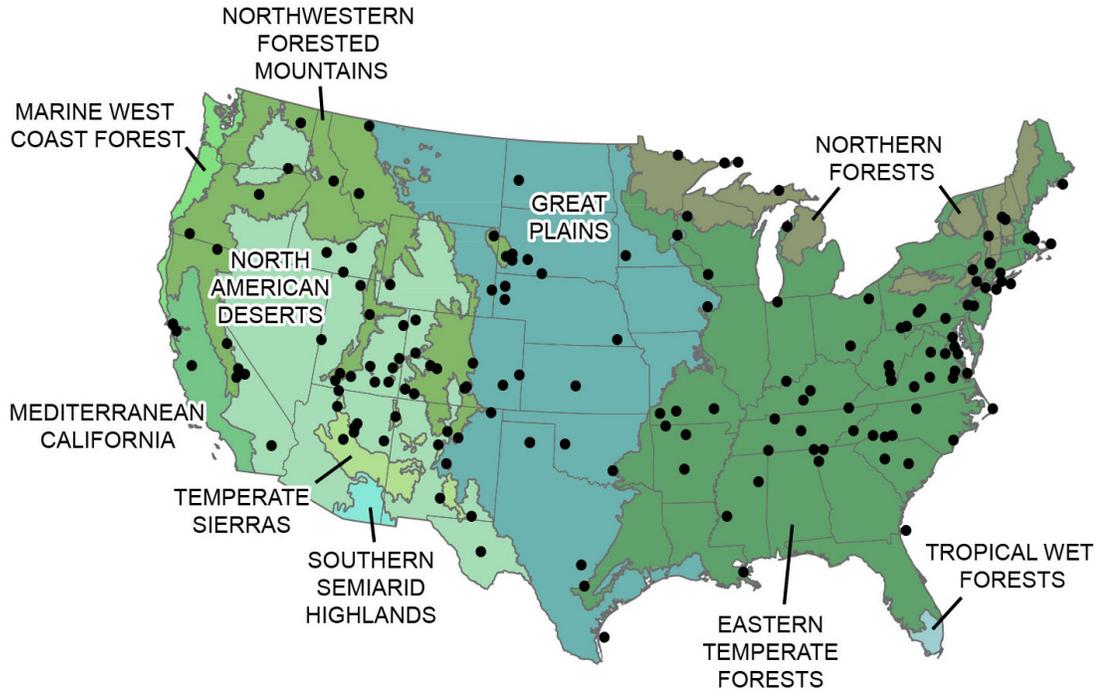


Figure 2.1 National Park Service site locations (n = 153) for plant surveys encompass a range of community types and ecoregions.

2.4 Results

We found a negative relationship between native richness and non-native occurrence across all community types and ecoregions ($Z = 22.53$, $P < 0.0001$, $SE = 0.02$). Although consistently negative, the strength of biotic resistance varied by habitat with more variation occurring among ecoregions than among community types (Figure 2.2,2.3).

For all community types, non-native occurrence was significantly higher in the Great Plains, Mediterranean California, and the Northwestern Forested Mountains when compared to the North American Deserts. Mediterranean California also had significantly greater non-native occurrence when compared with Temperate Sierras regardless of community type. On average, Mediterranean California and the Great Plains had the highest probability of non-native occurrence (0.14 and 0.12 respectively). Within each ecoregion, forests consistently had the

lowest likelihood of nonnative occurrence while herbaceous communities had the highest.

Shrublands and woodlands did not significantly differ in biotic resistance.

The negative slope of biotic resistance occurred in all habitats regardless of distance to urban/developed or agricultural land (Figure 2.4, Figure 5.1), although plots near human activity had significantly more non-native species, and thus higher likelihood of non-native occurrence ($Z = 18.74$, $P < 0.0001$, $SE = 0.009$). Hardiness zone had a significant positive effect on non-native occurrence ($Z = 13.62$, $P < 0.0001$, $SE = 0.009$), indicating that more non-native species occurred in warmer climates. Native richness had a greater effect on non-native occurrence ($b = 0.49$, $SE = 0.02$) than either distance to human activity ($b = 0.17$, $SE = 0.009$) or hardiness zone ($b = 0.33$, $SE = 0.02$). Deviance explained by the full model was 13%.

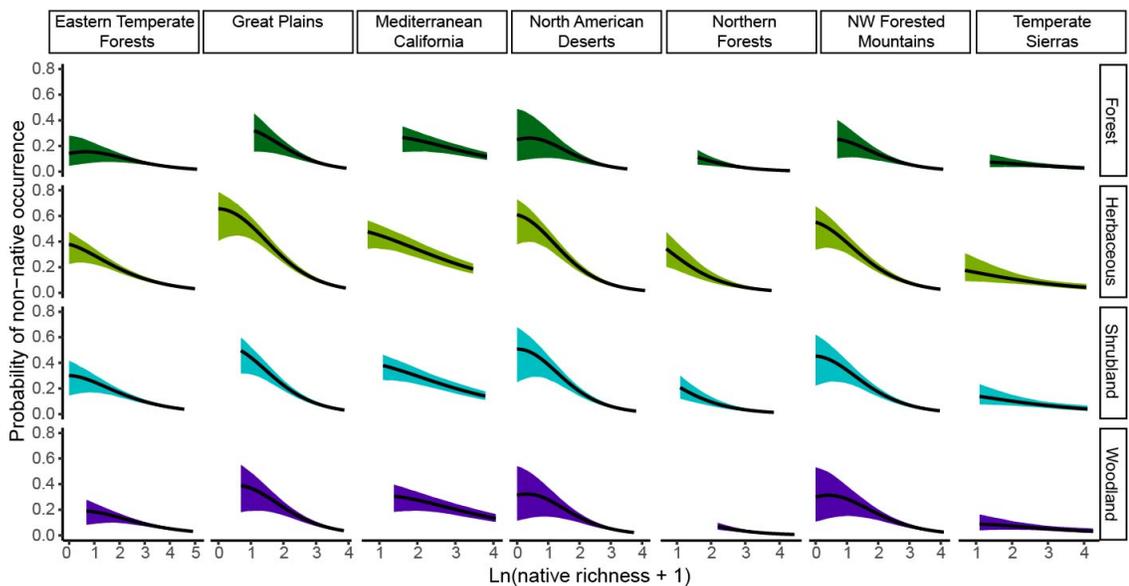


Figure 2.2 Predicted decline in non-native occurrence with increasing native richness across four community types (rows) and seven ecoregions (columns). Shaded polygons represent 95% credible intervals.

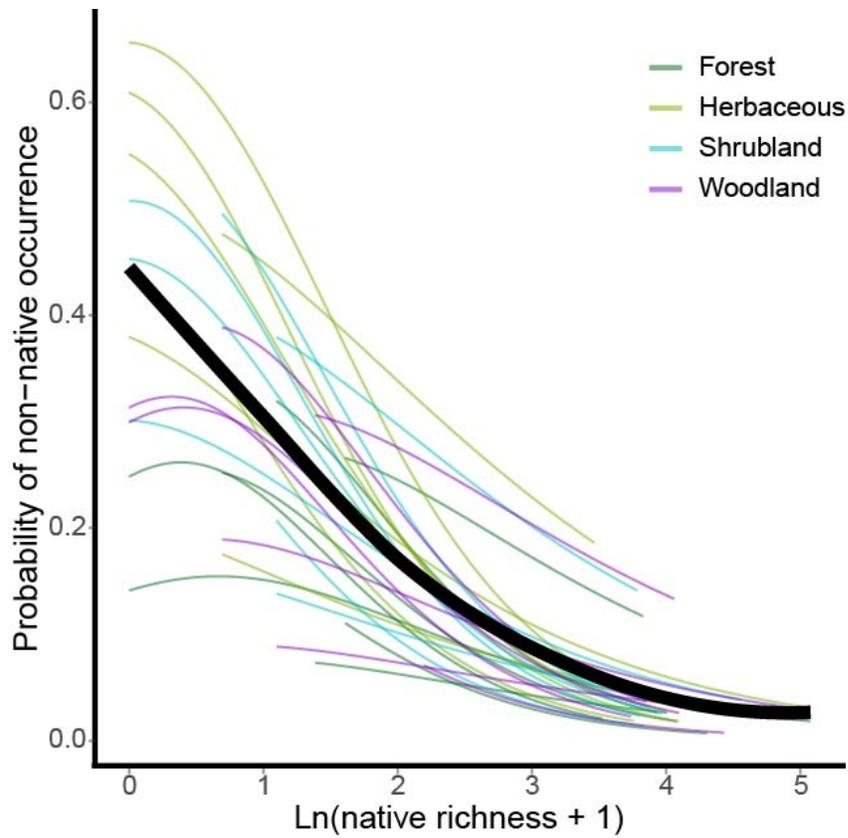


Figure 2.3 The overall negative relationship between native richness and non-native occurrence composed of unique curves of biotic resistance for each of the 28 combinations of community type (colors) and ecoregion (not labeled).

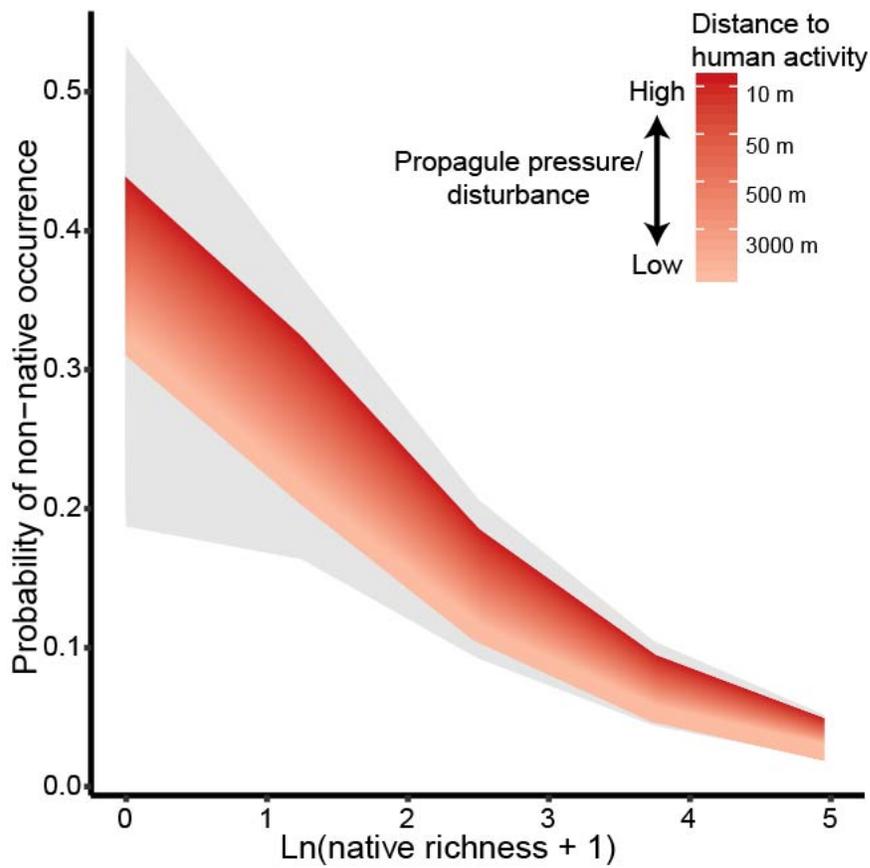


Figure 2.4 Predicted effect of proximity to human activity as a proxy for the effect of propagule pressure and disturbance on biotic resistance. Predictions and 95% credible intervals are for herbaceous communities in Eastern Temperate Forests.

2.5 Discussion

Higher native plant richness significantly reduced the probability of non-native plant occurrence across all community types and ecoregions sampled by the National Park Service. These highly valued ecosystems are some of the most iconic in the United States and span a diverse range of anthropogenic influence, habitat and species diversity. Although non-native species readily occurred in many areas, we found universal support for the biotic resistance hypothesis. This widespread evidence of biotic resistance provides support for conservation and restoration activities that promote native biodiversity to reduce non-native species establishment, thereby reducing the pool of potentially invasive plants.

Our results contrast with findings of previous broad-scale observational studies of biotic resistance, which often found a positive relationship between native and non-native species richness (Fridley et al. 2007; Peng et al. 2019; Smith & Côté 2019). Because our approach controlled for factors that covary with species richness (Moore et al. 2001; Rejmanek 2003; Iannone et al. 2016), our analysis characterized biotic resistance independent of the effects of habitat, distance to human activity and climate on plant richness. Environmental heterogeneity is less of a barrier for observational studies at small scales where within site variation is often limited. However, these studies remain difficult to compare due to differences in spatial grain (Peng et al. 2019), spatial extent (Smith & Côté 2019), statistical approach (Nunez-Mir et al. 2017) and how they measure invader success (e.g., the majority of broad-scale studies use richness data, whereas small-scale studies may use richness, cover, survival, etc., see Fridley et al. 2007). The quality and quantity of the National Park Service data allowed us to both account for environmental heterogeneity and compare fine-scale data across sites. By doing so, we demonstrate consistency in biotic resistance between many observational analyses, field experiments (Levine et al. 2004; Peng et al. 2019; Smith & Côté 2019), and analyses of both types that found variation in biotic resistance depending on site-specific characteristics (Stohlgren et al. 2006; Davies et al. 2007; Sandel & Corbin 2010; Von Holle 2013).

One limitation to using observational data is that we cannot establish directionality in the relationship between native richness and non-native occurrence. For example, the spread and impact of non-native species can significantly reduce native richness (Bradley et al. 2019). It could thus be possible that low native richness in this data set results from the increasing abundance/invasion of non-native species, which enables additional non-natives to establish via invasional meltdown (Simberloff & Von Holle 1999). However, ecosystems can absorb non-native species without a concomitant decline in native richness (Sax & Gaines 2003), and in this data set, native richness varied across ecosystems even in the absence of non-native species (i.e., low native richness was not always associated with high non-native occurrence). Furthermore,

our analysis included proximity to human activity, which is often strongly correlated to non-native species abundance (Lonsdale 1999; Shea & Chesson 2002; Brown & Peet 2003; Bartomeus et al. 2012; Seabloom et al. 2013). If biotic resistance was not in effect, we would expect areas of high human impact to have high non-native occurrence regardless of native diversity. Rather, non-native occurrence declined with native richness even in areas with high likelihood of invasion (Figure 2.4), which suggests that the pattern observed here is more likely attributable to biotic resistance than to non-native species impacts.

System-specific variation in biotic resistance suggests that a combination of local, landscape and regional factors influence the occurrence of non-native species (Figure 2.2,2.3). For example herbaceous communities, which can be more seasonally dynamic than other community types (Shea & Chesson 2002; Clark & Johnson 2011), had the highest probability of nonnative occurrence. Forests, which have less seasonal turnover and thus may provide fewer opportunities for non-native species to establish (Bartomeus et al. 2012; Nunez-Mir et al. 2017), had the lowest. At the ecoregion level, low richness areas of Mediterranean California (Baldwin et al. 2017) and the Great Plains are particularly vulnerable to incoming nonnative species. In general, systems with low native diversity were more likely to have a positive trend between native richness and non-native occurrence (Figure 2.3). In these cases, niche availability could allow both native and non-native plants to establish and coexist (Stohlgren et al. 2006; Davies et al. 2007).

Proximity to urban development and agricultural lands, which are related to propagule pressure and disturbance (Lonsdale 1999; Bartomeus et al. 2012), increased the likelihood of non-native occurrence across all habitats (Figure 2.4). This effect may explain why Mediterranean California and the Great Plains were particularly vulnerable to incoming non-native species. Sites in Mediterranean California – Point Reyes National Seashore and Golden Gate National Recreation Area – are part of the highly developed San Francisco Bay Area. This proximity to urban landscapes, coupled with the extensive history of intense land-use in California, has likely

resulted in high propagule pressure and regular disturbances promoting invasions in the habitats sampled in this analysis (Corbin & D'Antonio 2004). This is in stark contrast to the Temperate Sierras, which is a relatively remote, forest dominated ecoregion with few incidences of non-native species. In the Great Plains, sites have low native diversity and neighbor large swaths of agricultural lands, resulting in low biotic resistance, high propagule pressure and regular disturbance in surrounding areas, which may cause the high probability of non-native occurrence we observed. Managing post-disturbance is a well-supported recommendation for reducing invasions (Hobbs & Huenneke 1992; Guo et al. 2018), and our study confirms that anthropogenically affected areas require more management of incoming nonnative species with the potential to become invasive.

Our analysis also supports the hypothesis that species diversity follows a climatic gradient (Lomolino et al. 2010) such that warmer climates contain more species, including higher diversity of non-native plants. As the climate changes, warming areas with low native diversity could be increasingly vulnerable to invasion as non-native species shift poleward (Allen & Bradley 2016) or increase in abundance as temperatures become more suitable (Hulme 2017).

While assessing ecological vulnerability based on different anthropogenic and climatic contexts is informative, high native diversity was the strongest indicator of low non-native species occurrence. As a result, there is a potential positive feedback between managing native biodiversity to reduce invasions and reducing invasions to benefit native biodiversity (IPBES 2019). Our analysis provides support for biotic resistance during the earliest stages of the invasion process, when non-native species are first establishing (Blackburn et al. 2011). It remains unknown from these occurrence data whether species are indeed naturalised or simply casual nonnatives (sensu Richardson et al. 2000), but the strength of the relationship (Figure 2.3) suggests that both types of non-natives are likely suppressed by high native diversity. It is also unknown whether high native diversity can prevent the spread of one or more non-natives that do occur. Future broad-scale analyses could explicitly test diversity-invasibility by

incorporating non-native abundance as a proxy for invasive plant impact (Bradley et al. 2019). Lastly, diverse communities are still often invaded (e.g., Stohlgren et al. 2006). Although conserving native plant diversity decreases the likelihood of nonnative occurrence, more work is needed to understand the broad-scale anthropogenic and environmental factors that drive ecosystem vulnerability to non-native establishment and ultimately to invasion.

CHAPTER 3

INVASIVE PLANT IMPACTS VARY ACROSS RECIPIENT NATIVE COMMUNITIES AT THE CONTINENTAL SCALE

3.1 Abstract

Native biodiversity is continuously threatened by interacting forms of global change, such as habitat loss and the spread of non-native, invasive species. Understanding the negative impacts of invasions can therefore help societies direct resources to protecting the most vulnerable ecosystems. Although many studies have demonstrated how species invasions impact local biodiversity, we lack an understanding of how impacts vary across recipient native communities and at continental scales. Using thousands of vegetation surveys from ecosystems across the U.S., we asked how non-native plant cover interacts with the environment to determine invasion impact on native plant richness, diversity, and evenness. We hypothesized that invasive plant impacts would vary with resource availability, human modification, and the richness and evenness of the invading plant community. Across the U.S., highly invaded plant communities had lower native plant richness and diversity but higher evenness, suggesting a shift towards communities that lack many rare and/or dominant native plants. We also found that as non-native cover increased, native communities were most susceptible to diversity loss in areas with high resource availability, areas with high anthropogenic impact, and areas invaded by a dominant invasive species, accompanied by several less-dominant non-native plants. Our study suggests that at continental scales, invasive plant impacts are a function of invader abundance and the conditions of recipient native communities. Focusing management on the most vulnerable native ecosystems could therefore reduce biodiversity loss associated with plant invasions.

3.2 Introduction

Measuring and predicting the ecological impacts of invasive plants remains an elusive goal in invasion ecology. Recent studies have shown that negative impacts to native communities

are related to invader abundance (Bradley et al. 2019; Pearse et al. 2019), the identity of the invading species (Hejda et al. 2009; Pearse et al. 2019; Pearson et al. 2016), and the vulnerability of the native community (Catford et al. 2009). But aside from studies of these factors at local scales, few unifying patterns have emerged across taxa and habitat types (Crystal-Ornelas et al. 2020). We therefore lack an understanding of how plant invasions impact native communities across recipient environments and at continental scales.

Part of the challenge of identifying broad patterns in impacts stems from the difficulty of measuring impact (Verbrugge et al. 2010; Barney & Tekiel 2020), which typically limits inferences to a few high-impact species or ecosystem types (Hulme et al. 2013; Pyšek et al. 2008; Crystal-Ornelas et al. 2020). These biases limit our understanding of the geography of invasive plant impacts, which is a key need for identifying and directing resources towards vulnerable ecosystems (Latzka et al. 2016; Crystal-Ornelas et al. 2020). For example, Brewer (2011) found that the impact of stiltgrass (*Microstegium vimineum*) invasion depended on spatial variation in light availability. In open areas, stiltgrass reached high abundance, but native plant communities maintained diversity. In shaded areas, stiltgrass achieved lower abundance, but because the native plant community was more vulnerable to competition for light, stiltgrass had a stronger negative effect on native species diversity. This example hints at a complex relationship between invader abundance and the conditions of recipient communities that could be responsible for major trends in invasion impacts (Crystal-Ornelas et al. 2020; Ricciardi et al. 2021).

To better understand the geography of the impacts of plant invasions, we compiled thousands of vegetation surveys across all major ecosystems of the U.S. We define invasion impact as the slope of the relationship between native community diversity and the relative abundance of non-native plant cover (Sofaer et al. 2018; Bradley et al. 2019). At the continental scale, we investigated how the shape of this relationship varies depending on the conditions of recipient native communities (Figure 3.1). Specifically, we asked whether key factors that

influence plant competition (resource availability) and invasive plant presence and abundance (human activity) also affect invasion impacts.

First, we hypothesized that invasion impact depends on competition for resources. Variation in resource availability is associated with abiotic stress, species composition, and the outcomes of species interactions. But the directionality of these relationships is unclear, as evidence suggests that as resource availability and plant productivity increase, competition among species can become stronger (Grime 2002; Rees 2013), weaker (Goldberg et al. 1999), remain stable (Stotz et al. 2016), or depend on the type of limiting resources (Tilman 1988). For example, the Stress Gradient Hypothesis suggests that native species' competitive abilities might be weaker or incur a larger trade-off with growth under resource poor, high stress environments (Silliman & He 2018). If so, native species in resource-limited environments may be more vulnerable to competition by non-native plants, resulting in higher vulnerability to impacts (Didham et al. 2007). On the other hand, communities may be more vulnerable to invasion impacts in high resource environments if these environments support more impactful non-native species, which has been observed in many studies (Stohlgren et al. 1999; MacDougall et al. 2006; Gerhardt and Collinge 2007; Goldstein and Suding 2014). Thus, a general relationship between resource availability and invasion impact remains unknown.

Second, we hypothesized that impacts may vary with the degree of human modification of an ecosystem, potentially beyond the direct effect of human-induced disturbance on native communities. Evidence suggests that invasive species presence and abundance are tied to human activity (Lonsdale 1999; Seabloom et al. 2006; Beaury et al. 2020), but an open question is whether the factors that lead to higher abundance of invasive plants also lead to greater impacts. Although few studies have investigated this, Didham et al. (2007) reviewed several examples in which human activity altered competition between invasive and native species, resulting in stronger negative impacts in areas with high anthropogenic effects. For example, human disturbance can directly decrease native diversity and increase invader abundance, and it could

also amplify invasion impacts by shifting competitive interactions to benefit invading species. Therefore, we might expect high human activity to amplify invasion impacts.

Third, the number and evenness of co-occurring non-native species may influence the impact of invasion. Different invaders have different magnitudes of impact (Hejda et al. 2009; Pearson et al. 2016), so a larger non-native species pool increases the likelihood that one of the invaders interacts severely with the recipient community. If so, we might expect high invasion impacts in communities with multiple non-native species but low non-native evenness, indicating that one or a few invaders dominate cover. The presence of multiple non-native plants could also alter the abiotic environment, potentially creating niche space for more impactful invaders (i.e., invasional meltdown; Simberloff & Von Holle 1999; Ricciardi et al. 2013). Lastly, invasive plants could amplify the impacts of one another if they compete with native species at different times and across space (Simberloff & Von Holle 1999). Given these potential interactions, we hypothesized that communities with co-occurring non-native species will experience greater impacts.

Understanding how the conditions of recipient communities affect their vulnerability to invasive plant impacts would be a substantial step towards predicting and mitigating those impacts (Yokomizo et al 2009; Sofaer et al. 2018; Bradley et al. 2019; Ricciardi et al. 2021). In this study, we provide the first continental-scale analysis on how invasive plant abundance interacts with conditions of recipient ecosystems to impact native plant communities. We hypothesized that the effect of non-native plant cover on native community diversity would vary with resource availability, human modification, and the richness and evenness of non-native species.

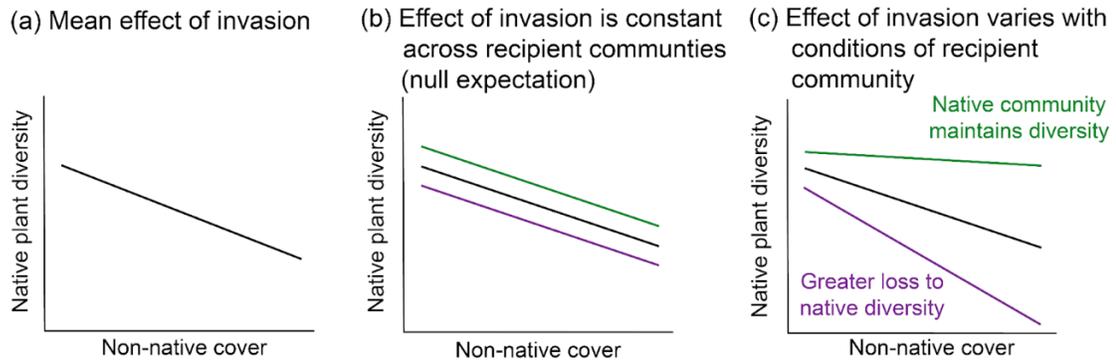


Figure 3.1 Conceptual figure showing how invasive plant impacts, measured as the slope of the relationship between native plant diversity and non-native plant cover, might vary depending on the conditions of recipient communities. (a) Mean effect of invasion across all recipient native communities. (b) The null expectation is that the effect of invasion is constant across recipient communities. In this example, communities (represented by different lines) differ in their native plant diversity, but not in the rate at which diversity declines with increasing non-native cover. (c)

Our hypothesis is that invasion impact varies depending on the conditions of recipient communities. In this example, communities differ in the magnitude of diversity lost to increasing non-native cover.

3.3 Methods

3.3.1 Vegetation data sources

We compiled surveys of terrestrial plant abundance for the lower 48 United States from the National Parks Service Inventory & Monitoring Program (NPS), the National Ecological Observatory Network (NEON 2019), Forest Inventory & Analysis Phase 3 vegetation surveys (FIA), the Bureau of Land Management Assessment Inventory and Monitoring data (AIM), and data stored in VegBank that follows the North Carolina Vegetation Survey protocol (NCVS). These datasets were selected because they provide species-level percent cover data for all plants located in plots or along transects. Plot size varied from 25m²-1000m², but average plot size was 400m². We identified each recorded taxon as native or non-native to the continental United States according to the USDA PLANTS Database. For unidentified taxa, we recorded nativity as unknown. For each plot, we summed cover across taxa to calculate relative cover of native, non-native, and unknown species. We based our analyses on plots with less than 10% relative cover of unknown nativity.

Input datasets differed in whether plots were distributed across the U.S. (e.g., NEON and NPS data) or focused on sampling a specific ecosystem type (e.g., FIA sampled forested ecosystems, AIM data largely sampled Western shrublands). To account for this, and for differences in plot size and sampling methods, we included data source, vegetation type (National Land Cover Database, Homer et al. 2012), and level 4 ecoregion (the finest scale categorization of similar ecosystem types provided by the Environmental Protection Agency) in models fit to the full dataset, and we conducted exploratory analyses to ensure that there were no major differences among datasets within similar ecosystem types. Datasets also differed in the continuous cover value assigned to species present in a plot but at very low abundance (e.g., FIA assigned trace abundance a cover value of 0.0025% while NPS assigned a value of 0.5%), which resulted in an uneven distribution of plots across low values of percent cover. We used a change point analysis (Fong et al. 2017) to understand the potential influence of these plots. This analysis suggested that the effect of non-native cover on native community diversity was significantly different between plots with less than and more than 2% non-native cover (Appendix B), most likely because of the uneven distribution of plots across cover values in this range. Therefore, plots with less than 2% non-native cover were removed from analyses ($n = 9,227$). This reduced differences among datasets and allowed us to focus on plots that were more likely to have an established population of non-native plants and thus more likely to experience measurable impacts on native communities.

For each plot, we calculated native plant richness, diversity (inverse of Simpson's diversity), and evenness (Evar; Camargo 1995, Smith & Wilson 1996) (Figure B4). Because diversity is calculated for plots with at least one native species and evenness for plots with at least two native species, sample sizes for each model differed with response variable (native richness: $n = 22,411$ plots; native diversity: $n = 22,285$; native evenness: $n = 21,862$). Five plots were identified as outliers in native diversity (native diversity was greater than 35, whereas the mean across plots was 5) and removed from analyses.

3.3.2 Data analysis

We defined invasion impact as the relationship between non-native cover and native plant richness, diversity, and evenness. We asked whether this relationship differed depending on resource availability, human modification, and the number and evenness of non-native species.

To quantify resource availability, we extracted values for net primary productivity (NPP) at each plot location using MODIS-250 remotely sensed data (Robinson et al. 2018). NPP can be considered a proxy for resource availability in many systems (Robinson et al. 2018), but in arid systems, NPP can be correlated with the abundance of non-native plants (Bradley & Mustard 2006; Vila & Ibáñez 2011). Thus, we also extracted values for several measures of water availability, including soil water deficit (Trabucco and Zomer 2019a), the Priestley-Taylor alpha coefficient (quantifies aridity stress on vegetation; Trabucco and Zomer 2019b), potential water deficit (Abatzoglou 2013), and the global aridity index (Trabucco and Zomer 2019b). Water resource variables were collinear with one another and with NPP. Results were consistent across measures of resource availability; we reported results of the best fit model given AIC (Table B1).

To test the hypothesis that human activity could alter the effect of non-native cover, we extracted a measure of human modification using the Global Human Modification Map (GHM; Kennedy et al. 2018). This dataset provides an estimate of the anthropogenic effect on the earth based on spatial data quantifying the impact of 13 different factors (e.g., transportation corridors, human population density). As a secondary measure of human modification, we calculated the Euclidean distance from each plot to the nearest parcel of land dominated by humans (developed and cultivated/planted land cover classes) based on land classifications in the National Land Cover Database (Homer et al. 2012). These variables were also collinear with one another and were compared using AIC (Table B2).

To test the hypothesis that the effect of non-native cover could be stronger in plots where co-occurring non-native species facilitate each other's impacts or have cumulative impacts, we

calculated plot-level non-native plant richness and evenness. Non-native richness allowed us to assess whether the effect of non-native cover was stronger in plots with more non-native species, and non-native evenness allowed us to assess whether this effect was driven by a dominant non-native species (low evenness) or whether the effect resulted from the cumulative abundance of multiple non-native species (high evenness). Non-native evenness can only be calculated for plots with two or more non-native species, which reduced the sample size to 14,908 plots. Therefore, for each response variable we fit a model with non-native richness as an explanatory variable and one with non-native evenness.

To test how resource availability, human modification, and the richness and evenness of invading species influenced the impact of invasive plant abundance, we fit generalized linear mixed effects models ('glmmTMB' v. 1.0.2.1 R package) to native plant richness, diversity, and evenness. Models fit to each response variable included interaction terms representing each of our hypotheses. Because the sample size differed depending on whether non-native richness or non-native evenness was used as a predictor variable, we fit two models to each response variable, one with non-native richness and one with non-native evenness in the third interaction term:

1. Native richness ~ Non-native cover*Resource availability + Non-native cover*Human modification + Non-native cover*Non-native richness
2. Native richness ~ Non-native cover*Resource availability + Non-native cover*Human modification + Non-native cover*Non-native evenness
3. Native diversity ~ Non-native cover*Resource availability + Non-native cover*Human modification + Non-native cover*Non-native richness
4. Native diversity ~ Non-native cover*Resource availability + Non-native cover*Human modification + Non-native cover*Non-native evenness
5. Native evenness ~ Non-native cover*Resource availability + Non-native cover*Human modification + Non-native cover*Non-native richness

6. Native evenness ~ Non-native cover*Resource availability + Non-native cover*Human modification + Non-native cover*Non-native evenness

A significant interaction would suggest that the relationship between the native community response and non-native cover depends on the conditions of the recipient community (Figure 3.1). We included longitude, latitude, and data source as fixed effects to reduce residual spatial autocorrelation. We also included dominant vegetation type (Homer et al. 2012) and level 4 ecoregion (Omernik 1995) as random effects on the intercept to account for any residual differences in our response variables associated with vegetation type. During data exploration, we observed a potential non-linear relationship between native plant evenness and non-native cover, so the model with native evenness as the response also included a quadratic effect of non-native cover. We used model selection based on AIC to select best fit models across collinear variables (Table B1-B2). All continuous predictor variables were rescaled using a z-score transformation.

3.4 Results

Higher non-native cover was associated with lower native plant richness and diversity and higher native plant evenness (Figure 3.3). There was a significant non-linear effect of non-native cover on native evenness, such that native evenness was much higher in plots with greater than 25% non-native cover (Table 3.1). The best fit model for all response variables included interactions between non-native cover and each of NPP, the Global Human Modification index, and non-native plant richness (Table 3.1). There was some residual spatial autocorrelation among plots (Figure B1-B3), but Moran's I values were greatly reduced compared to models without fixed effects and were close to the recommended value of zero (richness: 0.13, diversity: 0.08, evenness: 0.09; Gittleman & Kot 1990).

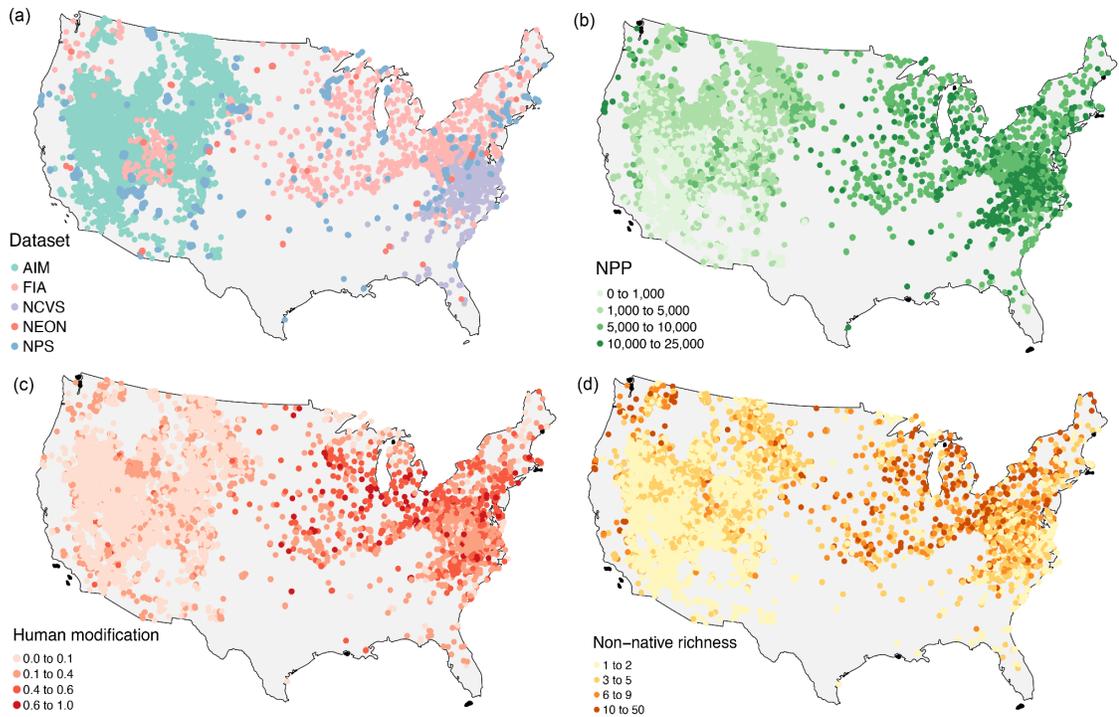


Figure 3.2 Focal predictor variables for plots included in the analysis: (a) data source, (b) net primary productivity (NPP) derived from remotely sensed data; higher values indicate more productive areas, (c) human modification, measured as a 0-1 index; higher values indicate more modified areas, and (d) non-native plant richness.

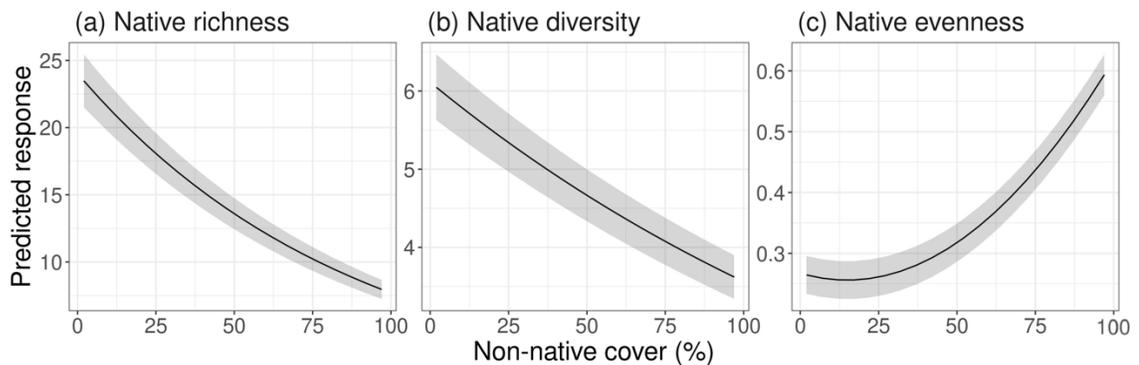


Figure 3.3 The effect of non-native cover on native plant (a) richness, (b) diversity, and (c) evenness. Each relationship is predicted from the best fit model for each response variable, with all predictor variables other than non-native cover held at their mean. All relationships are statistically significant ($p < 0.05$). Shaded regions represent 95% confidence intervals.

3.4.1 Resource availability

Native plant richness and diversity were higher in areas with high NPP, whereas native plant evenness was lower. There was a significant interaction between NPP and non-native cover on each of the three response variables (Figure 3.4 a-c), such that in areas with high NPP, non-native cover had a stronger effect on native richness and evenness (steeper slopes), and a weaker effect on native diversity, compared to areas with lower NPP.

3.4.2 Human modification

Highly modified areas had significantly fewer native species and lower native diversity across the gradient of invasion. There were also statistically significant interactions between human modification and non-native cover on native plant richness and diversity. In more modified areas (which were rare in the dataset given that most of the vegetation surveys sampled relatively pristine habitats), the effect of non-native cover was slightly stronger on native richness and weaker on native diversity (Figure 3.4 d-f). The interaction between human modification and non-native cover was nonsignificant for native plant evenness.

3.4.3 Non-native richness

Native richness and diversity were higher in plots with more non-native species, whereas high non-native richness was associated with low native evenness. For each of the three response variables, there was a significant interaction between non-native plant richness and non-native cover. Where non-native richness was high, the model predicted greater changes in native richness with increasing non-native cover, but less significant changes in native diversity, likely because of the steep increase in native evenness (Figure 3.4 g-i).

3.4.4 Non-native evenness

There was a significant interaction between non-native evenness and non-native cover on native richness ($B = 0.014$, $SE = 0.0062$, $p = 0.025$) and native evenness ($B = -0.010$, $SE = 0.0019$, $p < 0.005$). The effect of non-native cover was significantly stronger in plots where cover was dominated by fewer species (i.e., low non-native evenness) compared to plots where cover was evenly distributed across non-native species (Figure 3.4 j-l). The interaction between non-native evenness and non-native cover on native diversity was not significant ($B = -0.008$, $SE = 0.007$, $p = 0.24$).

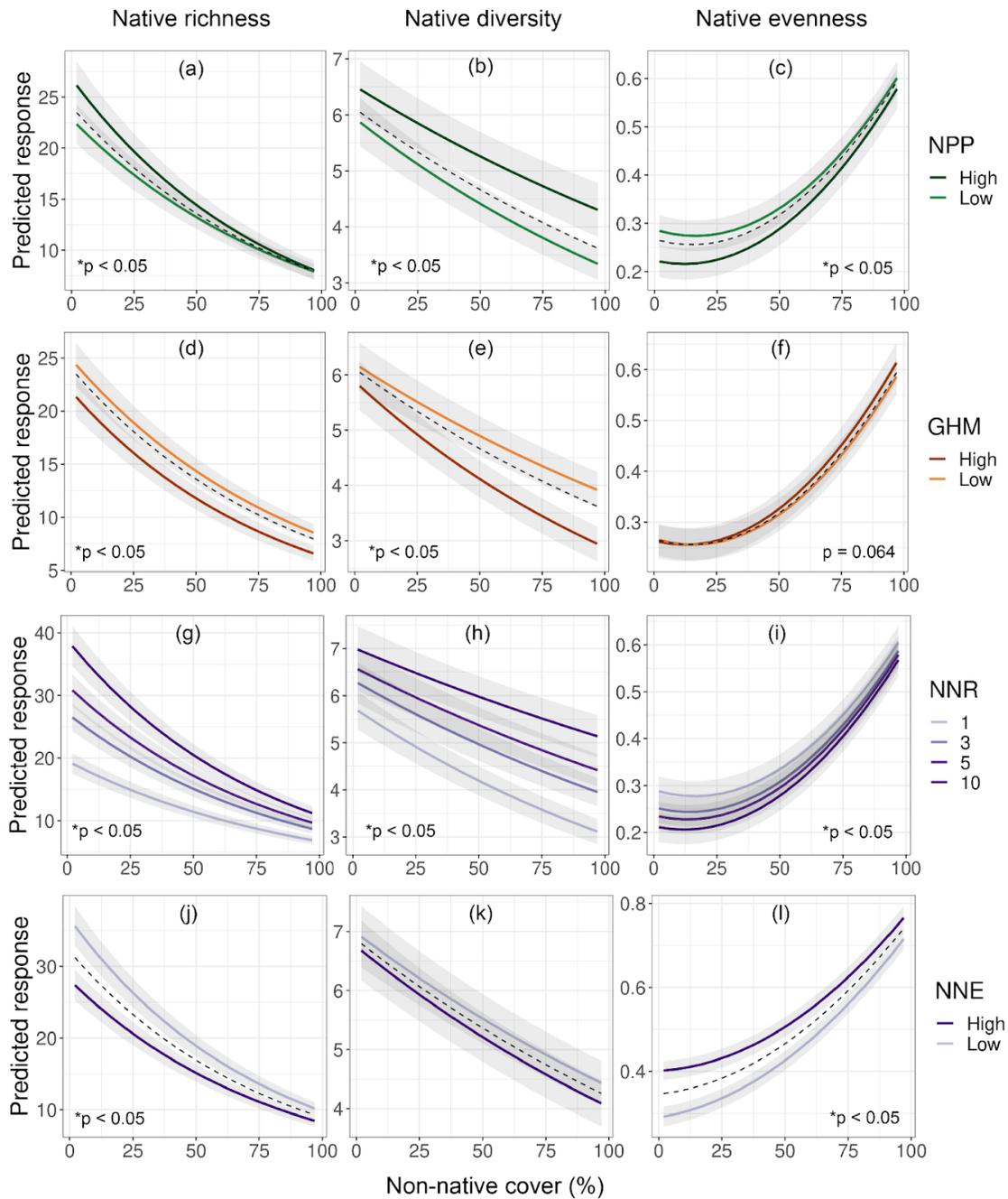


Figure 3.4. Invasion impact on native plant richness, diversity, and evenness across gradients of net primary productivity (NPP; a-c), global human modification (GHM; d-f), non-native plant richness (NNR; g-i), and non-native plant evenness (NNE; j-l). Impacts were strongest (steepest slopes) in productive and highly modified environments, as well as those with high non-native richness and low non-native evenness. For NPP, GHM, and NNE, dashed lines represent mean conditions, darker lines represent the mean plus two standard deviations of the mean, and lighter lines represent the minimum value (NPP, GHM, and NNE are right skewed, so the mean minus two standard deviations fell below the observed minimum value). Shaded regions are 95% confidence intervals. *P* values indicate significance of interactions.

Table 3.1 Model estimates (B), standard errors (SE), and p-values (P) for best fit models of native richness, diversity, and evenness. Dataset effects are reported in Table B3. Predictor variables were all standardized using a z-score transformation.

Fixed effects	Native richness			Native diversity			Native evenness		
	B	SE	P	B	SE	P	B	SE	P
Non-native cover	-0.108	0.003	<0.005**	-0.063	0.003	<0.005**	-0.016	0.001	<0.005**
NPP	0.055	0.009	<0.005**	0.032	0.01	0.002*	-0.022	0.003	<0.005**
GHM	-0.047	0.007	<0.005**	-0.019	0.008	0.015*	-0.002	0.003	0.493
Log non-native richness	0.299	0.007	<0.005**	0.086	0.008	<0.005**	-0.034	0.003	<0.005**
Non-native cover*NPP	-0.005	0.002	0.016*	0.006	0.002	0.014*	0.001	0.001	0.032*
Non-native cover*GHM	-0.005	0.002	0.014*	-0.009	0.002	<0.005*	0.001	0.001	0.064
Non-native cover*Non-native richness	-0.009	0.002	<0.005**	0.014	0.002	<0.005**	0.002	0.001	0.010*
Long	0.015	0.001	<0.005**	0.010	0.001	<0.005**	-0.001	0.0003	<0.005**
Lat	0.0003	0.003	0.914	-0.002	0.003	0.431	-0.004	0.001	<0.005**
Non-native cover ²	-	-	-	-	-	-	0.005	0.0002	<0.005**

*P < 0.05

**P < 0.005

3.5 Discussion

Plant invasions were associated with declines in native plant richness and diversity, and increases in native species evenness, but the magnitude of native biodiversity loss differed across recipient communities (Figure 3.4). Native plant communities were most vulnerable to changes in diversity in areas with high resource availability and high human activity, as well as high non-native plant richness and low non-native plant evenness, indicating the presence of a dominant invader. Our results are drawn from many thousands of rigorously sampled plots across ecosystem types of the United States, providing evidence that at continental scales, plant invasion impacts vary with invader abundance and the conditions of recipient communities.

High-resource environments had higher native plant richness and diversity, but these areas lost more native species to invasion compared to low-resource areas. Thus, the magnitude of invasion impact was greater in high-resource environments, at least partially because these native communities had more species to lose (e.g., vulnerability of biodiversity hotspots; Hrdina & Romportl 2017). Many experiments and some observational studies find that species-rich native communities have strong biotic resistance to invasive plant establishment (Levine et al. 2004; Beaury et al. 2020; but see Stohlgren et al. 1999). But, once invasive plants successfully establish, our findings show that diverse native communities are also susceptible to losing that diversity.

Impacts also varied with human modification, suggesting that anthropogenic activity not only contributes to higher invasive plant establishment (Beaury et al. 2020) and spread (Vila & Ibáñez 2011) but can also result in stronger negative impacts. These impacts presumably arise because human activity alters the interactions between native and non-native species. This is particularly concerning given that most of the vegetation surveys used in this analysis were located in relatively pristine areas (e.g., National Parks), so the effects shown in Figure 4d-e may be even stronger if more plots were in highly modified areas. Our findings reinforce recommendations to limit the spread of invasive plants in areas already facing other

anthropogenic impacts (Lopez et al. In Review). But interestingly, the effect of non-native cover was greater than that of human modification (Table 3.1), which informs the argument as to whether invasive species are truly a major threat to biodiversity.

Impacts were also strongest in plots with a dominant invader, but with multiple other non-native species present. This finding is consistent with the hypothesis that most non-native species have benign impacts on native ecosystems (Simberloff et al. 2012), but a larger non-native species pool increases the likelihood that at least one of the species will negatively impact native communities (Ricciardi et al. 2013). Because we found that communities with high non-native plant richness also had high native plant richness, it could be possible that these communities had greater diversity to lose, similar to the effect of high resource availability. Because we used observational data, we were unable to disentangle what factors in our analysis are drivers vs. passengers of invasion impact (e.g., Macdougall & Turkington 2005); understanding this should be a priority of future studies.

In general, opposing impacts of non-native cover on native richness and evenness limited effects on native diversity (Camargo 1995). At the continental scale, we found that plots with higher non-native plant cover had lower native plant richness and diversity but higher evenness. This suggests that heavily invaded communities had fewer rare species (e.g., McKinney 2004) and/or dominant native species were less abundant (Camargo 1995; Smith & Wilson 1996). While theoretical frameworks propose that the latter is more likely (Powell et al. 2011), to our knowledge no study has empirically investigated how frequently invasive plants impact rare vs. common native species. However, the concomitant decrease in native species richness and increase in evenness suggests that rare native plants are being lost. This is an important finding for conserving rare and endangered species, which are already threatened by other global changes (Bernardo et al. 2019).

Our study provides evidence that variation in invasive plant impacts across taxa and ecosystems is a function of the recipient environment, as well as the abundance and composition

of the invading non-native plants. Giving more attention to how environmental conditions might shape a recipient native community's ability to maintain diversity, and thus ecosystem function, could greatly improve our understanding and prediction of invasive plant impacts. This is particularly true in areas with high resource availability and high human modification, where native plant communities were most vulnerable to decreases in diversity. As multiple global changes continue to negatively affect native ecosystems, prioritizing the management of ecosystems most vulnerable to invasive species impacts can help reduce biodiversity loss.

CHAPTER 4

MODELING HABITAT SUITABILITY ACROSS DIFFERENT LEVELS OF INVASIVE PLANT ABUNDANCE

4.1 Abstract

Invasive plants have spread rapidly in the United States, negatively impacting native biodiversity, ecosystem services, and access to natural resources. Predicting where invasive plants are likely to spread and become abundant is critical for informing invasive plant management, and species distribution models are a key tool for informing the geography of invasion risk. However, most distribution models are limited by their use of occurrence-only data, which fail to capture variation in how abundant, and thus how impactful an invasive species is across its range. In this study, we ask how species distribution models predict suitability for different levels of abundance for three invasive plants: stiltgrass (*Microstegium vimineum*), sericea lespedeza (*Lespedeza cuneata*), and privet (*Ligustrum sinense*). For each species, we used an ensemble approach from five algorithms to compare suitability for percent cover $\geq 10\%$, $\geq 25\%$, and $\geq 50\%$ with suitability predicted from occurrence-only data. Across our focal species, we found that abundance models predicted 5-17% less area suitable for invasion compared to occurrence models. For stiltgrass and sericea lespedeza, the area suitable for invasion decreased linearly with higher levels of abundance but remained the same for privet. This suggests that stiltgrass and sericea lespedeza will only become highly abundant in a smaller portion of their abundance range, but anywhere privet can establish low abundance could be suitable for high abundance. We also identified important environmental predictors of each species distribution, which differed across levels of abundance and between occurrence and abundance. This indicates that habitats suitable for a species to occur in differ from those most vulnerable to high levels of abundance. These results highlight species-level differences in suitability for different levels of abundance but support previous findings that suitability for abundance is a subset of suitability for

occurrence. Selecting the appropriate level of abundance for assessing suitability for invasion, and thus invasion risk, may depend on species identity and management goals.

4.2 Introduction

Invasive plant species are one of the leading drivers of native biodiversity loss, with additional negative impacts to human economies, health, and access to natural resources (IPBES 2019). Species distribution models are important tools for assessing where invasive plants are likely to spread and have negative impacts, which can inform management of the risk posed by invasive species (Bradley 2011; Chapman et al. 2019; Jarnevich et al. 2021; O’Neil et al. 2021). Most existing efforts to model the distribution of invasive plants map suitability for invasion based on invasive species occurrence locations (e.g., Fernandes et al. 2019; Young et al. 2020). While occurrence data are useful for identifying all habitats suitable for an invasive species to establish in, occurrences fail to capture variation in invasive species abundance. Understanding the geography of abundance is critical because the negative impacts of invasion tend to be most severe at high levels of abundance (Bradley et al. 2019), and invasive plants are rare more often than they are abundant (Hansen et al., 2013). Because distribution models based on occurrences predict suitability for invasion even in areas where a species is unlikely to be common, these models often overestimate suitability for high abundance and thus the potential for negative impacts of invasion (Bradley 2016; Jarnevich et al. 2021; O’Neill et al. 2021).

The use of occurrence-only data in distribution modelling is partly due to a lack of reliable data on invasive species abundance (Bradley et al. 2018) as well as few modeling frameworks that leverage different types of abundance data (Pearce & Boyce 2005). Recent advances in data collection and curation have led to the release of many sources of geolocated abundance data, making it possible to predict where invasive plants are likely to reach high densities and thus have the greatest potential to negatively impact native ecosystems (Bradley et al. 2019). These newly available abundance data present an opportunity to understand the

geography and environmental predictors of invasive plant abundance, which can inform invasive species risk assessments and prioritizing management to reduce negative impacts.

The few existing studies that have incorporated abundance data into invasive plant distribution models created distribution datasets of points for where the invasive plant can be considered at ‘high abundance’. This can include point locations associated with a quantitative value above some level (e.g., percent cover greater than 10%, Jarnevich et al. 2021) or a qualitative description of cover (e.g., observations of monocultures, O’Neill et al. 2021). These high abundance points are then treated as occurrence data and used in species distribution models to generate spatial predictions of habitat suitability. By selecting a single definition of high abundance, this approach lumps together a range of observations that could represent very different levels of invasion and thus different magnitudes of impact on recipient ecosystems (Sofaer et al. 2018; Bradley et al. 2019). Flattening abundance information into a single category of ‘high abundance’ misses an opportunity to investigate how vulnerability to invasion changes as abundance increases.

Although abundance data informs predictions of impact, no study to date has mapped geographic variation in suitability for different levels of invasive plant abundance. In this study, we used species distribution models to compare suitability across multiple levels of invasive plant abundance as well as suitability based on occurrence-only data. We predicted habitat suitability for three common invasive plants in the Eastern United States: stiltgrass (*Microstegium vimineum*; also termed Japanese stiltgrass), sericea lespedeza (*Lespedeza cuneata*), and privet (*Ligustrum sinense*; also termed Chinese privet). These species represent distinct growth forms (grass, forb, and shrub) and spatial distributions in the U.S. (Figure C1), and thus different potential relationships between species ecology, occurrence, abundance, and the environment. By characterizing these differences, we identified areas of the U.S. that are most vulnerable to different levels of plant invasion, as well as highlighted limitations in using occurrence-only or a single level of abundance data for understanding the potential for negative impacts of invasion.

4.3 Methods

4.3.1 Focal species and data sources

Stiltgrass is a high-impact annual grass that can be found in a variety of environmental conditions (Kleczewski et al. 2011). It creates dense mats in forest understories, changing canopy structure and displacing native species. Sericea lespedeza is an aggressive semi-woody flowering plant that has spread throughout rangelands and grasslands of the eastern United States. Privet is a competitive invasive shrub that was originally introduced as an ornamental plant (Lehan et al. 2013). Privet is now common in natural areas of the Southeast U.S., where it forms dense thickets and outcompetes native plants, particularly in riparian zones (Batcher 2000). As the climate changes, models based on occurrence data predict that stiltgrass, sericea lespedeza, and privet will become serious management concerns for higher latitudes of the U.S. (Bradley et al. 2010; Allen & Bradley 2016).

We compiled point locations from four sources of occurrence data and twelve sources with both occurrence and abundance data (Table C1), totaling 68,442 data points across the three focal species. Abundance data included estimates of continuous percent cover or cover class, for which we took the median value within the range (e.g., a class of 10-15% cover was replaced with 12.5%). Across data sources, we removed duplicate entries, locations outside of the lower 48 United States, and any erroneous abundance data (e.g., values outside of 0-100% percent cover). Remaining data included more than 15,000 occurrence records for each species (Table C1), including 6451 records of abundance for stiltgrass, 3506 for sericea lespedeza, and 3814 for privet (Figure C2).

For each species, we created five distribution datasets based on locations where 1) the species occurs (including all locations with abundance information), 2) the species was recorded at $\geq 1\%$ cover (all records of abundance), 3) the species was recorded at $\geq 10\%$ cover, 4) the species was recorded at $\geq 25\%$ cover, and 5) the species was recorded at $\geq 50\%$ cover. We created

a sixth dataset based on locations where the species was recorded at $\geq 5\%$ cover, but the results from the species distribution models were similar to the $\geq 10\%$ cover models for each species (Figure C3) and are reported in Appendix C. To first assess potential biases in where occurrence versus any level of abundance data were collected, we compared the distribution of locations where each species occurs vs. locations with a record of the species abundance in geographic and environmental space. We also estimated the geographic overlap between predictions of habitat suitability for occurrence vs. abundance, which are described and reported in Appendix C (Tables C2-4; Figures C4-6). To avoid overrepresenting well-sampled geographies, each of the distribution datasets was spatially thinned by a distance of 0.9 kilometers using the ‘spThin’ v.0.2.0 R package (Aiello et al. 2015; Table 4.1).

Predictor data included a suite of 62 climate, landscape, and other environmental variables created and described by Engelstad et al. (In Review). If the Pearson, Spearman or Kendall correlation coefficient between a pair of variables was >0.7 (Dormann et al. 2013), we dropped one variable in the pair based on *a priori* hypotheses of factors that might influence the life history and ecology of our focal species (e.g., Chapman et al. 2019). Predictor variables were at a 90-m² resolution and used an Albers equal area projection (Engelstad et al. In Review).

4.3.2 Species distribution modeling

To predict habitat suitability for each level of abundance and for occurrence, we created ensemble species distribution models using the Software for Assisted Habitat Modeling (SAHM; Morisette et al., 2013) and following the methodology of Young et al. (2020) and Jarnevich et al. (2021). We generated pseudo-absence data using a targeted background approach (Morisette et al. 2013; Phillips et al. 2009) to reduce observation biases. A targeted background approach selects pseudo-absences from locations where vegetation data are likely to have been collected. From the same data sources we compiled for the focal species, we randomly selected 10,000 points from locations where the abundance of any non-native plant of the same growth form as the focal

species was recorded. While other methods of selecting pseudo-absence points, such as a kernel density estimator (KDE), have been used for modeling species in the early stages of an invasion (Elith et al., 2010), our three focal species have been in the U.S. for over a century (Lehan et al. 2013). Thus, it is reasonable to assume these species are in later stages of invasion and have had the opportunity to fill a substantial part of their potential range, making a targeted background approach most appropriate.

We created ensemble models of habitat suitability from five algorithms: boosted regression trees, generalized linear models, multivariate adaptive regression splines, Maxent, and random forest. Classic ensemble approaches select a threshold rule for binning the continuous output generated by each algorithm into either suitable or unsuitable habitat, identifying areas where multiple algorithms agree (Jiménez-Valverde & Lobo 2007; Araujo & New 2007). However, results are sensitive to the threshold rule used to distinguish unsuitable from suitable habitat (Jiménez-Valverde & Lobo 2007; Sofaer et al. 2019). We took an alternative approach to creating an ensemble model by combining first percentile and ten percentile threshold rules (suitability values associated with the lowest one percent and lowest ten percent of the training data) to categorize the continuous output from each algorithm into low (below the one percentile), moderate (between the one and ten percentile), and high (above the ten percentile) suitability. We then reassigned each category a value (low = 0, moderate = 1, and high = 2) and calculated the mean across the five algorithms, resulting in an ensemble map ranging from 0-2 (low to high suitability averaged across algorithms). For each species, we excluded areas where environmental conditions were dissimilar to conditions where the species was present using a Multivariate Environmental Similarity Surface (MESS; Elith et al., 2010).

We used a 10-fold cross-validation strategy (Kohavi 1995), in which we measured model performance by comparing model predictions to data that were not used to train the model (testing data). We evaluated model performance using the Boyce index, the area under the receiver operating characteristic curve (AUC), and the true skill statistic (TSS).

4.3.3. Model comparison

For each species, we compared predictions of habitat suitability by estimating overlap between distributions. We calculated the percent of each distribution that fell within the range predicted for the next level of abundance (i.e., the percent of the abundance $\geq 25\%$ distribution that fell within the abundance $\geq 10\%$ distribution). We also compared habitat suitability among distributions by estimating the proportion of pixels in the study area with high suitability (values > 1.5 out of 2) for each level of abundance and for occurrence. We also assessed invasion risk across lands managed by the National Park Service, U.S. Fish and Wildlife Refuge System, and the Bureau of Land Management ($n = 1038$ management units). We considered a management unit at risk of invasion if it contained a pixel with high suitability (values > 1.5).

We compared the relative importance of the different environmental predictors of each level of abundance and of occurrence for each species. Predictor variable importance was estimated for each algorithm as the change in AUC when values for that variable were permuted between occurrence and pseudo-absence locations. We converted this score for each predictor to its percent contribution relative to the other predictors and averaged these scores across the five algorithms (Young et al. 2020); higher values correspond to higher predictor variable importance.

4.4. Results

After spatial thinning, the number of data points used to train each model varied (Table 4.1), but all models had at least 190 training points. Evaluation statistics suggested moderate to high performance for all models with $AUC \geq 0.71$ and $TSS \geq 0.29$.

Table 4.1 The number of points used to train models after spatial thinning and the Boyce index, which is an evaluation statistic for models lacking true absence data (values closer to 1 suggest high model performance). Numbers reported for the Boyce index are the statistics associated with the training and testing data; the first set of values is for the first percentile threshold rule followed by the values for the tenth percentile threshold rule.

Species	Value	Occurrence points	≥10% cover	≥25% cover	≥50% cover
Stiltgrass	Sample size	7442	942	618	431
	Boyce index first train(test); tenth train(test)	1(1); 1(0.7)	1(1); 1(1)	0.4(0.2); 0.7(0.9)	1(1); 0.9(0.9)
Sericea lespedeza	Sample size	4559	854	472	318
	Boyce index first train(test); tenth train(test)	0.3(0.3); 0.9(1)	0.5(0.9); 0.9(0.7)	0.4(-0.9); 0.9(0.2)	0.8(-0.3); 1(0.7)
Privet	Sample size	4560	522	314	190
	Boyce index first train(test); tenth train(test)	0.9(0.6); 0.1(1)	0.6(0.4); 0.7(0.7)	0.2(0.1); 0.8(0.4)	0.5(0.9); - 0.4(0.9)

4.4.1 Spatial bias in occurrence vs. abundance data

Occurrence and abundance point locations overlapped in geographic and environmental space (Figure C4-5). But for each species, there were areas with only occurrence data or only abundance data, creating the potential for some spatial biases. This imperfect overlap in sampling of occurrence data versus abundance data likely contributed to differences in habitat suitability (Figure C6) and the importance of environmental predictor variables between models (Table C2-4). For example, sericea lespedeza occurrence was primarily limited by minimum winter temperature whereas all abundance points were more limited by nitrogen content, likely because there were records of sericea lespedeza occurrence but not abundance in areas with high nitrogen (Table C3; Figure C5). Thus, sericea lespedeza abundance data might not be directly comparable to occurrence data. For stiltgrass and privet, the top variables and variable contribution were

similar between models of occurrence and all abundance, suggesting that the two datasets encompassed similar environmental spaces and were more directly comparable (Table C2, C4).

4.4.2 Comparing habitat suitability

Across the study area, habitat suitability was more similar among the levels of abundance than between occurrence and abundance (Figure 4.1a-c; Figure 4.2-4.4). For all species, the highest percent of overlap was between the $\geq 25\%$ and $\geq 50\%$ abundance models: 89% overlap for stiltgrass, 90% for lespedeza, and 81% for privet. While there were often differences in suitability predicted from the $\geq 10\%$, $\geq 25\%$, and $\geq 50\%$ abundance models (e.g., suitability for sericea lespedeza in the Western U.S.), each overlapped more with one another than any did with suitability predicted from occurrence points. Habitat suitability for stiltgrass was the most similar across levels of abundance (average of 85% overlap) compared to the other two species (both averaged to 80% overlap).

Although there were geographic differences in where each model predicted suitable habitat, for each species, less area was predicted as highly suitable for all levels of abundance (Figure 4.1d-f) than area predicted as highly suitable for occurrence. For stiltgrass, the decrease in suitable area was nearly linear across models (Figure 4.1d). For sericea lespedeza, more of the study area was predicted as highly suitable for abundance $\geq 25\%$ compared to the other two levels of abundance because of high suitability predicted for abundance $\geq 25\%$ in the Western U.S. (Figure 4.1e; Figure 4.2). For privet, there was also a notable difference in suitability between occurrence and the levels of abundance (Figure 4.3), but there was almost no difference in the total area predicted as highly suitable across abundance models (Figure 4.1f).

Across management units, the number of units highly suitable invasion largely followed the geographic pattern of suitability for each species (Figure 4.1g-i) except for sericea lespedeza. Sericea lespedeza showed an unexpected pattern, where the abundance $\geq 25\%$ and $\geq 50\%$ models predicted more management units suitable for invasion than the occurrence model - again likely

due to suitable habitat in the Western U.S., which contains more public land managed by federal agencies than in the Eastern U.S.

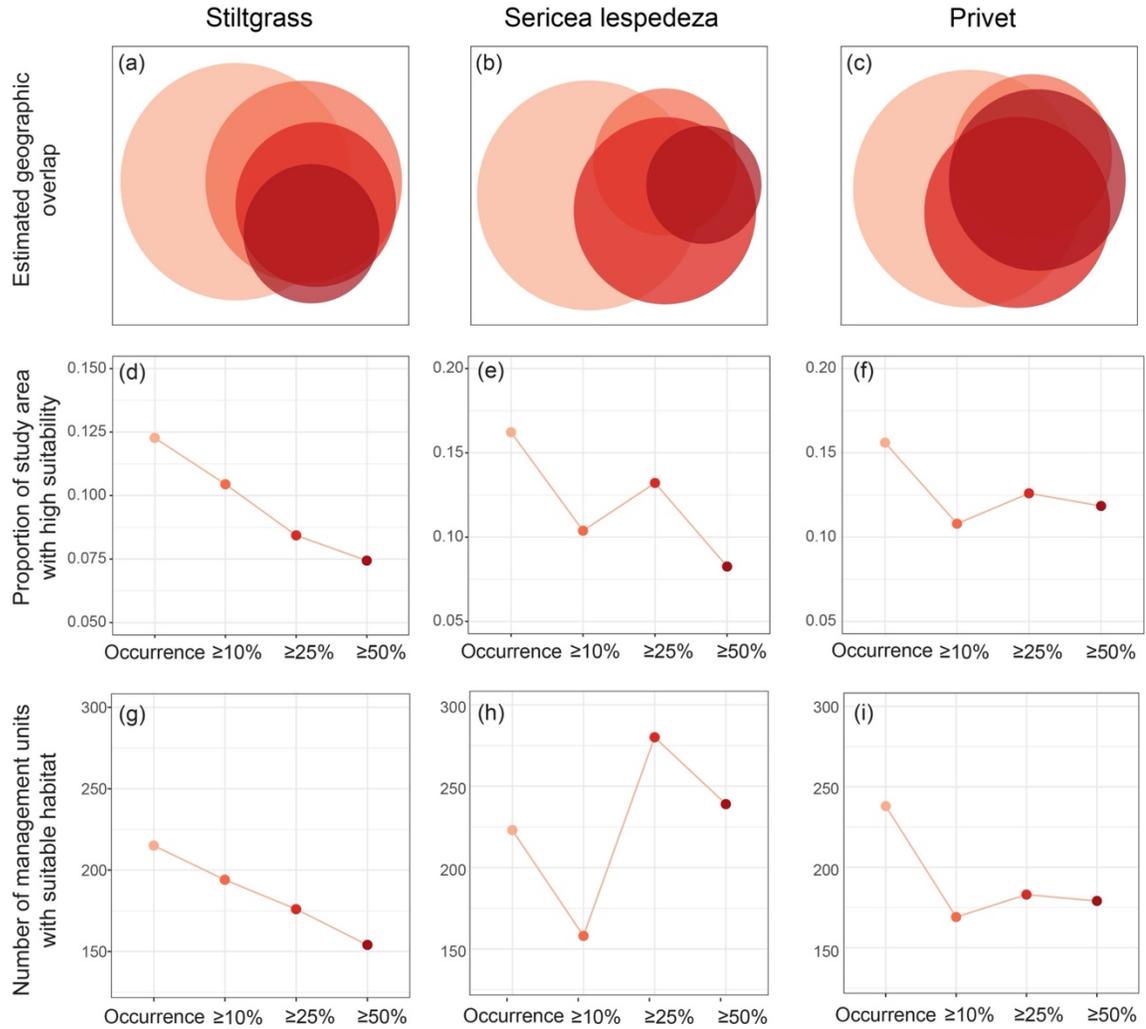


Figure 4.1 (a-c) Conceptual representation of geographic overlap in habitat suitability. Circle colors correspond to the models in d-i and are scaled based on the area with high suitability for invasion. Overlap is reported in Table C5. (d-f) Proportion of the study predicted with high suitability (values >1.5) for invasion. (g-i) The number of U.S. management units (out of 1038) with area highly suitable for invasion for each species.

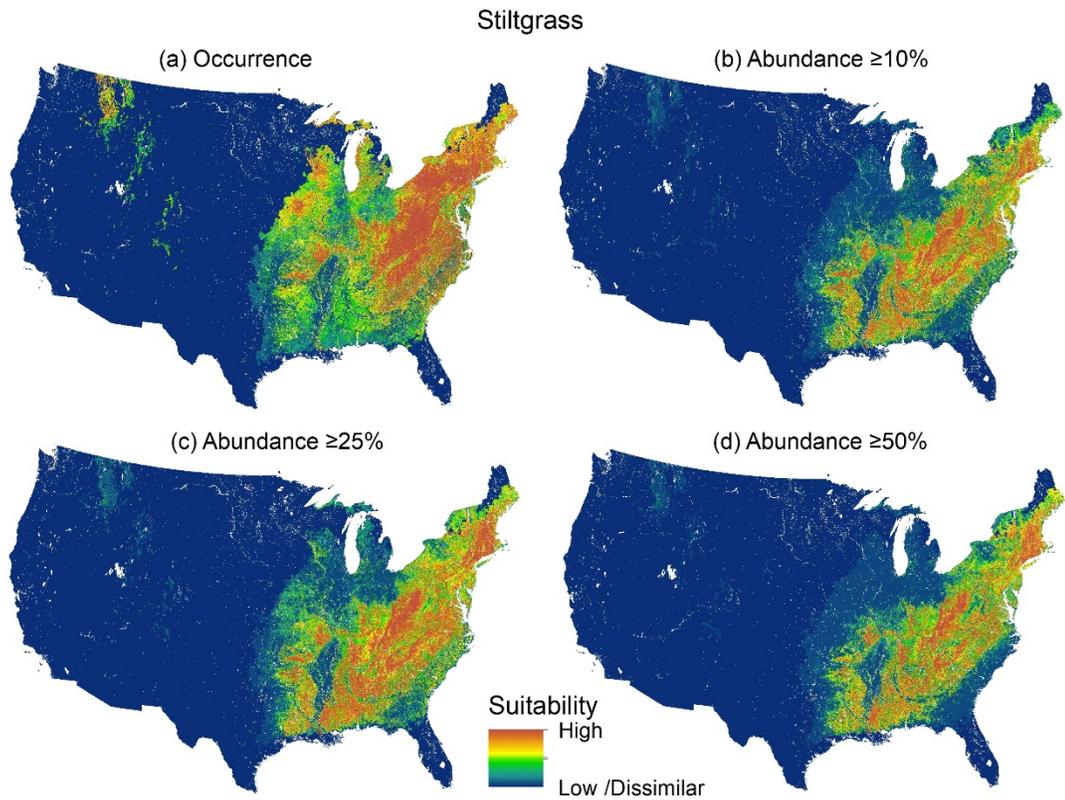


Figure 4.2 Habitat suitability for stiltgrass across models based on (a) occurrence points, (b) abundance of cover $\geq 10\%$, (c) $\geq 25\%$, and (d) $\geq 50\%$. Ensemble suitability represents the mean of categorized suitability values across algorithms. Dissimilar habitats, shown in blue, are beyond the range of environmental values represented by training data.

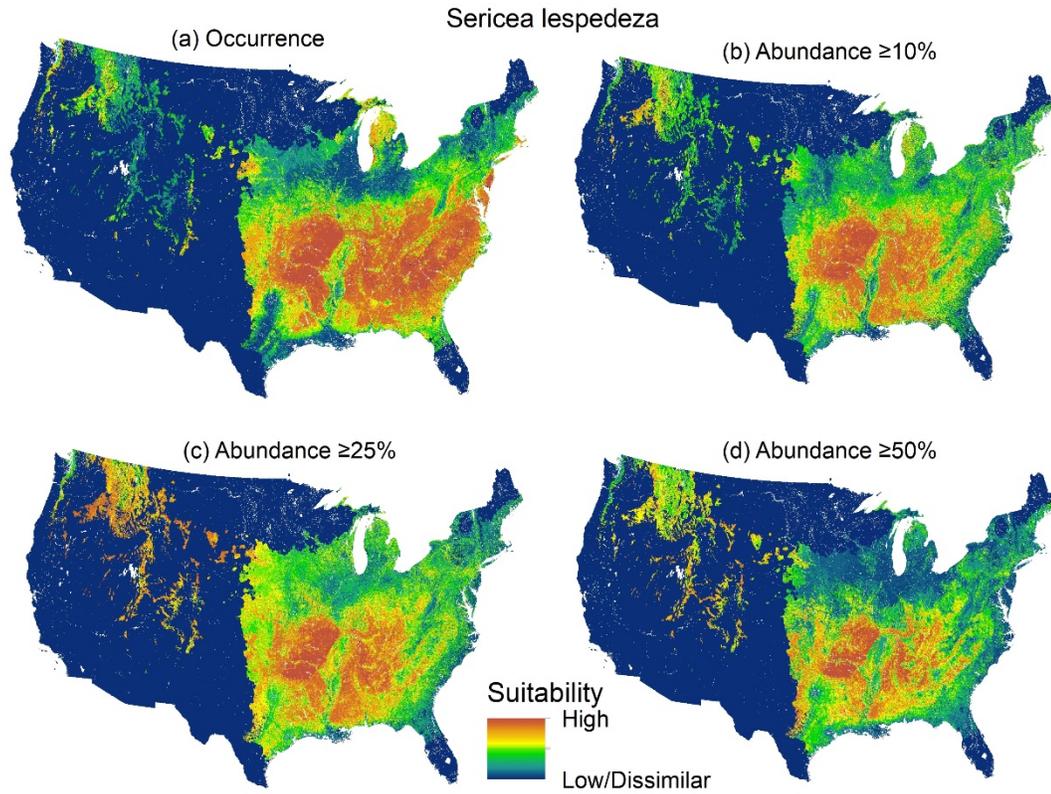


Figure 4.3 Habitat suitability for sericea lespedeza across models based on (a) occurrence points, (b) abundance of cover $\geq 10\%$, (c) $\geq 25\%$, and (d) $\geq 50\%$. Ensemble suitability represents the mean of categorized suitability values across algorithms. Dissimilar habitats, shown in blue, are beyond the range of environmental values represented by training data.

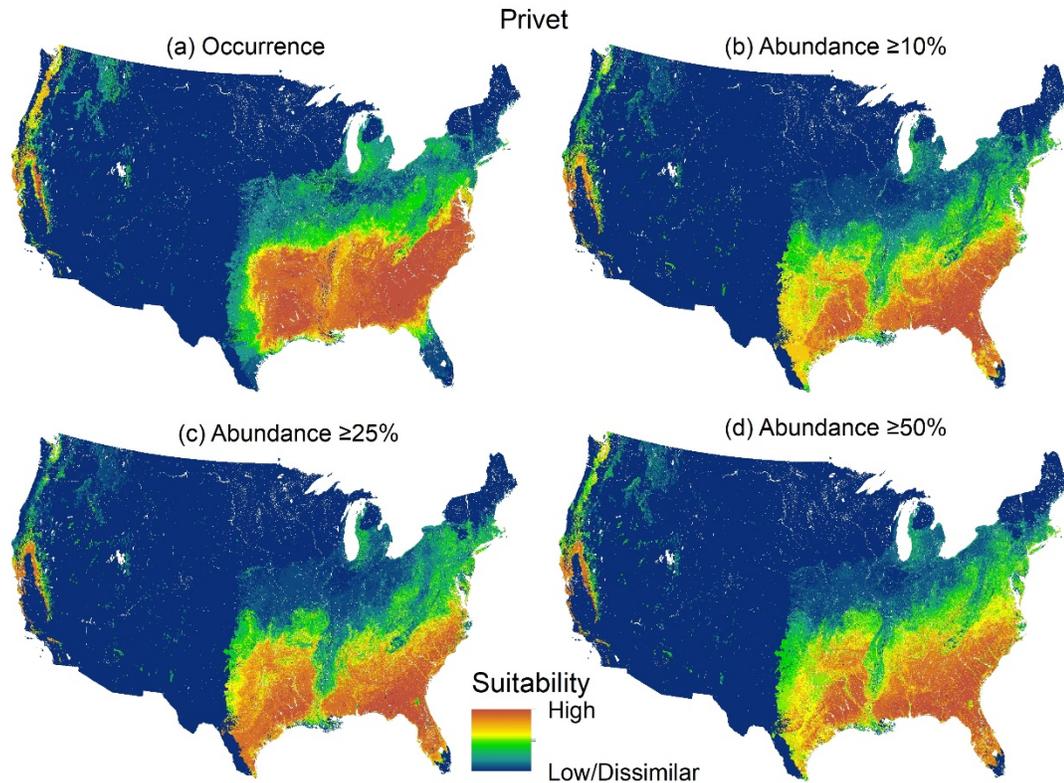


Figure 4.4 Habitat suitability for privet across models based on (a) occurrence points, (b) abundance of cover $\geq 10\%$, (c) $\geq 25\%$, and (d) $\geq 50\%$. Ensemble suitability represents the mean of categorized suitability values across algorithms. Dissimilar habitats, shown in blue, are beyond the range of environmental values represented by training data.

4.4.3 Top predictor variables

There were clear differences between the top predictor variables of occurrence and the top predictor variables of the different levels of abundance (Table 4.2; Tables C2-4). Privet was the only species where the top predictor was consistent for models of occurrence and across all models of abundance, which were all highly influenced by minimum winter temperature (60-65% contribution across all models). For stiltgrass, the most important variables for predicting occurrence were Normalized Difference Moisture Index (NDMI) and minimum winter temperature, but these predictor variables decreased in importance from 30-34% in the model of occurrence to 14-15% in the model of $\geq 50\%$ abundance. Precipitation seasonality, annual temperature range, and evapotranspiration were all important predictors of stiltgrass abundance,

with suitability for abundance decreasing in areas with greater seasonal variation in precipitation. These variables contributed less than 3% to predictions of stiltgrass occurrence.

The top variables were least consistent across models for sericea lespedeza, which must be interpreted with caution given the potential spatial bias between occurrence and abundance datasets (Table 4.2, Table C3). Nitrogen content was an important constraint on the abundance of sericea lespedeza (suitability for abundance decreased with higher levels of nitrogen) but did not affect occurrence (<3% contribution). Sericea lespedeza occurrence was primarily constrained by minimum winter temperature (34% contribution), which was only an important predictor of sericea lespedeza abundance $\geq 10\%$. Global human modification was the only variable that contributed more than 10% to the predictions of suitability across all models of lespedeza; unexpectedly, suitability for sericea lespedeza decreased in areas with greater anthropogenic impacts.

Table 4.2 The relative importance of environmental variables across ensemble models for each species. For each algorithm (n=5), variable contribution was estimated as the change in AUC when values for that variable were permuted between occurrence and pseudo-absence locations. The change in AUC was then converted to a percent contribution relative to the other predictors and averaged across the five algorithms. Variables with values <10% contribution for all models are reported in Tables C2-4. If there were no spatial biases in datasets, we expect contribution to be similar between models of occurrence points and abundance points.

Species	Predictor	Occurrence points	Abundance points	≥10% cover	≥25% cover	≥50% cover
Stiltgrass	Normalized Difference Moisture Index (NDMI) median	34.34	26.87	20.90	18.47	14.10
	Minimum Temperature Winter	30.71	28.1	18.39	14.63	15.45
	Precipitation Seasonality	0.52	5.43	14.12	13.42	22.22
	Temperature Annual Range	0.06	10.52	15.12	12.96	6.64
	Evapotranspiration (Apr-Oct)	1.86	3.31	9.24	11.90	11.25
Species	Predictor	Occurrence points	Abundance points	≥10% cover	≥25% cover	≥50% cover
Sericea lespedeza	Minimum Temperature Winter	34.11	12.34	14.78	2.37	6.67
	Global Human Modification	19.29	6.70	13.49	13.40	18.27
	Mean Summer Potential Water Deficit (Jun-Aug)	11.15	6.70	2.59	7.40	8.27
	Nitrogen Content	2.16	32.51	24.08	21.40	14.22
	Normalized Difference Moisture Index (NDMI) median	0.51	8.24	7.45	10.68	3.56
	Mean Annual Precipitation	6.34	4.95	9.12	13.75	18.61
Species	Predictor	Occurrence points	Abundance points	≥10% cover	≥25% cover	≥50% cover
Privet	Minimum Temperature Winter	62.45	72.55	61.59	65.19	60.56
	Mean Spring Potential Water Deficit (Mar-May)	11.28	6.53	3.46	3.94	4.08

4.5 Discussion

Understanding the geography of invasive plant abundance is critical for preventing the negative impacts of plant invasions (Bradley et al. 2019). By predicting habitat suitability for different levels of abundance, we identified areas of the United States that are vulnerable to high levels of invasion of stiltgrass, sericea lespedeza, and privet. Habitat suitability predicted from models that incorporated abundance data was distinct from suitability predicted from occurrence data, suggesting that occurrence records do not negate the importance of having information on species abundance, particularly when assessing potential risks associated with invasive plants reaching high densities.

Habitat suitability was more similar among abundance models than suitability between occurrence and abundance, but the level of similarity among abundance models varied by species. For example, NDMI explained a decreasing amount of variation across stiltgrass distributions, whereas seasonal variation in precipitation increased in importance for higher levels of abundance. This resulted in a smaller area predicted as highly suitable for stiltgrass abundance $\geq 50\%$ cover, suggesting that there may be optimal environmental conditions that support the highest abundance of stiltgrass and suboptimal conditions result in lower abundance. For stiltgrass management, our findings suggest that this species can occur in habitats that span a moisture gradient, but habitats with stable seasonal precipitation patterns are most vulnerable to high levels of stiltgrass invasion and its associated negative impacts.

Alternatively, for privet, all levels of abundance and occurrence were similarly limited by minimum winter temperature, and this variable explained 60-65% of variation in the distribution datasets. As the climate warms, monitoring habitats that will become more suitable for privet may help to prevent its spread and impact (Hellman et al. 2008). Further, given that suitability for privet invasion was most similar across models, anywhere privet is found at low abundance could also be vulnerable to high abundance. Therefore, managing existing infestations at low abundance

may be most effective for species like privet that show similar vulnerability to all levels of abundance.

For *sericea lespedeza*, the difference in predictors of occurrence and any location associated with abundance data shows that there are remaining spatial biases associated with data collection that can affect outcomes of distribution modeling. More work is needed to understand the environmental constraints on *sericea lespedeza* abundance; nevertheless, there were more variables that predicted *sericea lespedeza* abundance than occurrence, suggesting the potential that this species is rare more often than it is abundant. In such cases, or when capacity for management is limited (Beaury et al. 2019), selecting a high level of cover may be useful in targeting management and control to areas susceptible to the highest levels of invasion.

For all three species, the abundance models predicted less area suitable for invasion compared to the occurrence models, which is consistent with findings from other studies (Bradley 2016; Jarnevich et al. 2021; O'Neill et al. 2021; Van Couwenberghe et al. 2012). Thus, any definition of 'high abundance' in a distribution model is likely to create a more targeted representation of invasion risk. This finding is promising because there is still a paucity of abundance data for many invasive plants (Bradley et al. 2018; O'Neill et al. 2021), especially those in earlier stages of invasion. Defining suitability for abundance based on a lower level of cover can increase the number of point locations that can be included (Table C1), as well as accommodate temporal changes in abundance (i.e., species may be recorded at 10% cover because they can only reach that level of abundance, or because they have not had enough time to reach a higher density). We found that a few hundred well-dispersed data points with abundance information could produce high-performance species distribution models and predictions of suitability for invasion (Table 4.1).

Characterizing species-specific relationships between abundance and the environment provided critical information on the geography of invasive plant abundance and identified areas most susceptible to the negative impacts that can result from species reaching high densities. As

the climate changes, this information can be used to inform management decision-making, such as managing small populations in areas where abundance will no longer be constrained by the environment (e.g., sleeper populations; Spear et al. 2021), or monitoring habitats that will become more suitable for invasion (e.g., warming areas of the U.S.; Hellman et al. 2008). For our three focal species, modeling habitat suitability across levels of abundance provided critical information that would not have emerged from models based on occurrence data alone (Howard et al. 2014; Bradley 2016). Predicting suitability for invasion using abundance data $\geq 5\%$ or $\geq 10\%$ cover can help to target assessments of invasion risk, but more information is needed to understand which invasive species may reach high abundance everywhere they can establish a low abundance population versus those whose abundance is more restricted by the environment (Jarnevich et al. 2021). Where sufficient abundance data are available, modeling suitability for invasion across multiple levels of abundance may be most useful for guiding management.

APPENDIX A

SUPPORTING INFORMATION FOR CHAPTER 2: BIOTIC RESISTANCE TO INVASION IS UBIQUITOUS ACROSS ECOSYSTEMS OF THE UNITED STATES

Here we provide a description of model selection, validation, summary output, predictions, and credible intervals. Considering the many factors that likely influence plant richness, and collinearity between these variables, we used Akaike Information Criterion (AIC) to compare candidate models predicting non-native plant richness. We tested more candidate models than we report here, but given the large suite of possible models, we discuss only the final set of candidate models. Our candidate models included the following fixed effects based on a priori hypotheses:

- Native richness (NativeRich)¹
- Community type (Community)¹
- Ecoregion²
- Distance to human activity based on distance to developed or agricultural lands (DistLandCover)³
- Distance to human activity based on distance to roads (DistRoads)⁴
- Latitude¹
- Hardiness zone (HZ)⁵

Data sources:

1 National Park Service Vegetation Mapping Program

<https://www.nps.gov/im/vegetation-inventory.htm>

2 Environmental Protection Agency Level I Ecoregion spatial layer

<https://www.epa.gov/eco-research/ecoregions>

3 National Land Cover Database 2001 and 2011 spatial layers

<https://www.mrlc.gov/>

4 U.S. Census Bureau's Topologically Integrated Geographic Encoding and Referencing Database roads spatial layer

<https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>

5 PRISM Climate Group USDA Plant Hardiness Zone Maps

<http://prism.oregonstate.edu>

The model with the lowest AIC included the fixed effects of native richness, community type, ecoregion, distance to human activity using land cover, and hardiness zone. This model also included site as a random effect such that each site (e.g., parks, monuments, historic sites, forts) had a unique intercept.

Model	AIC	Delta AIC	Df
NativeRich*(Community + Ecoregion) + DistLandCover + HZ	60373.1	0.0	32
NativeRich*(Community + Ecoregion) + DistRoads + HZ	60484.4	111.2	32
NativeRich*(Community + Ecoregion) + DistLandCover + Latitude	61096.5	723.3	32
NativeRich*(Community + Ecoregion) + DistRoads + Latitude	61281.2	908.0	32

Best fit model: `glmmTMB(cbind(NonRich, NativeRich) ~ zNativeRich*(Ecoregion+Community) + zPropagule + zHZ + (1 | Site), ziformula = ~ zNativeRich+ Community + (1 | zPropagule) + (1 | zHZ) + (1 | Ecoregion) + (1 | Site), data=plots, family="binomial", control=glmmTMBControl(optCtrl=list(iter.max=1e3,eval.max=1e3), profile = TRUE))`

Variables preceded with ‘z’ (e.g., zNativeRich) were log transformed and Z standardized to place all numeric variables on the same scale and avoid correlation between the slope and intercept of the different effects. Distance to human activity using land cover types is now labeled as ‘Propagule’. This model explained 13% of variation in the data measured as deviance explained compared to a null model absent of fixed effects.

We fit a zero inflated mixed effects model with the binomial distribution using the `glmmTMB` package in R to test the effect of different predictors on non-native species occurrence. Much of the model set-up is the result of collinearity between species richness and any description of habitat. Ideally, we would be able to predict the independent effects of native richness, ecoregion, and community type, as well as interactions between these variables. However, in a model including these predictor variables, collinearity resulted in variance inflation factors in the thousands:

```
mod = glm(cbind(NonRich, NativeRich) ~ Ecoregion*Community*zNativeRich +
zPropagule + zHZ, data=parks, family="binomial")
vif(mod)
```

	GVIF	Df	GVIF^(1/(2*Df))
Ecoregion	1.862832e+08	6	4.888562
Community	3.324577e+02	3	2.632021
zNativeRich	6.208301e+00	1	2.491646
zPropagule	1.421633e+00	1	1.192323
zHZ	1.870160e+00	1	1.367538
Ecoregion:Community	5.054588e+11	18	2.113987
Ecoregion:zNativeRich	2.388663e+08	6	4.990908
Community:zNativeRich	2.177709e+02	3	2.452825
Ecoregion:Community: zNativeRich	7.669276e+10	18	2.006108

We fit multiple models using combinations of native richness, ecoregion, and community type, and different interactions between them. The model discussed in this paper was the best fit model that included as much information as we could with variance inflation factors around or below 10. We accepted a higher variance inflation factor than the typical rule of thumb considering the inclusion of interactions between native richness and the habitat predictors.

	GVIF	Df	GVIF^(1/(2*Df))
zNativeRich	4.941534	1	2.222956
Ecoregion	11.108359	6	1.222187
Community	2.803392	3	1.187446
zPropagule	1.365789	1	1.168670
zHZ	1.824461	1	1.350726
Ecoregion: zNativeRich	10.456703	6	1.216045
Community: zNativeRich	7.261963	3	1.391583

Because richness varied depending on ecological context, we chose to use the binomial distribution to analyze proportion data. In doing so, we are able to analyze the relationship between native and non-native species richness across habitats with varying diversity. Using the Poisson or negative binomial distributions to analyze richness data is incorrect in this context because there is no control of factors that covary with species richness. Rather, using proportion

data allowed us a more standardized means of making comparisons across extremely different habitats. In early studies of biotic resistance, this approach was criticized because native richness is the denominator of the response and used as a predictor. Critics of this method suggested that this approach biased the response towards support of biotic resistance because diverse systems will always have a lower proportion of non-native species as the denominator of the response is large. This is true when converting richness data to a proportion by hand, but the glmmTMB binomial framework allows us to use raw counts of richness much like the Poisson or negative binomial distribution. This modeling framework did not bias results towards acceptance of the biotic resistance hypothesis. We demonstrate this using the following simulation, results of which are displayed in Figure A1:

```

#set up blank plot to fill in with model predictions
  plot(0,0, type="n",lwd=2, ylim=c(0,0.3), xlim=c(0,150),xlab="nat",
ylab="prob(nonnat)")
  abline(h=0.1, lwd=2, col=2)
#simulate data using range of total richness from observed data and average proportion of
native species per plot (0.9)
  for(i in 1:500){
    #simulated Total richness:
    n <- 50
    tot <- sort(sample(1:165, n, replace=T))
    #simulate native richness (p=0.9)
    nat <- rbinom(length(tot), tot, 0.9)
    #compute non-native richness
    nonnat <- tot-nat
    #create proportions
    props <- cbind(nonnat,nat)
    #model this:
    null <- glm(cbind(nonnat,nat) ~ 1, family = binomial)
    denom <- glm(cbind(nonnat,nat) ~ nat, family = binomial)
    #plot
    lines(predict(denom, type="response") ~ nat, type="l",lwd=2, ylim=c(0,1),
col=adjustcolor("gray",0.05))
  }

```

Randomly simulated data did not produce consistently negative relationships (Figure A1), demonstrating that this model setup, and specifically the use of the binomial distribution with native richness in the denominator of the response and as a predictor, did not bias the results towards evidence of biotic resistance.

Site was included as a random intercept effect to account for spatio-temporal autocorrelation between plots. We considered including it as a random slope and intercept effect using native richness ($z_{\text{NativeRich}} \mid \text{Site}$), but sites sampled habitats based on the vegetation contained in that site, so sample sizes for each habitat within each site were too small to estimate individual random slopes. We also tested for autocorrelation by performing a Moran's I test using weighted distances between plots.

```
Moran.I(PearsonResiduals, Weights)
  $observed [1] 0.1932561
  $expected [1] -4.089143e-05
  $sd [1] 0.0004346337
  $p.value [1] 0
```

Results of the Moran's I suggest there is slight spatial autocorrelation between plots, indicating some regularity in the way plots are distributed across the U.S. This is somewhat unsurprising considering the National Park Service's effort to hold protected areas in all 50 states. We accounted for spatial autocorrelation in our model by including the geographic variables of ecoregion, hardness zone, and site. We tried adding geographic region (e.g., South, West) and geographic subregion (e.g., Southeast, Southwest) to account for the remaining autocorrelation, but these variables were highly collinear with ecoregion.

```
glm.subregion <- glm(cbind(NonRich, NativeRich) ~
zNativeRich*(Ecoregion+Community) + zPropagule + zHZ + Subregion,
data=plots, family="binomial")
```

```
vif(glm.subregion)
```

	GVIF	Df	GVIF^(1/(2*Df))
zNativeRich	5.874350	1	2.423706
Ecoregion	466.504290	6	1.668801
Community	2.831289	3	1.189408
zPropagule	1.428727	1	1.195294
zHZ	2.484724	1	1.576301
Subregion	193.414057	8	1.389650
Ecoregion:zNativeRich	11.563071	6	1.226279
Community:zNativeRich	7.480496	3	1.398476

```
glm.region <- glm(cbind(NonRich, NativeRich) ~
zNativeRich*(Ecoregion+Community) + zPropagule + zHZ + Region,
data=plots, family="binomial")
```

```
vif(glm.region)
```

	GVIF	Df	GVIF^(1/(2*Df))
zNativeRich	5.514900	1	2.348382
Ecoregion	156.158894	6	1.523341
Community	2.735949	3	1.182637
zPropagule	1.408195	1	1.186674
zHZ	2.195556	1	1.481741
Plot_Geog_region2	39.000734	3	1.841530
Ecoregion:			
zNativeRich	10.984745	6	1.221047
Community:			
zNativeRich	7.265666	3	1.391701

The data were highly zero inflated, with 50% of the 24,456 plots having zero non-native species. This is unsurprising because we would hope that many areas within the United States remain uninvaded, and this is especially true considering many of the sites in the National Park Service dataset are protected areas. We therefore used a zero inflated model, but considering the variation in the data and the size of the database itself, the glmmTMB package could not fit a model with additional fixed effects in the zero inflated component ('ziformula') other than those included in the best fit model above. We tried all combinations of predictor variables, including

fixed vs. random effects. The model reported in this paper was the best fit model with the most information we could include without glmmTMB crashing.

Model summary table:

Family: binomial (logit)

Formula: cbind(NonRich, NativeRich) ~ zNativeRich* (Ecoregion + Community) + zPropagule + zHZ + (1 | Site)

Zero inflation: ~zNativeRich + Community + (1 | zPropagule) + (1 | zHZ) + (1 | Ecoregion) + (1 | Site)

Data: plots

AIC	BIC	logLik	deviance	df.resid
60373.1	60632.5	-30154.6	60309.124424	

Random effects:

Conditional model:

Groups Name	Variance	Std.Dev.
Park (Intercept)	0.8041	0.8967

Number of obs: 24456, groups: Park, 153

Zero-inflation model:

Groups Name	Variance	Std.Dev.
zPropagule (Intercept)	0.05539	0.2354
zHZ (Intercept)	2.90025	1.7030
Ecoregion (Intercept)	1.46479	1.2103
Park (Intercept)	5.92492	2.4341

Number of obs: 24456, groups: zPropagule, 7989; zHZ, 16; Ecoregion, 7; Park, 153

Conditional model:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-2.409963	0.091389	-26.370	< 2e-16 ***
zNativeRich	-0.488926	0.021704	-22.527	< 2e-16 ***
EcoregionGREAT PLAINS	0.239456	0.070081	3.417	0.000633 ***
EcoregionMEDITERRANEAN CALIFORNIA	0.378448	0.146959	2.575	0.010018 *
EcoregionNORTH AMERICAN DESERTS	-0.255962	0.110532	-2.316	0.020573 *
EcoregionNORTHERN FORESTS	-0.136066	0.150251	-0.906	0.365153
EcoregionNW FORESTED MOUNTAINS	0.115489	0.106698	1.082	0.279075
EcoregionTEMPERATE SIERRAS	-0.415970	0.194578	-2.138	0.032533 *

CommunityHerbaceous	0.367754	0.026820	13.712	< 2e-16	***
CommunityShrubland	0.238326	0.027729	8.595	< 2e-16	***
CommunityWoodland	0.244325	0.029220	8.362	< 2e-16	***
zPropagule	-0.166146	0.008866	-18.740	< 2e-16	***
zHZ	0.332131	0.024381	13.623	< 2e-16	***
zNativeRich:Ecoregion	-0.391186	0.036219	-10.801	< 2e-16	***
GREAT PLAINS					
zNativeRich:Ecoregion	0.060803	0.031365	1.939	0.052551	.
MEDITERRANEAN CALIFORNIA					
zNativeRich:Ecoregion	-0.423672	0.027652	-15.321	< 2e-16	***
NORTH AMERICAN DESERTS					
zNativeRich:Ecoregion	-0.341404	0.074749	-4.567	4.94e-06	***
NORTHERN FORESTS					
zNativeRich:Ecoregion	-0.302726	0.028071	-10.784	< 2e-16	***
NW FORESTED MOUNTAINS					
zNativeRich:Ecoregion	0.111929	0.109938	1.018	0.308626	
TEMPERATE SIERRAS					
zNativeRich:Community	0.019628	0.022033	0.891	0.373018	
Herbaceous					
zNativeRich:Community	0.025968	0.025062	1.036	0.300136	
Shrubland					
zNativeRich:Community	0.062078	0.024891	2.494	0.012632	*
Woodland					

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Zero-inflation model:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-2.50156	0.74981	-3.336	0.000849 ***
zNativeRich	-0.79839	0.04539	-17.588	< 2e-16 ***
CommunityHerbaceous	-1.94492	0.11719	-16.596	< 2e-16 ***
CommunityShrubland	-1.32415	0.11247	-11.773	< 2e-16 ***
CommunityWoodland	-0.38159	0.09182	-4.156	3.24e-05 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

>

We used matrix multiplication and simulation to generate and visualize model predictions of binomial probabilities based on the observed data (Bolker 2008a). In Figure 2.2, the probability of non-native occurrence was predicted across the observed range of native richness for each habitat with distance to human activity and hardiness zone fixed at the mean for that

habitat. In Figure 2.3 and Figure 2.4, the effect of propagule pressure using a range of distances (m) observed in each habitat was predicted across a range of values for native richness.

To produce model predictions, we used the model variance-covariance matrix (i.e., uncertainty and correlations between uncertainties around fitted model estimates) to simulate 1000 sets of parameter estimates from a multivariate normal distribution around model fitted parameter estimates (Bolker 2008b). We then used matrix multiplication to multiply each set of simulated parameter estimates with the values for native richness, distance to human activity, and hardiness zone described for each figure. We then selected the middle 95% of simulations to represent 95% credible intervals (Bolker 2008c). Figures show the simulated credible intervals (colored regions) distributed around the fitted parameter estimates.

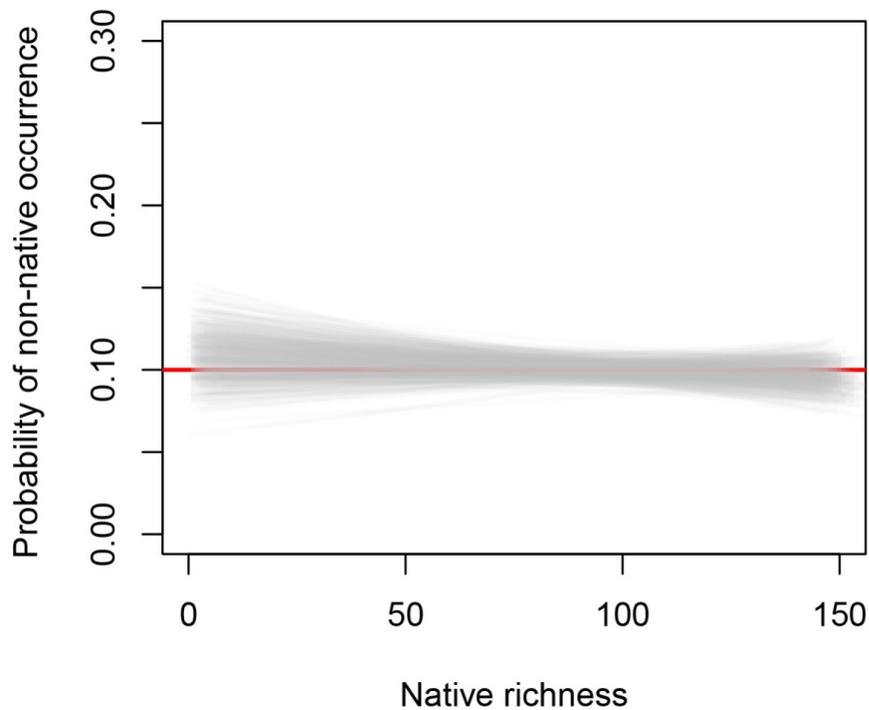


Figure A1 Random simulations of the relationship between native and non-native richness to demonstrate that using a binomial probability distribution does not bias results towards acceptance of the biotic resistance hypothesis.

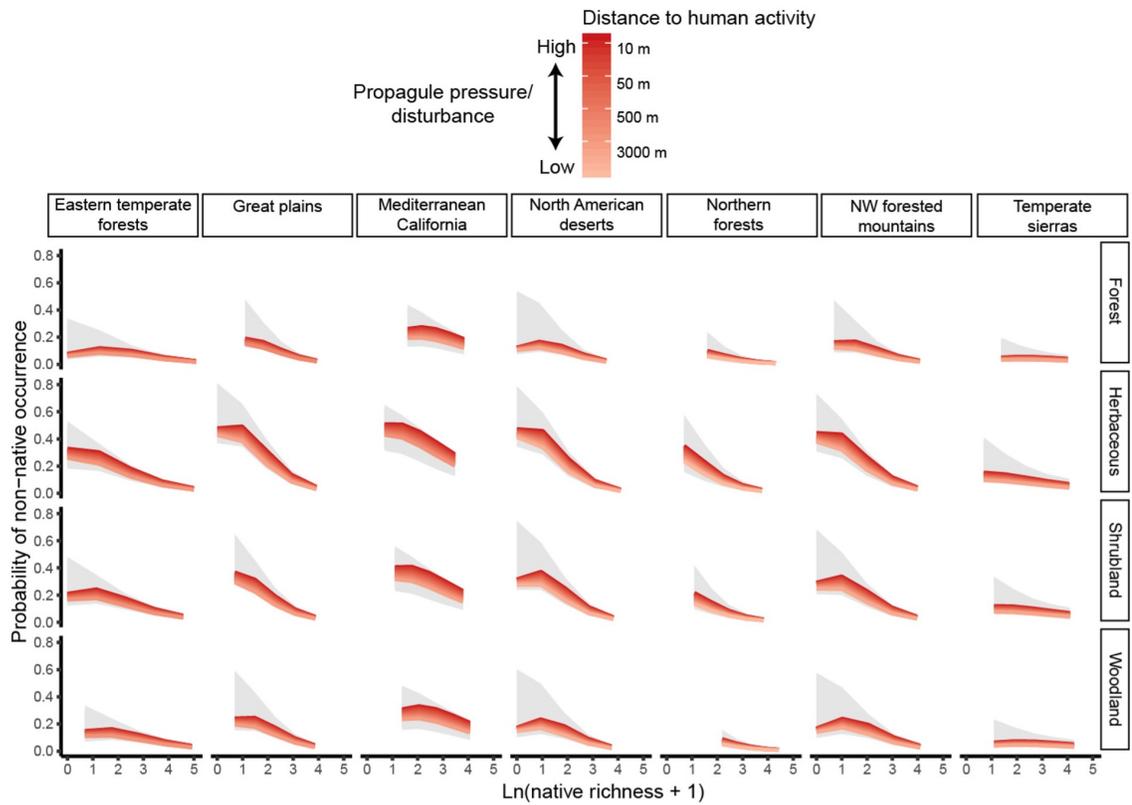


Figure A2 Predicted effect of proximity to human activity as a proxy for the effect of propagule pressure and disturbance on biotic resistance. The ranges of distance to human activity and native richness are from the observed data for each habitat. Grey regions represent 95% credible intervals.

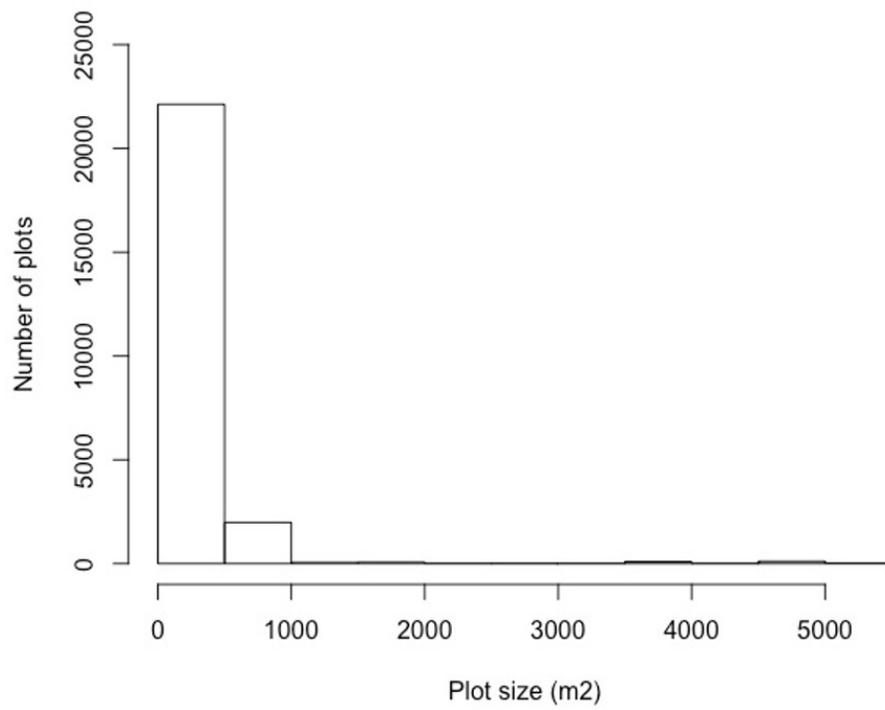


Figure A3 Distribution of plot size for data used in this analysis. Ninety percent of the plots sampled less than or equal to 400 m².

APPENDIX B

SUPPORTING INFORMATION FOR CHAPTER 3: INVASIVE PLANT IMPACTS VARY ACROSS RECIPIENT NATIVE COMMUNITIES AT THE CONTINENTAL SCALE

Results of change point analysis using the 'chngppt' R package.

```
chngpptm (formula.1=Native Richness ~ 1,  
          formula.2= ~Non-native cover,  
          data = plots, type="M11", family="poisson")
```

No variance estimate available.

\$coefficients

	est
(Intercept)	3.1241339
Non-native cover	-1.888958
(Non-native cover-chngppt)+	-0.3602604

\$chngppt

est 8.287938

Table B1 Comparison of model fit (for native richness as the response) among productivity and water availability variables as a quantification of a gradient of resource availability: net primary productivity (NPP), potential water deficit (PWD), soil water deficit (SWD), Priestley-Taylor alpha coefficient (PT), sum of annual precipitation (PSUM), global aridity index (AR), and a null model (the global model without a term for resource availability). The model with NPP had a significantly lower AIC ($\Delta AIC > 2$) compared to models with other variables.

Variable	Df	si	$\Delta AICc$	AIC weight	Cumulative weight	Log Likelihood
NPP	32	134712	0	1	1	-67323
PWD	32	135724	1012	0	1	-67830
SWD	32	136154	1442	0	1	-68045
PT	32	136156	1444	0	1	-68046
PSUM	32	136518	1806	0	1	-68227
AR	32	136618	1906	0	1	-68277
Null	30	136929	2217	0	1	-68434

Table B2 Comparison of model fit (for native richness as the response) between variables quantifying human modification: global human modification index (GHM) and euclidean distance (ED) to land parcels dominated by humans (developed and cultivated/planted land cover classes). The null model is the global model without a term for human modification. The model with GHM had a significantly lower AIC ($\Delta AIC > 2$) compared to the model with euclidean distance.

Variable	Df	AICc	$\Delta AICc$	AIC weight	Cumulative weight	Log Likelihood
GHM	32	134712	0	1	1	-67323
ED	32	134766	54	0	1	-67351

Spatial autocorrelation tests

Native richness

DHARMA Moran's I test for spatial autocorrelation

data: rich_resid

observed = 1.2955e-01, expected = -4.4623e-05, sd = 1.1085e-03, p-value < 2.2e-16

alternative hypothesis: Spatial autocorrelation

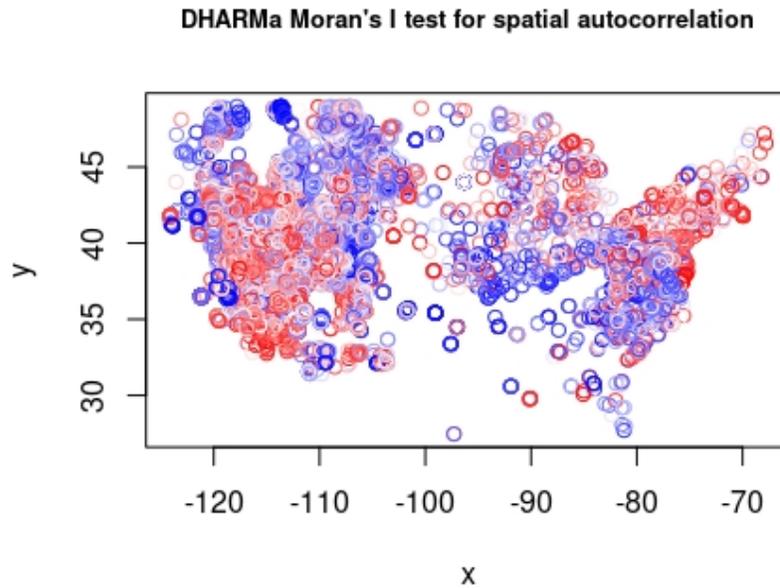


Figure B1 Spatial pattern in residuals across plots from a model fit to native species richness. Red areas signify where the model underestimated native richness and blue areas where native richness was overestimated.

Native diversity

DHARMA Moran's I test for spatial autocorrelation

data: div_resid

observed = 8.1247e-02, expected = -4.4875e-05, sd = 1.1129e-03, p-value < 2.2e-16

alternative hypothesis: Spatial autocorrelation

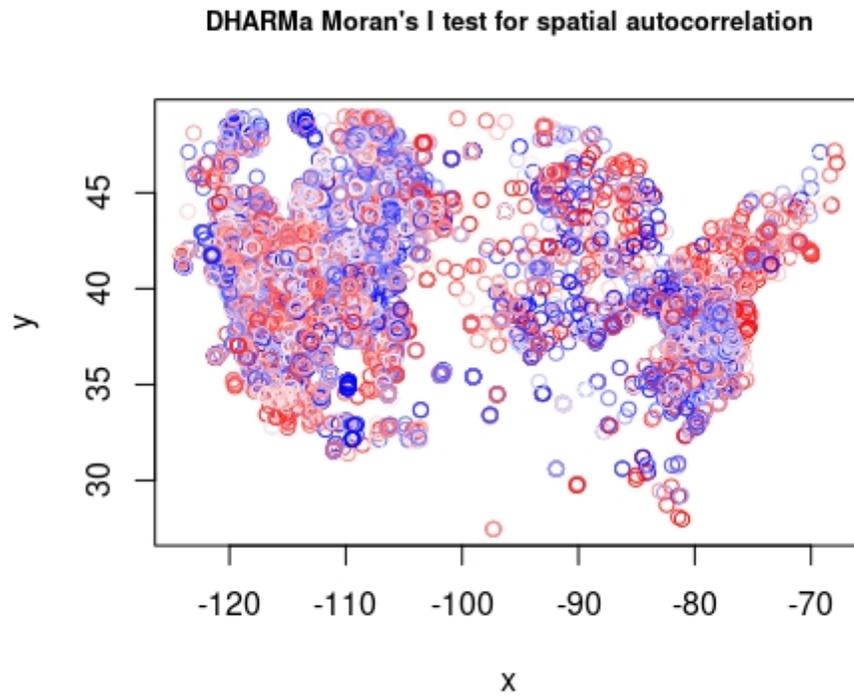


Figure B2 Spatial pattern in residuals across plots from a model fit to native species diversity. Red areas signify where the model underestimated native diversity and blue areas where native diversity was overestimated.

Native evenness

DHARMA Moran's I test for spatial autocorrelation

data: eve_resid

observed = 9.3975e-02, expected = -4.5744e-05, sd = 1.1384e-03, p-value < 2.2e-16

alternative hypothesis: Spatial autocorrelation

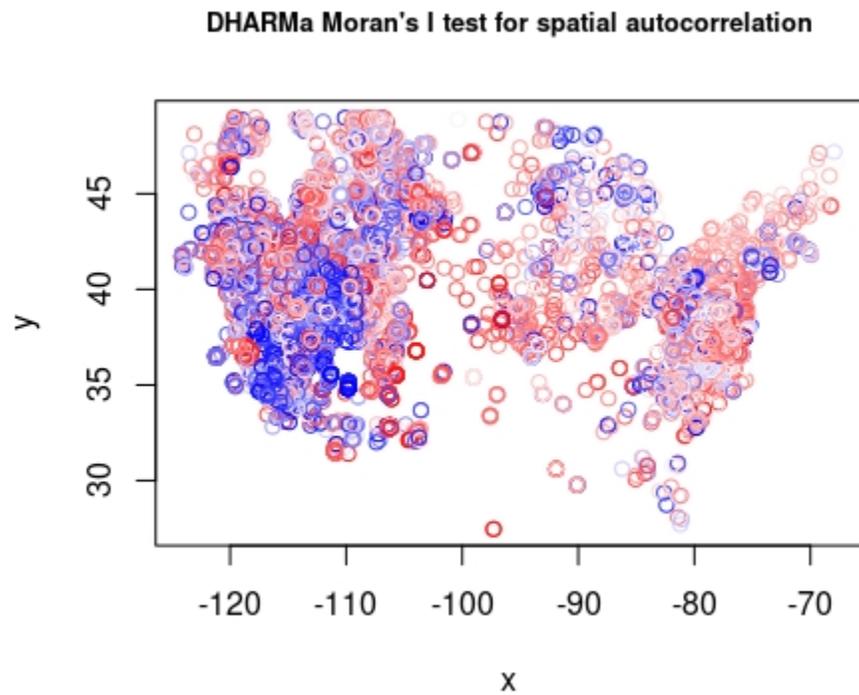


Figure B3 Spatial pattern in residuals across plots from a model fit to native species evenness. Red areas signify where the model underestimated native evenness and blue areas where native evenness was overestimated.

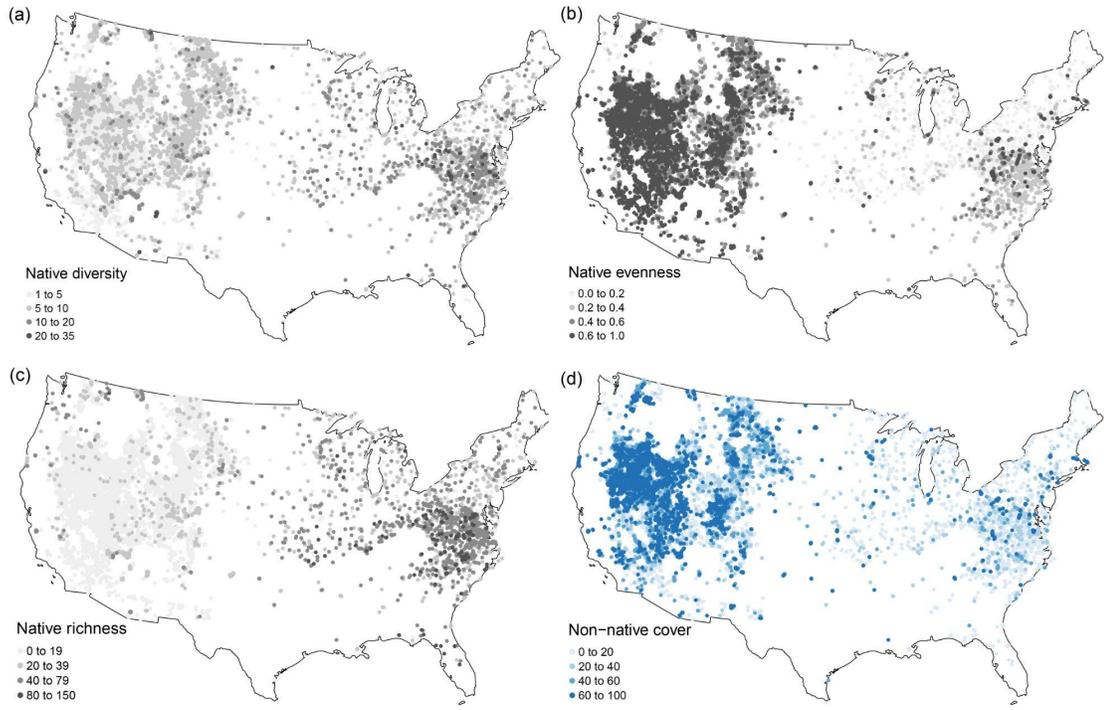


Figure B4 Native community response variables, (a) diversity, (b) evenness, (c) richness, and (d) non-native cover across plots included in the analysis.

Table B3 Model estimates (B) and standard errors (SE) for the effect of data source in models of native richness, diversity and evenness. Because the model of native evenness had a smaller sample size, low-sampled sites that followed the North Carolina Vegetation Survey (NCVS) protocol were combined into one group.

Data source	Native richness		Native diversity		Native evenness	
	B	SE	B	SE	B	SE
Bureau of Land Management Assessment Inventory and Monitoring	3.971	0.177	2.69	0.163	0.531	0.0488
Forest Inventory & Analysis	0.671	0.026	0.272	0.028	-0.196	0.009
National Ecological Observatory Network	0.275	0.035	0.003	0.039	-0.134	0.012
National Park Service Inventory & Monitoring	0.117	0.020	-0.173	0.022	-0.097	0.006
North Carolina Vegetation Survey Sites (coded by state and/or source project)						
AL	0.326	0.215	-0.045	0.226	-0.128	0.013
FL	1.38	0.156	0.703	0.134		
GA	0.488	0.134	0.107	0.141		
MS	0.362	0.289	-0.44	0.38		
NC (coastal)	0.434	0.068	-0.229	0.078		
NC (mountains)	0.376	0.074	-0.18	0.08		
NC (Piedmont plots)	0.682	0.045	0.142	0.048		
SC	0.516	0.062	-0.083	0.07		
TN	0.305	0.116	-0.287	0.13		
VA	0.326	0.215	-0.051	0.108		
WV	0.555	0.098	--	--	-0.11	0.011
VA (Natural Heritage)	0.644	0.031	0.145	0.034	-0.070	0.011

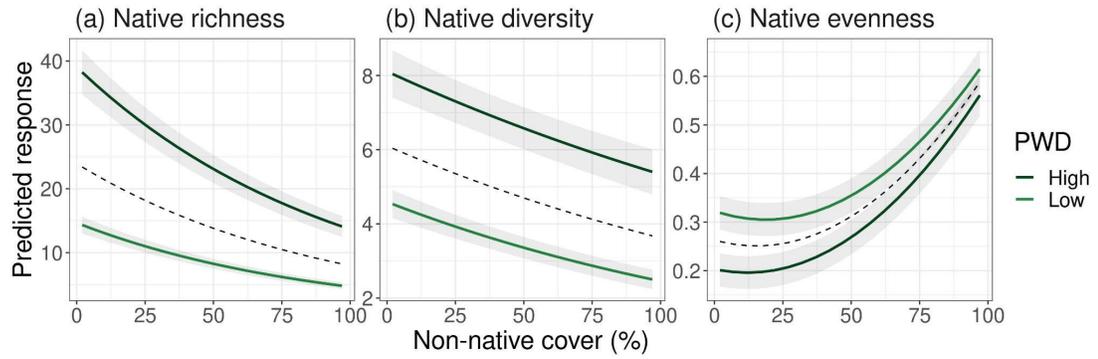


Figure B5 The relationship between non-native plant cover and native plant (a) richness, (b) diversity, and (c) evenness across a gradient of potential water deficit (PWD). High PWD corresponds to wetter areas. There was a nonsignificant interaction between PWD and non-native cover in the model for native richness ($P = 0.20$), but there was a significant interaction on native diversity ($SE = 0.0021$; $P < 0.02$) and native evenness ($SE = 0.00062$; $P < 0.007$).

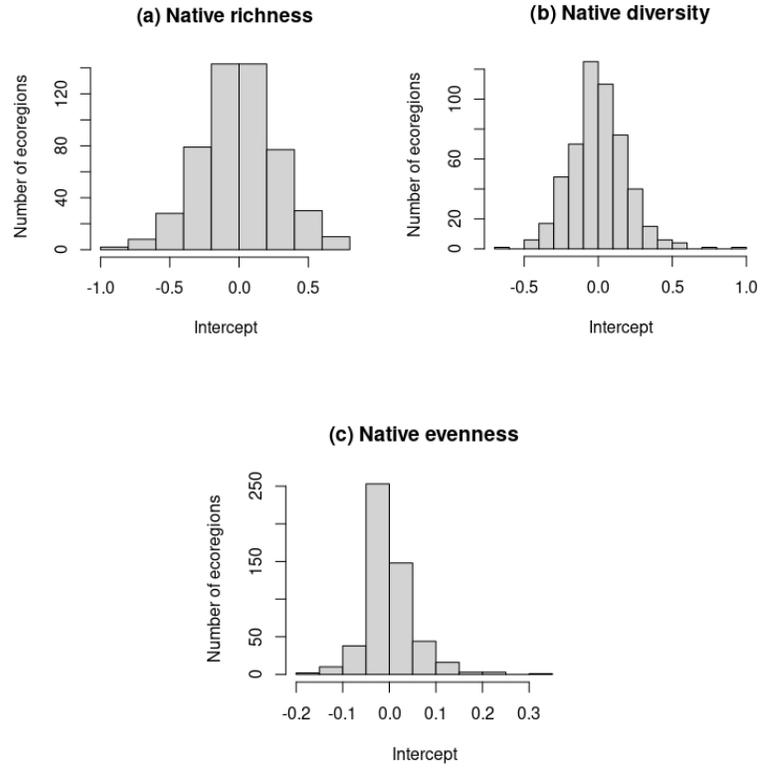


Figure B6 Distribution of random intercepts associated with level 4 EPA ecoregions (n = 520).

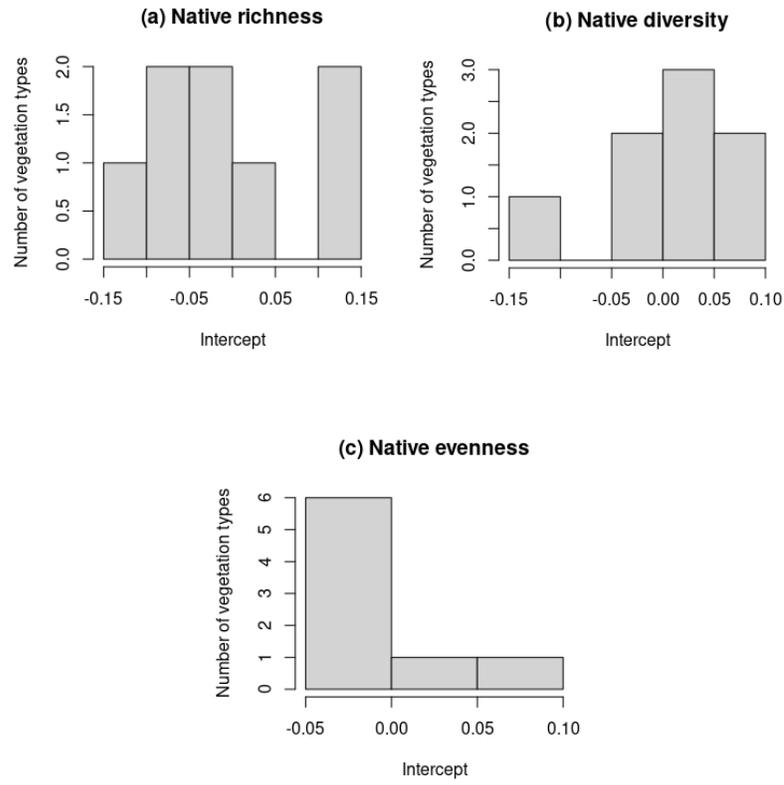


Figure B7 Distribution of random intercepts associated with dominant vegetation type (n = 8).

APPENDIX C

SUPPORTING INFORMATION FOR CHAPTER 4: MODELING HABITAT SUITABILITY
ACROSS DIFFERENT LEVELS OF INVASIVE PLANT ABUNDANCE

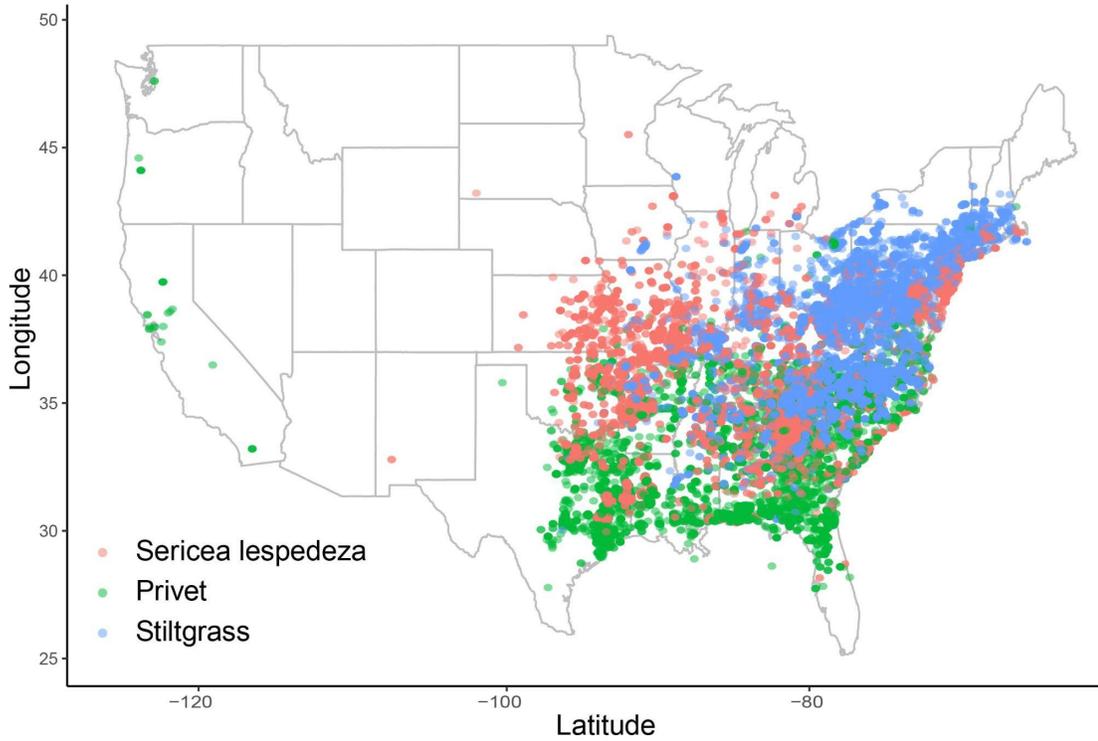


Figure C1 Geographic distribution of all available point locations in the United States for stiltgrass, sericea lespedeza, and privet.

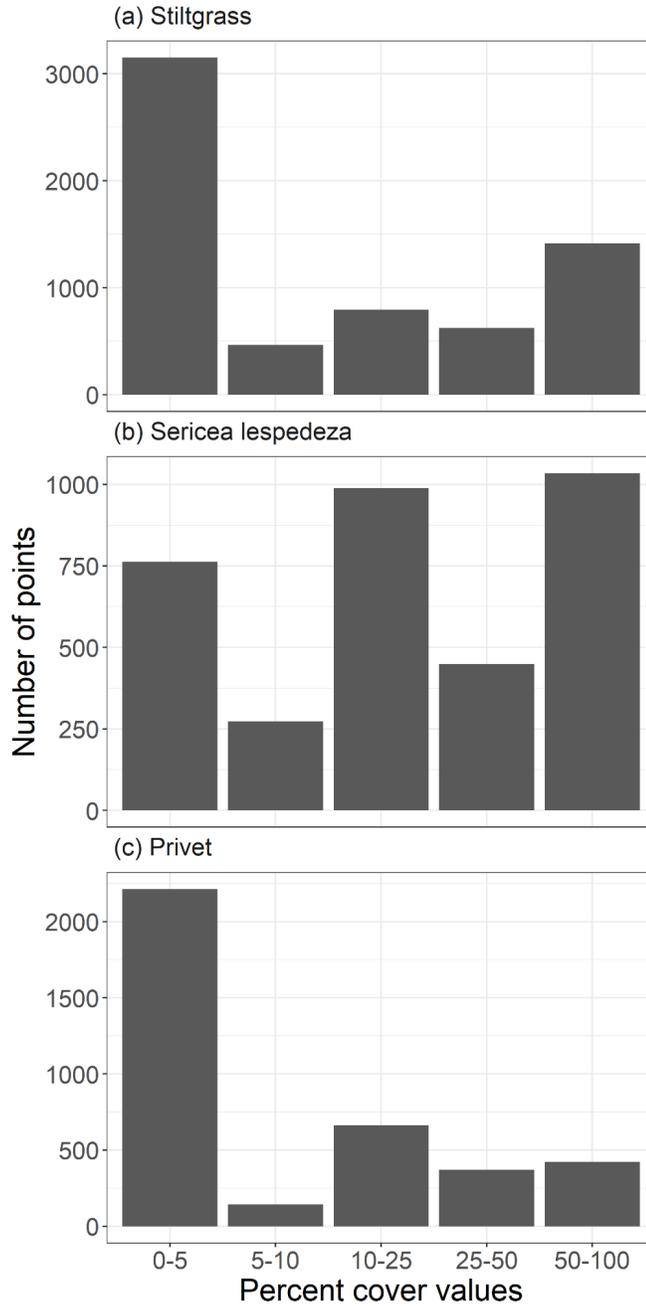


Figure C2 Distribution of percent cover data across bins of (0-5), [5-10), [10-25), [25-50), [50-100]. For each species, this includes all available abundance records prior to spatial thinning. Total sample sizes are stiltgrass $n = 6451$, sericea lespedeza $n = 3506$, and privet $n = 3814$.

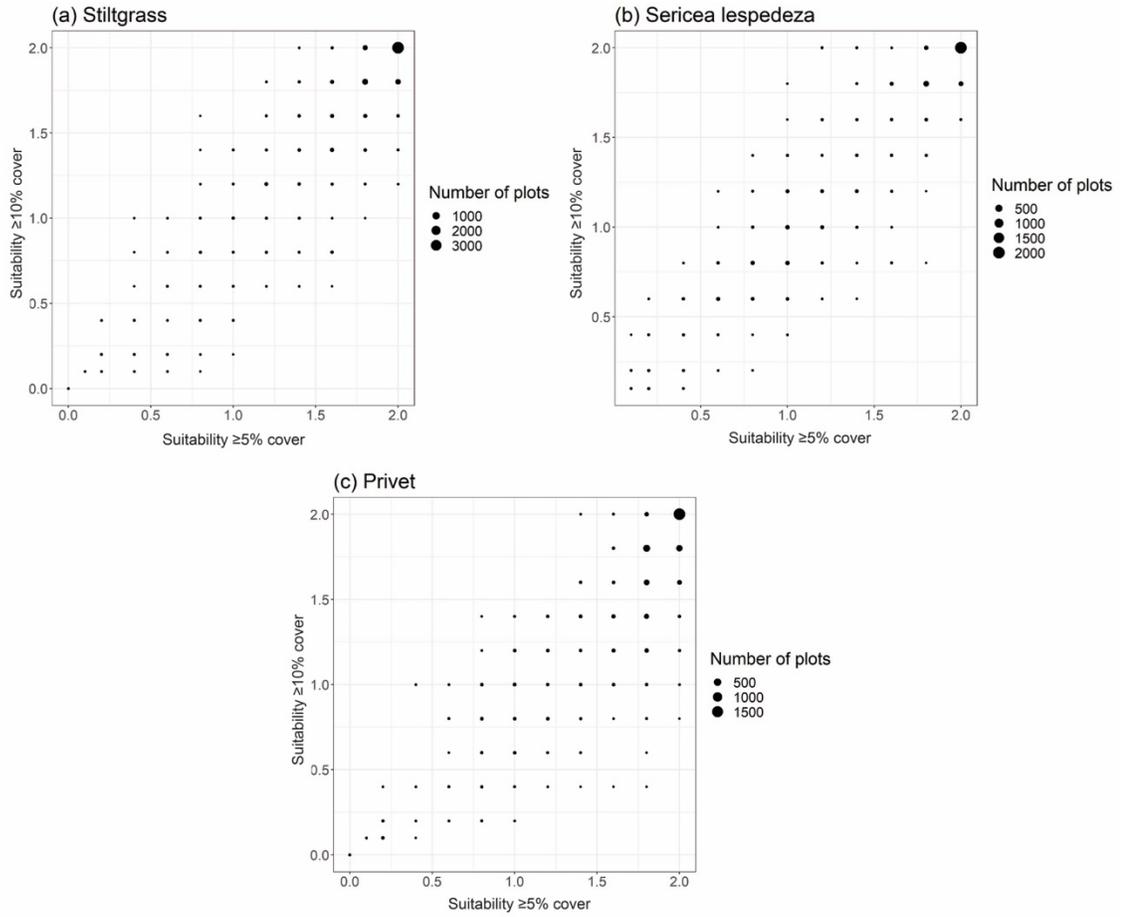


Figure C3 Comparing suitability between a model based on $\geq 5\%$ cover and $\geq 10\%$ cover. Suitability values were joined to all the available abundance data for each species.

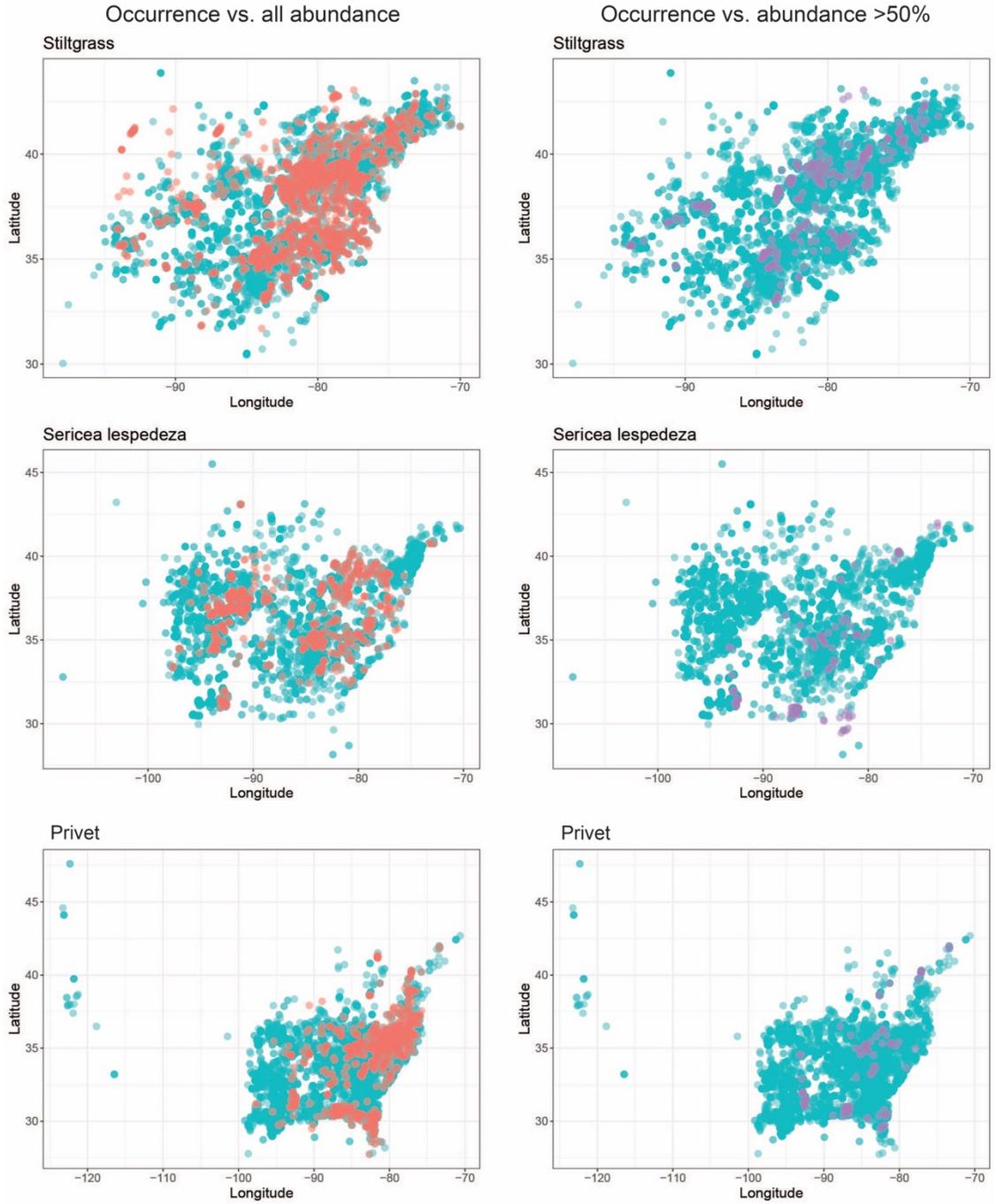


Figure C4 Distribution of occurrence (blue points) vs. abundance data (red = all abundance data; purple = >50% cover) in geographic space for stiltgrass (top panels), sericea lespedeza (middle panels), and privet (bottom panels).

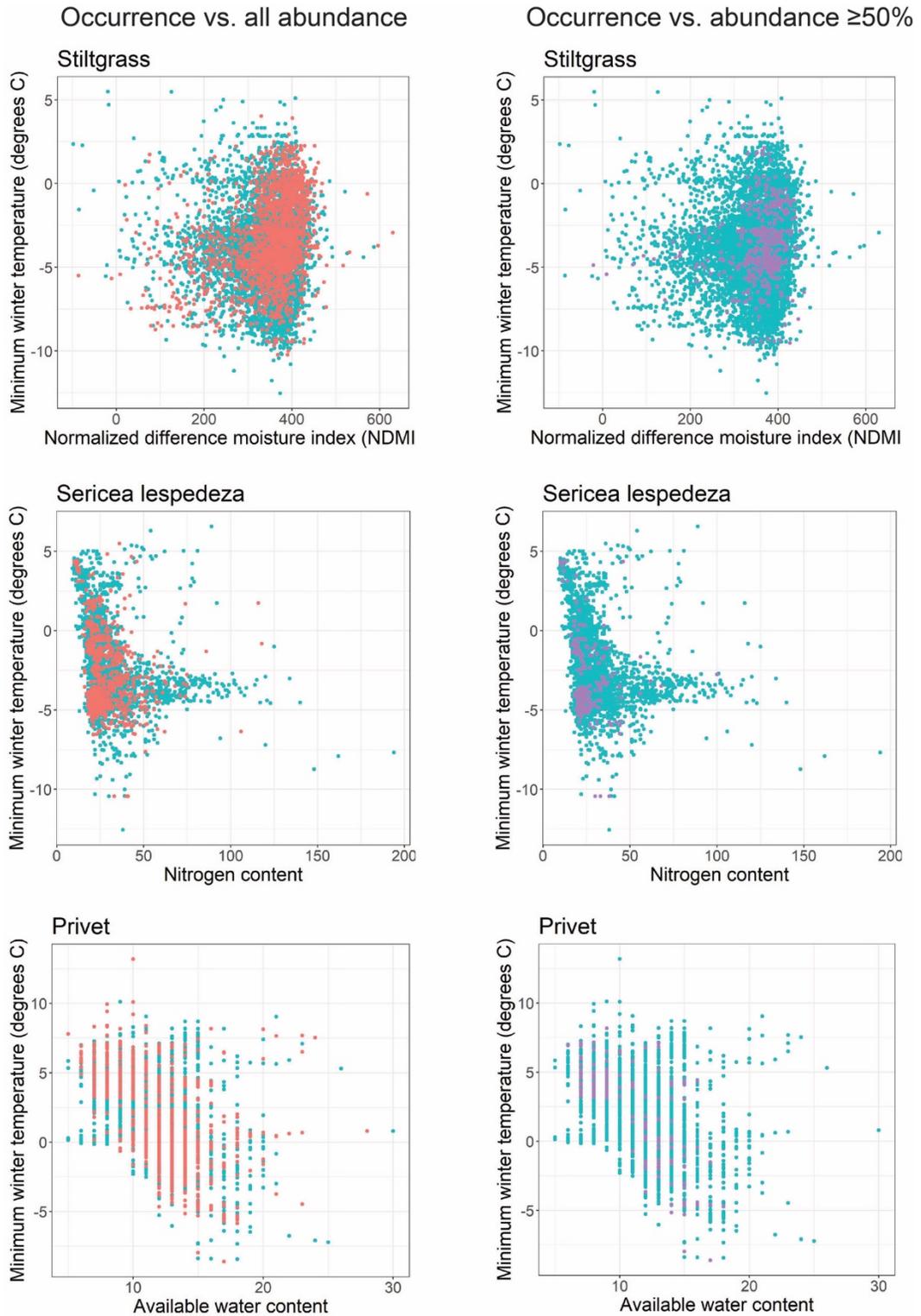


Figure C5 Distribution of occurrence (blue points) vs. abundance data (red points) in environmental space for stiltgrass (top panels), sericea lespedeza (middle panels), and privet (bottom panels). For each species, variables represent a top predictor variable from the occurrence model and a top predictor variable across abundance models.

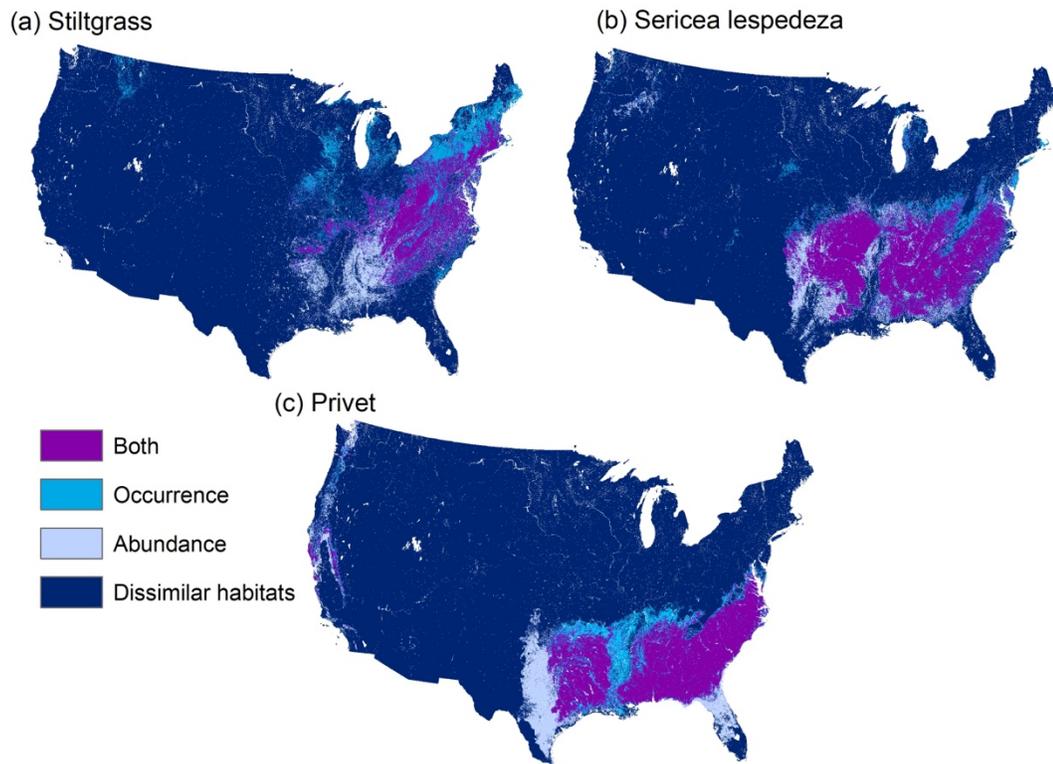


Figure C6 Habitat suitability according to models based on occurrence data and on any data associated with abundance for each species. Purple areas indicate places where both models predicted high suitability for invasion (values >1.5 out of 2). Dissimilar habitats, shown in blue, are beyond the range of environmental values represented by training data.

Table C1 Data source, data type, access notes (whether the data was publicly available or requested by the authors), and the number of points for each species. Data type includes occurrence only, continuous percent cover, and percent cover identified as a class within a range of values (i.e., 5-10%). Number of points refers to the total sample size available; sample sizes used to train models are provided in Table 4.1 of the main text.

Source	Data type(s)	Access notes	Stiltgrass	Sericea lespedeza	Privet	Total
Bureau of Land Management National Invasive Species Information Management System	Occurrence	Privately requested (https://bison.usgs.gov/ipt/resource?r=blm_nisms)	37	156	-	193
CalFlora	Percent cover, cover class	Publicly available (https://www.calflora.org/)	-	-	9	9
Early Detection and Distribution Mapping System	Occurrence, percent cover, cover class	Publicly available (https://www.eddmaps.org/)	21594	12460	11163	45217
Florida Natural Areas Inventory	Cover class	Privately requested (https://www.fnai.org/)	-	-	376	376
Forest Inventory & Analysis phase 3 vegetation surveys	Percent cover	Publicly available (https://www.fia.fs.fed.us/tools-data/other_data/index.php)	152	20	11	183
Global Biodiversity Information Facility	Occurrence	Publicly available (https://www.gbif.org/)	2681	1481	3741	7903
Illinois Critical Trends Assessment Program	Percent cover	Privately requested (https://www.inhs.illinois.edu/research/ctap/data-access/)	8	42	-	50
iMapInvasives Network	Percent cover, cover class	Privately requested (https://www.imapinvasives.org/)	158	9	-	167
National Ecological Observatory Network	Percent cover	Publicly available (https://www.neonscience.org/)	73	22	37	132
National Parks Service Inventory & Monitoring Program	Percent cover	Publicly available (https://irma.nps.gov/DataStore/)	349	76	107	532
National Parks Service National Invasive Species Information Management System	Occurrence	Privately requested (https://irma.nps.gov/NISIMS/)	375	587	223	1185

Table C1 continued.

Source	Data type(s)	Access notes	Stiltgrass	Sericea lespedeza	Privet	Total
National Wetland Condition Assessment	Percent cover	Publicly available (https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys)	56	8	28	92
Carolina Vegetation Survey	Percent cover	Privately requested (http://cvs.bio.unc.edu/)	1131	171	715	2017
U.S. Geological Survey Biodiversity Information Serving Our Nation database	Occurrence	Publicly available (https://bison.usgs.gov/)	3716	1989	1667	7372
VegBank	Percent cover	Publicly available (http://vegbank.org/vegbank/index.jsp)	1433	123	929	2485
Virginia Natural Heritage Program	Percent cover	Privately requested (https://www.dcr.virginia.gov/natural-heritage/)	405	46	78	529
Total			32168	17190	19084	68442

Table C2-4 The relative importance of all environmental variables included in the models of stiltgrass (Table C2), sericea lespedeza (Table C3), and privet (Table C4). For each algorithm (n=5), variable contribution was estimated as the change in AUC when values for that variable were permuted between occurrence and pseudo-absence locations. The change in AUC was then converted to a percent contribution relative to the other predictors and averaged across the five algorithms. Sources for predictor variables are provided following Table C4.

Table C2 Stiltgrass variable contribution.

Predictor	Occurrence points	Abundance points	≥ 5%	≥10%	≥25%	≥50%
Normalized Difference Moisture Index (NDMI) median ¹	34.34	26.87	21.53	20.90	18.47	14.10
Minimum Temperature Winter ²	30.71	28.1	19.04	18.39	14.63	15.45
Mean Annual Precipitation ²	7.09	NA	NA	NA	NA	NA
Potassium Content ³	6.65	1.82	3.61	1.27	0.65	6.18
Global Human Modification ⁴	5.36	2.00	2.78	2.15	3.68	2.27
Mean Spring PET (Mar-Jun) ²	5.30	NA	NA	NA	NA	NA
Percent Calcium Carbonate In Soil ⁵	4.61	0.09	0.17	0.13	0.73	0.69
Topographic Diversity ⁶	2.4	4.23	3.33	5.40	3.21	4.77
Available Water Content (Mean Depth, cm) ⁵	2.25	0.21	0.59	0.27	0.39	0.38
Percent Clay ³	2.04	0.64	1.2	0.49	0.99	2.33
Burning Index ²	2.02	NA	NA	NA	NA	NA
Evapotranspiration (Apr-Oct) ²	1.86	3.13	8.43	9.24	11.90	11.25
Mean Tree Cover ⁷	1.78	3.90	5.05	8.95	7.75	8.50
Percent Sand ⁵	1.75	0.21	1.08	0.28	1.44	1.31
Multi-Scale Topographic Position Index ⁶	1.70	1.17	2.13	2.22	1.67	1.34
Isothermality ⁸	0.90	2.41	0.64	0.37	2.3	1.12
Mean Summer PET ²	0.56	11.74	9.7	8.32	7.67	7.19
Mean Annual Flow ⁹	0.53	1.12	0.2	0.16	1.38	0.71
Precipitation Seasonality (Cv) ⁸	0.52	5.43	13.33	14.12	13.42	22.22
Normalized Difference Moisture Index (NDMI) standard deviation ¹	0.36	0.23	0.46	0.64	0.72	1.06
Depth To Restriction Layer (Mean) ⁵	0.34	0.82	0.79	0.86	0.71	2.41
Continuous Heat-Load Index ⁶	0.33	0.14	0.46	0.20	0.54	0.62
Soil Organic Carbon ³	0.23	NA	NA	NA	NA	NA

Table C2 continued.

Predictor	Occurrence points	Abundance points	≥ 5%	≥10%	≥25%	≥50%
Soil pH ³	0.22	NA	NA	NA	NA	NA
Burn Frequency ¹⁰	0.17	NA	NA	NA	NA	NA
Distance to Water (coarse-scale) ¹¹	0.16	0.80	0.20	0.14	0.85	0.92
Available Water Content (Variance in Depth, cm) ⁵	0.07	1.06	0.98	0.99	0.59	0.18
Temperature Annual Range ⁸	0.06	10.52	11.14	15.12	12.96	6.64
Bare Ground Standard Deviation ⁷	0.04	0.59	1.25	1.28	1.2	1.37

Table C3 Sericea lespedeza variable contribution.

Predictor	Occurrence points	Abundance points	≥ 5%	≥10%	≥25%	≥50%
Minimum Temperature Winter ²	34.11	12.34	8.42	14.78	2.37	6.67
Global Human Modification ⁴	19.29	6.70	10.96	13.49	13.40	18.27
Mean Summer PET ²	11.15	1.91	2.63	2.59	7.40	8.27
Bare Ground Standard Deviation ⁷	9.05	NA	NA	NA	NA	NA
Mean Annual Precipitation ²	6.34	4.95	4.35	9.12	13.75	18.61
Precipitation Seasonality (Cv) ⁸	5.53	2.71	1.63	1.47	1.35	2.32
Evapotranspiration (Mar-May) ²	4.74	6.38	15.77	6.68	7.95	7.98
Available Water Content (Mean Depth, cm) ⁵	4.67	4.53	0.70	0.91	0.76	1.96
Potassium Content ³	3.49	6.89	5.31	5.63	2.91	1.93
Normalized Difference Moisture Index (NDMI) standard deviation ¹	2.47	1.62	1.00	1.12	1.22	1.16
Topographic Diversity ⁶	2.39	1.59	2.35	4.02	2.89	4.95
Percent Sand ⁵	2.23	1.51	0.76	0.72	1.59	1.32
Nitrogen Content ³	2.16	32.51	31.97	24.08	21.40	14.22
Depth To Restriction Layer (Mean) ⁵	1.89	5.1	4.39	5.68	8.81	8.89
Bulk Density ³	1.30	NA	NA	NA	NA	NA
Percent Clay ³	0.92	1.91	1.97	3.28	2.70	1.74
Soil pH ³	0.85	1.14	1.62	3.44	0.84	0.61
Mean Spring PET (Mar-May) ²	0.83	2.13	8.50	5.13	6.62	5.00
Mean Diurnal Range (Bio2) ⁸	0.74	1.7	0.76	1.34	1.49	2.01
Percent Calcium Carbonate In Soil ⁵	0.66	1.17	0.57	0.40	0.75	0.36
Normalized Difference Moisture Index (NDMI) median ¹	0.51	8.24	7.43	7.45	10.68	3.56
Mean Annual Flow ⁹	0.36	1.71	1.01	1.19	1.97	2.65
Distance to Water (coarse-scale) ¹¹	0.08	1.02	0.98	0.82	1.17	1.04
Burn Frequency ¹⁰	0.01	NA	NA	NA	NA	NA

Table C3 (continued).

Predictor	Occurrence points	Abundance points	≥ 5%	≥10%	≥25%	≥50%
Continuous Heat-Load Index ⁶	0.01	1.56	1.49	0.84	1.07	0.82
Multi-Scale Topographic Position Index ⁶	0	2.44	0.63	0.71	1.24	0.80
Available Water Content (Variance in Depth, cm) ⁵	0	0.79	0.13	0.28	0.38	0.43

Table C4 Privet variable contribution.

Predictor	Occurrence points	Abundance points	≥ 5%	≥10%	≥25%	≥50%
Minimum Temperature Winter ²	62.45	72.55	70.72	61.59	65.19	60.57
Mean Spring PET (Mar-Jun) ²	11.28	6.53	1.45	3.46	3.94	4.08
Mean Annual Precipitation ²	6.22	NA	NA	NA	NA	NA
Mean Tree Cover ⁷	4.83	1.54	2.62	1.38	1.78	2.27
Percent Calcium Carbonate In Soil ⁵	4.32	0.67	0.56	0.23	0.28	0.47
Available Water Content (Mean Depth, cm) ⁵	4.28	2.9	2.89	6.33	9.71	8.01
Nitrogen Content ³	3.88	2.37	2.26	2.27	1.71	2.49
Continuous Heat-Load Index ⁶	2.72	1.72	2.08	3.02	2.2	1.25
Soil pH ³	2.3	0.91	0.91	1.9	1.08	0.98
Global Human Modification ⁴	2.25	1.8	2.3	1.39	1.28	2.3
Normalized Difference Moisture Index (NDMI) median ¹	1.91	1.62	0.99	2.34	2.96	2.43
Percent Clay ³	1.62	1.06	2.09	7.11	3.5	2.68
Depth To Restriction Layer (Mean) ⁵	1.06	3.65	3.35	3.44	3.45	3.33
Evapotranspiration (Jun-Aug) ²	1.06	1.73	2.48	2.03	1.22	2.77
Topographic Diversity ⁶	0.54	NA	NA	NA	NA	NA
Bare Ground Standard Deviation ⁷	0.5	0.73	0.89	0.93	1.27	4.13
Mean Diurnal Range ⁸	0.47	4.96	6.79	5.81	4.31	2.07
Distance to Water (coarse-scale) ¹¹	0.28	0.73	1.11	1.32	1.14	1.36
Multi-Scale Topographic Position Index ⁶	0.19	1.66	1.54	2.29	4.52	5.89
Available Water Content (Variance in Depth, cm) ⁵	0.14	NA	NA	NA	NA	NA
Mean Annual Flow ⁹	0.14	1.09	0.77	1.01	0.78	0.94
Burn Frequency ¹⁰	0.04	NA	NA	NA	NA	NA
Normalized Difference Moisture Index (NDMI) standard deviation ¹	0.004	1.01	1.2	1.3	1.36	1.5

Sources for predictor variables:

- ¹Kennedy, R.E., Yang, Z., Gorelick, N., Braaten, J., Cavalcante, L., Cohen, W.B., Healey, S. (2018). Implementation of the LandTrendr Algorithm on Google Earth Engine. *Remote Sensing*. 10, 691.
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- ²Abatzoglou J. T. “Development of gridded surface meteorological data for ecological applications and modelling “ *International Journal of Climatology*. (2011) doi: 10.1002/joc.3413.
- ³Nauman, T., Ramcharan, A., Brungard, C., Thompson, J., Wills, S., Waltman, S., & Hengl, T. (2017). *Soil Properties and Class 100m Grids United States* [Dataset]. PennState University Libraries. <https://doi.org/10.18113/S1KW2H>
- ⁴M. Kennedy, Christina; Oakleaf, James; M. Theobald, David; Baruch-Mordo, Sharon; Kiesecker, Joseph (2018): Global Human Modification. figshare. Dataset. <https://doi.org/10.6084/m9.figshare.7283087.v1>
- ⁵Chaney NW, Wood EF, McBratney AB, Hempel JW, Nauman TW, Brungard CW, Odgers NP. 2016. POLARIS: A 30-meter probabilistic soil series map of the contiguous United States. *Geoderma* 274: 54-67.
- ⁶Theobald, D. M., Harrison-Atlas, D., Monahan, W. B., & Albano, C. M. (2015). Ecologically-relevant maps of landforms and physiographic diversity for climate adaptation planning. *PLoS one*, 10(12), e0143619 <https://doi.org/10.1371/journal.pone.0143619>
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- ⁸ Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., Pasteris, P.P. “Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States”. *International Journal of Climatology*. (2008) 28, 2031–2064. <https://doi.org/10.1002/joc.1688>.

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⁹U.S. Environmental Protection Agency (USEPA) & U.S. Geological Survey (USGS). (2012). *National Hydrography Dataset Plus - NHDPlus - ScienceBase-Catalog* (2.1) [Dataset]. <https://www.sciencebase.gov/catalog/item/56c38ad8e4b0946c6520aa52>

¹⁰Eidenshink, J., B. Schwind, K. Brewer, Z. Zhu, B. Quayle, and S. Howard. (2007). A project for monitoring trends in burn severity. *Fire Ecology* 3(1): 3-21.

¹¹ESRI, National Atlas of the United States, & U.S. Geological Survey (USGS). (2010). *USA Water Bodies, Rivers & Streams* [Dataset]. <https://www.arcgis.com/home/item.html?id=0eb5f7b586ea4e08b5003b3554032453>; <https://www.arcgis.com/home/item.html?id=8206e517c2264bb39b4a0780462d5be1>

Table C5 Number of pixels of high suitability (>1.5 out of 2) for invasion shared between models.

Stiltgrass	Occurrence	≥10%	≥25%	≥50%
Presence	96149492			
≥10%	55821389	81875807		
≥25%	46022289	63905596	66076978	
≥50%	40931069	56262903	52029687	58297551
Sericea lespedeza	Occurrence	≥10%	≥25%	≥50%
Presence	127105094			
≥10%	68342115	81328138		
≥25%	67263965	68481360	103515724	
≥50%	48422816	45342510	57996022	64707160
Privet	Occurrence	≥10%	≥25%	≥50%
Presence	122247453			
≥10%	70606836	84567594		
≥25%	72927926	74654119	98707969	
≥50%	75594805	72074144	75306780	92819570

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