Plant Invasion in Forests Understories: A Native Community Perspective and Implications Ior Management

by

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Dedication

This dissertation is dedicated to all first-generation students who, against all the odds, have made this far.

And it also dedicated to my furry friends, Pantera and Whitie.

days in the forests of Michigan. SEAS and EEB PhD community, especially Jiayang Li and Divya Solomon– we made it to the finish line!!!

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Abstract

Forest ecosystems provide humans with a wide array of ecosystem services, e.g., water, clean air, extreme weather mitigation, flood and landslide prevention, products, and aesthetic, spiritual, and recreational values. Still, in the face of global change, these systems are at increasing risk of losing their functionality, with one major threat coming from the introduction of harmful invasive species. As a result, numerous resources, in research and management, have been allocated towards studying their ecology and promoting their control. These efforts, however, are rarely successful, and positive outcomes only last for a short period of time before the forest understories are invaded again. In an effort to address these shortcomings, my research deviates from the conventional perspective on management and research of biological invasions by switching the focus from the invader to the invaded community. By focusing on the invaded community, research can investigate means of ensuring this community resists and recovers from invasion instead of attempting to predict which species will be the next invader. I adopted a three-pronged approach to investigate the processes by which ecosystem functionality changes with invasion and to assess how management could enhance the native community's resistance to and recovery from invasion. First, I synthesized the existing knowledge on the mechanisms underlying shrub invasion in forest understories across the globe and their impacts on the native community by using a meta-analytical approach. Despite no differences in invasive species performance across mechanisms of invasion, the native community was significantly more impacted when the invasion was driven by low biotic resistance. Additionally, the results of this

chapter underscore the importance of a wide representation of resource-use strategies and competitive abilities among the native community to resist shrub invasion. Second, I carried out a four-year-long field experiment in southeast Michigan forest understories to investigate whether priority effects, i.e., the ability to arrive first, could be a successful mechanism of native community recovery in terms of coverage percentage after invasive species removal. I also assessed which characteristics of the native community led to faster native coverage recovery rates. Contrary to expectations, priority effects were not the primary mechanism driving community assembly post-invasive removal. However, rich native understory communities displaying higher values of acquisitive leaf traits related to rapid carbon processing strategies showed the fastest recovery rates. Third, I collected observational data on the plant community and composition of invaded forest understories at a local forest in Michigan. There, I compared the role of increasing levels of invasion, in relation to leaf trait distributions which I used a proxy to understand potential changes in ecosystem functions. The results revealed that invasion led to a significant increase in community-level leaf nitrogen. The native community leaf trait values, however, remained unchanged across the entire range of invasion levels. These findings have important management implications. Given the complementary effect of invasion rather than the displacement of trait values and functions, the removal of invasives will likely restore function to levels similar to pre-invasion conditions. My research takes a novel approach to the study of biological invasions by focusing on the native community rather than on the species invading, which provides further and unique insights into the field of invasion ecology. My research additionally addresses how we can use ecological principles to make native forests more resistant to invasive species.

Chapter 1 Introduction

Forests occupy approximately 3.9 billion hectares worldwide (Pan *et al.* 2011), providing humans with a wide array of essential ecosystem services, e.g., water, clean air, extreme weather mitigation, flood and landslide prevention, products, and aesthetic, spiritual and recreational values (Thompson *et al.* 2011; Decocq *et al.* 2016; Liang *et al.* 2016; Brockerhoff *et al.* 2017; Mori, Lertzman & Gustafsson 2017). Still, in the face of global change, i.e., climate change, land-use change, pollution, and species introductions, forest ecosystems face escalating risks to their functionality and biodiversity (Díaz *et al.* 2019). Invasive species, introduced species harmful to the native community, pose a significant threat to the long-term survival of temperate forests (Seebens *et al.* 2017; Link *et al.* 2018; Ward, Williams & Linske 2018). Therefore, it is imperative to develop ecological knowledge that advances our understanding of invasion in ways that can inform evidence-based management actions and enhance the success of restoration efforts in invaded forests.

The long-term persistence of forests relies on the maintenance of their structure, composition and diversity. Although most of the focus is on the canopy due to its role in carbon storage and acting as a carbon sink during growth (Pan *et al.* 2011; Castro *et al.* 2021), understories play a crucial role for tree recruitment and regeneration, as well as harboring most of the forest biodiversity (Landuyt *et al.* 2019; Spicer, Mellor & Carson 2020). However, introduced plants often dominate forest understories when they become invasive, leading to biodiversity loss, suppression of tree recruitment, and impacts on ecosystem functions and services (Mack *et al.* 2000; Simberloff *et al.* 2013; Link *et al.* 2018; Díaz *et al.* 2019). Current research approaches to biological invasion

typically focus on the traits of introduced species (van Kleunen, Dawson & Maurel 2015), the contexts in which they become invasive (Klironomos 2002), their interactions with native species in pair-wise comparisons (Golivets & Wallin 2018; Sheppard 2018), and/or the risk posed by specific invasive species (Chai *et al.* 2016). Despite these efforts, there remains considerable uncertainty in predicting which communities are most vulnerable to invasion. In response to this challenge, my work proposes a shift in research focus from invasive species to the affected community itself.

Management of invaded forests commonly involves controlling or eradicating an invasive plant species, the one with major impact (D'Antonio *et al.* 2017). Besides considering impact, the decision of which invasive species to remove is also based on costs and labor efforts (Simmons *et al.* 2007; Wilson *et al.* 2011). However, the suppression of targeted invasive plant species without further restoration actions may not lead to the system's recovery (Thomson 2005; Pearson *et al.* 2016). This is because management practices that reduce plant density and increasing resource availability can make the system vulnerable to secondary invasion, particularly by non-targeted alien species (Thomson 2005; Pearson *et al.* 2016). Combined with infrequent long-term monitoring of the native community reestablishment success, these negative unintended effects of controlling invasives (Myers *et al.* 2000; Rinella *et al.* 2009; Kettenring & Adams 2011) reinforce the need to switch focus from the invader, species-specific, to the native community (Ibáñez *et al.* 2021). In my work I aimed at gaining a better understanding of the native community response to invasion. For this I used a three-pronged approach, i.e., a quantitative systematic review, a field experiment and an observational data collection. My goals were to investigate the processes by which ecosystem functionality changes with invasion and assess how management could

enhance the native community's resistance to and recovery from invasion. By advancing

ecological knowledge in ecosystem resistance to such an impactful stressor as invasive

plants, I hope to contribute to moving biological invasions from a descriptive science to

a more predictive one.

Mechanisms and impacts of shrub invasion in forests

Forests face multiple anthropogenic stressors, with plant invasions being

particularly important due to the continuous movement of plants across the globe (Jauni,

Gripenberg & Ramula 2015; Seebens *et al.* 2017). In forest understories, plant invasions

hinder the recruitment of native species affecting forest structure and function (e.g.,

Pysek *et al.* 2012; Link *et al.* 2018; O'Loughlin *et al.* 2019). These impacts of plant

invasion on native communities are guided by analogous mechanisms to those observed

during classical community assembly principles (HilleRisLambers *et al.* 2012). By

integrating the mechanisms of community assembly in the context of plant invasion

(Pearson *et al.* 2018), we can gain a better understanding of whether invasive shrub

performance and invasion impact on the native community of forest understories varies

across mechanisms of invasion, i.e., high propagule pressure, low biotic resistance, or

use of empty niches. To the best of my knowledge, this is the first attempt to synthesize

knowledge on shrub invasion in forested ecosystems and to link native community

performance to mechanisms of invasion.

High propagule pressure of invasive seeds enables successful population

establishment via founder effects (Bradley *et al.* 2019). In other cases, introduced

species can become highly abundant by exploring underutilized resources in the native

community particularly after disturbances, which is often described as exploring empty

niches (Davis, Grime & Thompson 2000; Chase & Leibold 2003; Hierro, Maron &

Callaway 2005). Another mechanism of invasion occurs when native communities lack competitive abilities, resulting in a lack of biotic resistance (Shea & Chesson 2002). This becomes particularly prominent when the native community lacks specific traits that would allow for a rapid response to environmental changes (Catford, Jansson & Nilsson 2009). Understanding these invasion mechanisms is crucial for assessing the potential impacts on the native community and guiding effective management strategies.

In **Chapter 2**, I conducted a meta-analytical study to quantitatively synthesize the existing knowledge on the mechanisms underlying shrub invasion in forest understories and their impacts on the native community. After screening 3,389 publications, I selected 124 studies that yielded a total of 377 observations. I extracted data on both native community and invasive species performance under high and low levels of invasion. I then calculated effect sizes and analyzed them as a function of mechanisms of invasion and abiotic features of the resident community, while also including study random effects. I also explored model residuals in relation to several climatic variables, and covariates (i.e., study type, global ecoregion, forest community, forest type, occurrence of disturbance and type), to try to better understand and explain the residual variability from the analysis of the effect sizes.

The role of priority effects and native community responses after invasive plant removal

Once invaded, forests are managed via the removal of the impactful agent, which leaves behind unused resources, such as light, soil water, and nutrients, previously exploited by the removed plants (Thomson 2005; Pearson *et al.* 2016). The composition and structure of the subsequent community likely take place via priority effects, a mechanism of community assembly in which community composition is

determined by the order of species arrival (Fukami 2015; Fukami, Mordecai & Ostling 2016; Hess, Mesleard & Buisson 2019). However, in disturbed landscapes, particularly invaded forest understories post-management actions, native seed pools may be depleted, while invasive seeds are frequently abundant (Vilà & Ibáñez 2011; Pearson *et al.* 2016; Schuster, Wragg & Reich 2018). If priority effects are driving plant recovery after vegetation removal, promoting early arrival of natives could curtail the risk of re-invasion. Being able to identify under which conditions priority effects promote native recovery will allow better protection and restoration of natural areas. Studies testing the timing of arrival as a potential management tool have focused almost entirely on grassland (e.g., Dickson, Hopwood & Wilsey 2012; Uricchio *et al.* 2019) and old-field communities (e.g., Stuble & Souza 2016), but rarely on forests (Sarneel, Kardol & Nilsson 2016) or in the context of invasion (Weidlich *et al.* 2021).

In **Chapter 3**, I conducted a four-year-long field experiment to test whether priority effects could be a successful mechanism of forest recovery and investigated the features of the native community that led to faster recovery. The experiment consisted of 36 plots, each divided into six 1 m^2 subplots, where I applied several treatments in a full factorial design consisting of adding seed mixes and different invasive removal frequencies. Before implementing the treatments, I removed invasive species by clipping stems at the soil level avoiding extra soil disturbance. To investigate if priority effects drove community assembly after invasive removal, I added two seed mixes (forbs only or forbs and grasses) to a third of the subplots. This ensured that native seeds would arrive first, representing priority effects, after the removal of invasives. Another third of the subplots was left untreated as a control. Additionally, I continued to remove invasive species in half of each plot three times annually to examine whether priority effects interacted with prolonged release in competition with reinvaders. I

analyzed the native community recovery rates each year, taking into account year-to-year variability and autoregressive dependency.

Complementarity vs. displacement of ecosystem functionality via alterations in leaf trait distributions impacted by plant invasions

Plant invasion can have significant effects on the functioning of forested ecosystems via alterations in community-level trait distributions (e.g., Livingstone, Isaac & Cadotte 2020; Fernandez *et al.* 2021). Invasion can impact the trait distribution of co-occurring native species by *displacing* native community trait values or by *complementing*, adding to the existing community. If invasive species displace native community trait values, the removal of invasive species may not result in a complete functional recovery given the loss of function during the invasion process. In contrast, if invasive species complement native community trait values, their removal has the potential to restore functionality to its original level. To discern between these two processes, analytical approaches should involve separate analyses based on total community trait values to diagnose change and based solely on native community trait values to diagnose impact (Thomsen *et al.* 2016), while also considering trait correlations (Poggiato *et al.* 2023). Despite its relevance for assessing impact, there is little work done to discern overall change versus impact of plant invasion on community traits, and therefore, ecosystem functionality, while simultaneously accounting for trait correlations in a joint modeling fashion by using a multinormal distribution. This modeling approach has been widely used to model species distributions since its proposal (Clark *et al.* 2014; Pollock *et al.* 2014), but only very recently introduced as a way to account for community-level covariation of traits (Poggiato *et al.* 2023).

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In **Chapter 4**, I collected observational data to examine changes on community-level trait distributions driven by plant invasion and to determine whether invasion impacted native trait distributions via complementarity or displacement. I collected data on composition and abundance of understory plant communities in 150 plots within the Edwin S. George Reserve. I then linked community composition to trait data from the TRY database (Kattge, Díaz & Lavorel 2011) on leaf nitrogen content, specific leaf area and leaf dry matter content, representing resource use strategies on both ends of the leaf economic spectrum (Wright *et al.* 2004). I adopted a joint modeling approach to address simultaneously trait correlations and the potential effects of biotic factors and environmental factors. By calculating community-weighted means of these traits with and without including invasive species, I was able to differentiate impact in ecosystem functionality occurring as a result of displacement or complementarity.

In **Chapter 5,** I provide a summary of the main results and key take home messages from the research conducted in **Chapters 2 to 4**. Additionally, I acknowledge limitations I encountered during the study and discuss their potential implications. Through this this three-pronged approach, i.e., quantitative systematic review, field-experiment and observational data collection, I was able to develop evidence-based recommendations for the management of plant invasion in forest understories, with an emphasis on temperate forests. Future forests depend on effective restoration practices to maintain their functionality and native plant recruitment. My work represents a step forward in this endeavor, aiming to ensure the functionality and sustainability of forests for generations to come.

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Chapter 2 Assessing the Mechanisms and Impacts of Shrub Invasion in Forests: A Meta-analysis

2.1 Abstract

1. The encroachment of invasive shrubs in forest understories can have detrimental effects on native plant recruitment. As a result, removal of invasive species is a common practice although long-lasting success is rare. In order to effectively conserve and manage invaded forests, it is crucial to understand the mechanisms that drive shrub invasion, i.e., high propagule pressure, low native resistance, and exploitation of empty niches.

2. To gain a deeper understanding of the invasion process in forest ecosystems we conducted a meta-analysis of the work done in this topic. We collected data on invasive species and native community performance, and on the abiotic conditions of forest understories under low and high levels of shrub invasion. We analyzed data from 124 articles that yielded 377 unique observations.

3. Our results revealed that while invader performance did not vary by the mechanism of invasion, the impact on the native community was significantly detrimental when invasion occurred via low biotic resistance, and only marginally significant via propagule pressure. Invasive species performance was associated with increases in light availability, but not with other resources (soil water, or nutrients). When assessing impact on native performance as a function of invasive performance, results were again only significant under the low biotic resistance mechanism. Lastly, impacts were stronger when invasion took place by a single invader.

4. *Synthesis and applications:* Taken together, these results suggest that restoration efforts should focus on (i) increasing the presence of strong native competitors or functionally diverse native communities, (ii) decreasing sources of invasive shrub propagules while keeping the canopies closed when invasion occurs via high propagule pressure, (iii) avoiding management techniques that degrade or diminish canopy cover, and (iv) prioritizing management of forest understories dominated by particularly impactful invasive shrubs.

2.2 Introduction

Forests provide a diversity of ecosystem services critical to humans and play a major role in nature-based solutions to global warming (Führer 2000; Peltzer *et al.* 2010; FAO 2020). However, these services may be jeopardized due to an increased risk of diminished forest functioning caused by invasive plant species (Liao *et al.* 2008; Peltzer *et al.* 2010). In particular, invasive shrubs are encroaching on forest understories suppressing native plants' recruitment (Clark *et al.* 1999; Pyšek *et al.* 2012; Link et al. 2018; Ward, Williams & Linske 2018; Dharmadi, Elliott & Miniat 2019), affecting carbon and nitrogen cycling (Liao *et al.* 2008; Peltzer *et al.* 2010; Martin, Newton & Bullock 2017), and negatively impacting biodiversity (O'Loughlin *et al.* 2019). Understanding the mechanisms by which shrub invasions in forest understories occur, and what their impacts on the native community are, is thus fundamental for providing evidence-based recommendations to prevent, or successfully control, plant invasions (Byun, de Blois & Brisson 2018; Prior *et al.* 2018).

The invasion process is by nature a community assembly process (Shea & Chesson 2002; Catford, Jansson & Nilsson 2009; Pearson et al. 2018), which is characterized by three main components: (i) arrival of propagules, (ii) availability of resources for establishment and population growth, and (iii) high enough performance

to outcompete existing vegetation (HilleRisLambers *et al.* 2012). The impacts of plant invasion on native communities are governed by similar mechanisms to those found in community assembly of native communities. Large availability of invasive propagules would ensure population establishment of the invasive, i.e., overcoming founder effects (Bradley *et al.* 2019). The performance of invasive species can be strongly influenced by their ability to exploit available resources unused by the resident community. Unused resources might be a result of directional selection that may preclude communities from fully utilizing all resources available (Fussmann, Loreau & Abrams 2007) or of unprecedented disturbance events (e.g., Fowler *et al.* 2013). These circumstances are commonly associated with exploitation of unused resources by invasive species, i.e., the availability of empty niches (Davis, Grime & Thompson 2000; Chase & Leibold 2003, Hierro, Maron & Callaway 2005). How much invasive performance is associated with an impact on forest understory plants, would then depend on the native plant community's competitive ability to resist or not invader species, i.e., biotic resistance (Shea & Chesson 2002), particularly when the native community might lack a suite of traits that allows rapid response to environmental changes (Catford, Jansson & Nilsson 2009).

A common mechanism of invasion success is the arrival of sufficient propagules to ensure population establishment and growth – propagule pressure (Figure 2.1) (Richardson *et al.* 2000; Lockwood, Cassey & Blackburn 2005). Human-dominated landscapes are a source of invasive propagules via ornamental gardens, agriculture, and accidental introductions (Vilà & Ibáñez 2011; Cadotte *et al.* 2017). Anthropogenic landscapes also contribute to invasive propagule availability by providing dispersal corridors and vectors (Ibáñez *et al.* 2009; Vilà & Ibáñez 2011; Ibáñez *et al.* 2014a). For example, introduced species in parks and gardens act as a constant source of propagules

into nearby forest remnants, with an increased likelihood of invasion when initial planting effort is high (Dawson et al. 2008; Petri, Aragaki & Gomes 2018). High propagule pressure is therefore identified as one of the main mechanisms of invasion since it leads to increases in invasive abundance over time (Catford *et al.* 2011; Stuble & Souza 2016; Ibáñez *et al.* 2021).

Another mechanism by which invasive plant species can establish in new ecosystems is by utilizing resources that are not being fully utilized by native plant species – empty niches (Figure 2.1) (Elton 1958; Hierro, Maron & Callaway 2005). In forest ecosystems, the understory is considered a highly competitive environment, where most of the light, soil nutrients, and soil water are taken up by large trees (Dawson, Burslem & Hulme 2015). This has resulted in relatively low levels of invasion in comparison to other vegetation types (Dawson, Burslem & Hulme 2015). However, human activities, such as disturbance and global climatic changes, can alter the availability of resources, creating opportunities for introduced species to exploit them. For example, disturbance can lead to increased light via removal of or changes in canopy cover (van Lierop *et al.* 2015), climate change can alter water availability regimes (Bradley *et al.* 2010), and the excessive use of fertilizers can elevate soil nutrient levels (Sala *et al.* 2000). Given evolutionary constraints of the native community, e.g., low growth rates (Fussmann, Loreau & Abrams 2007; Fridley *et al.* 2022), these novel changes in resources may lead to unused resources, creating empty niches (Davis, Grime & Thompson 2000; Hierro, Maron & Callaway 2005). Under these conditions, introduced species, especially those having high growth rates and selected to tolerate harsh environmental conditions (Van Kleunen, Weber & Fischer 2010; van Kleunen, Dawson & Maurel 2015), could exploit such unused resources more efficiently (Davis, Grime & Thompson 2000; Hierro, Maron & Callaway 2005).

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The third mechanism of invasion within the community assembly framework is associated with low competitive ability by the native community – low biotic resistance (Figure 2.1) (Shea & Chesson 2002; Nunez-Mir *et al.* 2017; Byun, de Blois & Brisson 2018). The native community's ability to collectively outcompete invaders by limiting their establishment (biotic resistance, Catford, Jansson & Nilsson 2009) or by preventing their populations' growth (biotic containment, Levine, Adler & Yelenik 2004) can result from native species' identity, richness, associated traits, niche requirements, and/or performance (Catford, Jansson & Nilsson 2009). Diverse native communities tend to utilize available resources more thoroughly– a phenomenon known as the diversity effect (Levine & D'Antonio 1999). Additionally, native communities that have a more diverse representation of traits and niche requirements also have higher resistance to introduced species, since they are probably occupy available niches that invasive species might explore (niche similarity, MacArthur & Levins 1967). In other instances, high native competitive ability within a specific environment, such as high shade tolerance (Vojik & Boublik 2018; Gómez *et al.* 2019), or rapid response to disturbance (Moles *et al.* 2012; Driscoll 2017), can prevent the establishment and population growth of invasive plants via interspecific competition (Shea & Chesson 2002). When these different strategies are lacking or did not evolve in the native community, low biotic resistance may be the mechanism driving invasion (Shea & Chesson 2002; Nunez-Mir *et al.* 2017).

The impact of plant invasion on native vegetation is commonly associated with high abundance of invasive species (Bradley *et al.* 2019). However, there has been little research assessing if similar levels of species abundance have similar impacts across invasive events. Both the mechanism driving invasion, and the features of the native community likely affect invader impact (Byun, de Blois & Brisson 2018; Ibáñez *et al.*

2021). In some instances, the invader impact might be the result of higher abundance of invasive propagules or more suitable growing conditions for invasives than for native species; but it may also be due to low biotic resistance or containment, features of the native community. Thus, understanding what drives both invasion and impact becomes essential for developing effective conservation and management practices.

Despite its relevance in forest functioning, to date, it is unclear how prevalent each of these invasion mechanisms (i.e., high propagule pressure, empty niches, low biotic resistance) is in forest understories, or how impact varies across them. To improve our understanding of shrub invasions with respect to the mechanisms of invasion and the impacts on plant communities in forest ecosystems, we conducted a meta-analysis of articles (i.e., publications published in peer-reviewed scientific journals) published on this topic. We selected articles that quantified invasive and native community performance and abiotic conditions in the same forest understory community under low and high levels of shrub invasion. We aimed at answering: (Q1) is invasive success associated with the mechanism of invasion (Figure 2.1)? (Q2) Given forests generally low invasibility status (Chytrý *et al.* 2009; Martin, Canham & Marks 2009) and the unprecedented fluctuations of resources in human-dominated landscapes (Haddad *et al.* 2015), what are the abiotic conditions most suitable for invasion success? And, (Q3) does invasive impact on the native community in forest understories vary across mechanisms of invasion? By understanding the invasion mechanisms underlying invasive success and impact on forest ecosystems, we can provide critical information to improve management practices and conservation of these ecosystems (Byun, de Blois & Brisson 2018; Ibáñez *et al.* 2021).

2.3 Methods

2.3.1 Systematic search and data extraction

We performed a comprehensive literature search in Web of Science Core Collection in February 2019, with years considered from 1900 to 2018. We used the following keywords: (invasi* OR invade* OR alien OR exotic OR ruderal OR weed OR non-native OR nonnative OR introduced OR naturaliz* OR nonindigenous OR non-indigenous) AND (shrub OR scrub OR bush OR brush OR "woody plant*") AND (forest OR forests). We carried out a second complementary search, using the same keywords, in April 2020 to expand the end year of considered articles up to 2019. We then excluded all books, book sections, and conference abstracts. We included only articles written in English, Portuguese, or Spanish.

The selection criteria we used were: 1) articles had to study shrub (or subshrub) invasions within forest communities; 2) articles had to report invasive species performance and native community performance and/or abiotic resources under two levels of invasion (i.e., low and high shrub invasion) in the same forest. We excluded articles that only reported presence or absence of invasive species when comparing two forested areas to avoid absences due to lack of dispersal into the area. We also excluded articles that had actively removed invasive species as their performance at low levels of invasion were artificially obtained by these management actions hampering comparable parallels across articles. Based on the information presented in each article, each study (i.e., observations within each included article) was assigned to one of three main mechanisms of invasion: (i) propagule pressure (i.e., invasion was driven by invasive species propagules being present and abundant); (ii) empty niches (i.e., invasion took place because invasive species tapped into unused abiotic resources by the native plant community); and (iii) low biotic resistance (i.e., native community was not competitive enough to resist invasion; Figure 2.1) (for more detail on classification criteria see Text S 2.1 in the Supporting Information).

For each study, we extracted data on the following response variables: performance of both invasive species and native community (e.g., abundance, growth, fecundity), and, when reported, resource availability (light, water, or/and nutrients). We also collected associated data on geographic and climatic information, characteristics of the forest community, invasive species identity, study type, occurrence, and type of disturbance, among other variables (see the complete list in List S2.1 and additional details in Text S 2.1). Data entries were further classified as invaded by one or by multiple invasive shrub species to assess if impact is mostly driven by invasive abundance or by the presence of particular invasive species, e.g., higher chances of having a more competitive invader when multiple invaders are present (Kuebbing, Nunez & Simberloff 2013). Some articles have multiple data entries, i.e., different metrics of plant performance or different abiotic factors were measured. We extracted data on sample size, mean value, and, when reported, associated variance metric (SD, SE, or upper maximum value) of both invasive (see the complete list in List S2.2) and native performance (List S2.3). Data were extracted from text, tables, or graphs. In graphs, we used the Web Plot Digitizer online application (Rohatgi 2020) to retrieve mean and associated variance values. Additional information on how data was extracted can be found in Text S 2.1. A schematic view of the study's selection process can be found in Figure S 2.1 as a PRISMA flow chart (Page *et al.* 2021) and detailed criteria following PRISMA Eco-Evo v1.0 (O'Dea *et al.* 2021) can be found in Table S 2.2. The full dataset and derived files can be found in Dryad https://doi.org/10.5061/dryad.msbcc2g33 (Petri & Ibáñez, 2023).

2.3.2 Effect size calculations

We calculated effect size (ES) as the differences in invasive species (*inv*) and native community (*nat*) performance (*P*) under high and low levels of invasion as (Eq. 1):

$$invES \; or \; natES = \frac{P_{high \, inv} - P_{low \, inv}}{|P_{average}|} \qquad (1)$$

We used this calculation of ES to avoid issues with zero and negative values (Sorte *et al.* 2013), and it highly correlates with other standards ES calculation, e.g., natural log of the ratio (Persons $r > 0.95$). As a result, this calculation for ES invasive species is only positive while native community ES values range from negative to positive. We also estimated an ES (*resES*) for the differences in resources (*R*) at high and low invasion levels as:

$$resES = \frac{R_{high \, inv} - R_{low \, inv}}{|R_{average}|} \qquad (2)$$

In this case, negative ES means resources are lower under high invasion, while a positive ES indicates resources are higher in forests with high level of invasion. We ran simulations to estimate ES means (**ESm*) and variances (**ESvar*), where sample sizes were accounted for. For more detail see Text S 2.1 in the Supporting Information.

2.3.3 Data analysis

To assess if invasion performance varied as a function of mechanism of invasion (Q1), we analyzed our estimates of ES, mean (*invESm*), and precision (1/*invESvar*) (Eq. 3), as a function of the mechanisms of invasion (i.e., low biotic resistance, high propagule pressure, and empty niches) (Eq. 4). We also included study random effects (SRE). For each observation *i*:

$$invESm_i \sim Normal \ (E_i, \tau_{mechanism(i)} + 1/invESvar_i) \qquad (3)$$

$$E_i = \alpha_{mechanism(i)} + SRE_{study(i)} \qquad (4)$$

Parameters α_* reflect overall invasive performance under each mechanism, while parameter τ_* are the precisions (1/variance) associated with each mechanism. We also analyzed differences in invasive species performance as a function of other variables, such as type of experiment, ecoregion, forest type, forest community, disturbance, and type of disturbance. We carried out a similar analysis on native community ES estimates (*natESm* and *natESvar*).

To investigate which abiotic conditions invasive shrubs are taking advantage of in forests understories (Q2), we analyzed invasive ES (*invESm*) (Eq. 5) as a function of resource availability (*resES*), for light, water, and nutrients (Eq. 6). For observation *i*:

$$invESm_i \sim Normal \ (E_i, \tau_{resource(i)} + 1/invESvar_i) \qquad (5)$$

$$E_i = \mu1_{resource(i)} + \mu2_{resource(i)} \cdot resES_i + SRE_i \qquad (6)$$

In this case, parameters $\mu1_*$ reflect a different intercept per resource type, parameters $\mu2_*$ represent the slope of the relationship between invader performance and the availability of each resource type, and parameters τ_* are the precisions (1/variance) estimated for each resource type. Here again we added study random effects (SRE) to the model.

Next, to assess if impact of invasion on the native community is associated with invasive performance and dependent on the invasion mechanism (Q3) (Eq. 7), we analyzed native ES (*natESm*) as a function of invasive ES (*invESm*) under each mechanism (Eq. 8). For observation *i*:

$$natESm_i \sim Normal\ (E_i, \tau_{mechanism(i)} + 1/natESvar_i) \tag{7}$$

$$E_i = \lambda_{mechanism(i)} \cdot invESm_i + SRE_i \tag{8}$$

We did not include an intercept as native ES should be zero at zero invasive performance. Parameters λ_*, the slope of the relationship between native community performance and invasive species performance, and τ_*, the precisions (1/variance), were estimated for each mechanism. We also included study as random effects (SRE). We implemented a similar model structure and analysis to identify whether impact of invasion is associated with invasive performance and dependent on single or multiple invading species.

To accommodate missing variances and still use those observations (26%; Ibáñez *et al.* 2021) we used a Bayesian approach in the estimation of parameters. We estimated parameters α, μ, and λ from non-informative prior distributions, $\alpha^*, \mu^*, \lambda^* \sim$ Normal (0, 0.0001). Random effects were estimated as $SRE_i \sim$ Normal (0, τ_*), and variances (σ:$1/\tau$) as $\sigma^* \sim$ Uniform (0, 10). Missing invasive and native ES variances were estimated as latent variables from distributions with mean equal to the largest ES variance estimated among observations that reported response variability, $ESvar \sim Normal(MaxVar, 1)$ limited to be ≥ 0 (Ibáñez *et al.* 2014b; Ibáñez *et al.* 2021). Lastly, we investigated publication bias by visually checking funnel plots, plotting the precision (i.e., 1/variance) as a function of estimated effect sizes of the response variables (Figure S 2.2) and by performing the Egger's regression test (Table S 2.3).

To investigate whether covariates could be added to the models to help explain unaccounted variability in effect sizes, we explored the correlations of each ES (i.e., invES, natES, and resES) with metrics used to calculate effect sizes (Figure S 2.6-S

2.8). We also explored all three ES with climatic variables, i.e., elevation, annual precipitation, average January, July, and annual temperatures and year of data collection (Figure S 2.9-S 2.11). Given the low correlation values, the highest being 0.18, we decided to not include climatic variables in the models. In addition to investigating climatic variables, we explored the residuals of all five models (Equations 3-8, the equivalent of Equation 3 for natESm, and the equivalent of Equation 7 per number of invaders) against multiple covariates (Figures S 2.12-S 2.16), i.e., study type, global ecoregion, forest community, forest type, occurrence of disturbance and type. We found weak associations across all analyzed covariates, and opted for the simplest version of each model. Across all analyses, we considered statistically significant effect sizes or slopes if credible intervals (CI) did not overlap zero, and significant differences between effect sizes when their CIs did not overlap. We performed all data wrangling and plotting in R (R Core Team 2022), using the 'tidyverse' family of packages (Wickham *et al.* 2019). We estimated ES via simulation directly in OpenBUGS (Thomas *et al.* 2006). For the simulation code, see Code S1 in the Supporting Information. We ran the mixed-effects models in OpenBUGS through R by using the 'R2OpenBUGS' (Sturtz, Ligges & Gelman 2019) and 'mcmcplots' (Curtis 2018) packages. The full reproducible modeling code can be found on https://github.com/laispetri/ShrubInvasionInForests_Meta-analysis, which also includes the full list of packages used.

2.4 Results

Overview – We obtained a total of 3,389 publications, and from those, after applying the selection criteria 124 articles were selected for data extraction (see List S2.4 in the Supporting Information) (see Figure S 2.1 for PRISMA flow chart). Articles included in this meta-analysis were published between 1988 and 2019, with the 50th

percentile after 2010. On-the-ground data collection was performed between 1973 and 2019, with observations above the 50th percentile occurring after 2004. Data extraction yielded a total of 377 observations and 56.5 % of the articles generated more than one observation. In total, 58 invasive shrubs were represented across articles, with the three most frequent species being: *Lonicera maackii* (Rupr.) Maxim., *Lantana camara* L., and *Elaeagnus umbellata* Thunb. (Table S 2.1 has a complete list of invasive shrubs). Most of the articles only reported one invader (67.5 % of the observations). All parameter values from the analyses are reported in Text S 2.2. Visual inspection of funnel plots (Figure S 2.2) indicated that *invES* had publication bias while *natES* and *resES*, did not. These results were corroborated by Egger's regression test (Table S 2.3) which indicated asymmetry in the *invES* funnel plots, and symmetry for the others.

The sample sizes between invasive species and native community performance differed, being respectively, 265 and 103. Invasive species and native community performance were similar across study types (all credible intervals overlap Figure S 2.3a), indicating that performance (e.g., abundance) was not influenced by a particular manner of investigating the invaded system (i.e., field experiment, observational study, or greenhouse experiment). Although 6 continents were represented in the data, 65.3 % of the observations originate from studies performed in North America, followed by Oceania with 14.1 % and Africa with 7.96 % (see Figure S 2.4 for a spatial representation of the articles). Studies were distributed across 11 different global ecoregions (Figure S 2.3b), 14 forest communities (Figure S 2.3c), and seven forest types (Figure S 2.3d). No ecoregion, forest community, or type yielded significantly different invasive species or native community performance. Disturbance and disturbance type did not differentially impact invasive species' performance, but significantly and negatively affected native community performance, specifically when

caused by human activities (Figure S 2.3e and Figure S 2.3f). Still, there was no

particularly different disturbance effect across mechanisms of invasion (Figure S 2.5).

Invasive shrub success and mechanisms of invasion (Q1) – Neither invasive

species nor native community performance significantly varied across mechanisms of

invasion (Figure 2.2). However, native ESs were always significantly lower than

invasive ES (Figure 2.2a, 95% predicted intervals [PI] do not overlap), but native ES

was only statistically significantly different from zero under low biotic resistance

(Figure 2.2a, 95% PI do not overlap the zero line).

Effects of limiting resources on invasion success (Q2) – Next, we investigated

under which level of resources invasive shrub performance was higher in forest

understories. Invasive effect sizes increased, marginally statistically significant (alpha =

0.05), with increasing levels of light (Figure 2.3a), while there was no association with

varying levels of nutrients (Figure 2.3b) or water (Figure 2.3c). All slopes were not

statistically significant (Figure 2.3d).

Invasive shrub impact on the native community (Q3) – Finally, we assessed how

impacts of invasive species on native community performance varied across

mechanisms of invasion or number of invasive shrub species. Only under low biotic

resistance, did the native performance significantly decrease with increasing invasive

performance (Figure 2.4a). Unlike our expectations, performance of single invaders was

significantly associated, negatively, with native community performance while the

effect of multiple invaders was non-significant (Figure 2.4b).

2.5 Discussion

Invasive shrubs can strongly impact forest understories by reducing native plant

recruitment and by changing forest structure and functioning (Führer 2000; Peltzer *et al.*

2010; FAO 2020). As a result, removal and control of invasive shrubs is a common

practice, although in most cases success is generally low, i.e., the removed species, or other invaders, recolonize the treated area (Kettenring & Adams 2011). A better understanding of the mechanisms of shrub invasion and their impact on the native community could provide information relevant to improving these practices. In this meta-analysis, where we assessed the effectiveness and impact of the main mechanisms of invasion, we found that invasive performance did not vary by mechanism of invasion. However, we showed that impacts of shrub invaders were more detrimental in native communities experiencing invasion via low biotic resistance. As expected, invasion impact increased with invasive performance, but only significantly when lack of biotic resistance was identified as the invasion mechanism. From the three most limiting resources in forests understories, invasive shrub performance was only positively associated with higher light resources, with no clear association with soil water or nutrients. Lastly, we showed that invasive shrub impact on the native community was stronger under single species invasion. These results demonstrate the complexity of the invasion process while providing relevant information to management and conservation of forest ecosystems.

2.5.1 Invasive shrub success and mechanisms of invasion (Q1)

The mechanisms underlying the establishment of invasive plants can be classified as being part of three main processes: propagule pressure, use of empty niches, and low biotic resistance of the native community, an extension of the classic assembly principles in natural communities (Shea & Chesson 2002; Catford, Jansson & Nilsson 2009; Pearson *et al.* 2018). In our meta-analysis, invasive shrubs performance did not vary across these mechanisms (Figure 2.2). Our results suggest that invasion success is more likely associated with the wide array of traits invasive plants possess rather than the process that facilitated the invasion. In the biological invasions literature,

invasive plants are generally characterized by having acquisitive traits (e.g., high germination and growth rates, high photosynthetic rates) (Bazzaz 1979; Martin, Canham & Marks 2009; van Kleunen, Dawson & Maurel 2015) that give them advantage in disturbed and high resource sites (70 % of our observations took place in disturbed ecosystems) (Funk 2013; Jauni, Gripenberg & Ramula 2015). Still, this literature has also documented the ability of invasive shrubs and trees to take over low-resource environments, such as forest understories (Martin, Canham & Marks 2009). These shade-tolerant invasive shrubs (39% of the species in our data; Table S 2.1) usually rely on leaf trait plasticity (Heberling & Fridley 2013; Martinez & Fridley 2018), explore available resources more efficiently (Funk & Vitousek 2007; Heberling & Fridley 2013), or possess a combination of fast growth and long leaf duration (Fridley *et al.* 2022). These are all strategies that allow them to have a longer growing season, which likely benefits their populations' growth. For example, in North American temperate forests (65.3% of our observations), invasive shrubs and tree saplings leaf out earlier and postpone their leaf senesce when compared to other native plants in the understory (Miller *et al.* 2022). Invasive species do not only have longer growing season, but also take advantage of a longer period of time under higher light levels, before canopy leafs out and after canopy senesces. For native species, leafing out later has evolved as a strategy to avoid damage from late frost events (Inouye 2000). However, with the frequency and severity of extreme cold events predicted to decrease due to global warming, this strategy may no longer be advantageous (Ma *et al.* 2019). Invasive species however, might be already adapted to take advantage of the extended growing season (Fridley 2012; Martinez & Fridley 2018; Schuster, Wragg & Reich 2018). In summary, the ongoing introductions of invasive plants in forest ecosystems represented in our data constitute a species pool with a wide array of resource

acquisition strategies. Therefore, to increase management success, invasive control practices should consider promoting a functionally diverse native species pool with a wide array of resource use strategies and competitive abilities.

2.5.2 Effects of limiting resources on invasion success (Q2)

Forest understories are extremely competitive with respect to essential resources for plant establishment and growth, such as light, soil water, and soil nutrients (Dawson, Burslem & Hulme 2015). Healthy understory native plant communities are, however, adapted to low light environments and to taking advantage of sunflecks and canopy gaps (Chazdon & Pearcy 1991; Sax & Brown 2000; Way & Pearcy 2012). Our results showed an increase in performance of invasive species under high light availability in forests understories (Figure 2.3). This result agrees with the general recognition that invasive plants usually perform better under high-resource environments as they tend to be selected based on early successional and acquisitive traits (Martin, Canham & Marks 2009; Funk 2013). We were unable to investigate similar relationships between resource levels and the native community performance due to limited sample size of observations.

The high light levels found in our dataset are likely associated with disturbance events (70% of our observations were disturbed at least once; from those 52.5 % were anthropogenic-induced), which frequently increase light levels inside forests. Natural disturbances such as windthrow, insect outbreaks, and natural tree mortality decrease plant biomass and temporarily increase canopy opening (Turner 1989). Environmental heterogeneity promoted by natural disturbances, in time and space, promotes variability in resources that native communities evolved to respond to (Davis, Grime & Thompson 2000; Hierro, Maron & Callaway 2005). However, anthropogenic disturbances such as human land use has reduced native herbaceous (Flinn & Vellend 2005) and shrub

(Martin, Canham & Marks 2009) diversity (Gilbert & Lechowicz 2005) of forest understories, while invasive propagules are plentiful and readily available in such landscapes (Vilà & Ibáñez 2011; Brym, Allen & Ibáñez 2014; Jauni, Gripenberg & Ramula 2015). Given the short evolutionary history in which native communities experience these novel disturbances, they probably had insufficient time to reassemble and adapt to these novel conditions (Shea & Chesson 2002). Under these conditions, invasive species tend to be particularly stronger competitors (Jauni, Gripenberg & Ramula 2015; Ibáñez *et al.* 2021). Our results are consistent with this pattern, disturbance was negatively associated with native plants performance, specifically when caused by human activities, while the association was positive for invasive species (Figure S 2.3e and Figure S 2.3f). This suggests that the management of forests invaded by shrubs should focus on reducing the incidence of anthropogenic disturbance while promoting shaded conditions.

We suggest two main explanations for the non-significant effects of soil water and nutrients on invasive shrub performance. First, different limiting resources might play an essential role in distinct life stages of an invasive species. Given that we compared the same forest under low and high levels of invasion, most of the observations likely measured populations of adult shrub individuals representing only part of the environmental challenges these individuals face through their life spans. For example, the invasive shrub, *Elaeagnus umbellata*, is limited by soil moisture in the seedling stage while growth is limited by the availability of light and space in a temperate forest (Brym, Allen & Ibáñez 2014). Second, a combination of small sample size and large variation of invasive species performance associated with changes in soil water and nutrients decreased our ability to infer the effects of these limiting resources on invasive species performance.

2.5.3 Invasive shrub impact on the native community (Q3)

There is plenty of evidence demonstrating the negative impacts of invasive plants on native communities, e.g., Vilà *et al.* 2011; Corbin & D'Antonio 2012; Pyšek *et al.* 2012; Ibáñez *et al.* 2021. However, studies that differentiate impacts across invasion events are rare (Ibáñez *et al.* 2021). If impact varies as a function of the mechanism of invasion, management strategies could then be more targeted. The results of our meta-analysis indicate higher impact on the native community when invasion occurs via low biotic resistance (significant results) or high propagule pressure (marginally significant results; Figure 2.4a). This finding is consistent with a global meta-analysis across terrestrial ecosystems that identified both propagule availability and lack of biotic resistance as the main drivers of vulnerability to plant invasion (Ibáñez *et al.* 2021). Thus, already depauperated native communities will be less able to withstand invasions than healthy ones. This may be due to the loss of species that could have outcompeted the invader, had higher dispersal abilities, and/or occupied particular niche requirements that now are unused (Flinn & Vellend 2005; Martin, Canham & Marks 2009). Therefore, management should ensure that invasive control happens in healthy native understory communities or that it is followed by the restoration of native species pool.

Invasion is contingent on, and frequently, driven by high propagule pressure of invaders (Holle & Simberloff 2005; Lockwood, Cassey & Blackburn 2005; Ibáñez *et al.* 2009; Catford *et al.* 2011). Invasion via this mechanism possibly reflects two co-occurring processes, priority and legacy effects. Priority effects (i.e., arriving first) facilitate invasion in human-dominated landscapes as they tend to be a rich source of invasive seeds dominating dispersal events (Vilà & Ibáñez 2011; Cadotte *et al.* 2017). While the legacy of anthropogenic disturbances is commonly associated with depleted native richness and abundance (Flinn & Vellend 2005; Martin, Canham & Marks 2009).

Given the nature of these processes and the potential larger impact when invasion occurs via high propagule pressure, management should target the sources of propagules at the landscape level, by diminishing invaders while promoting native seed dispersal.

Research on invasive plants in forest ecosystems often focuses on studying a single species, while managers more frequently face the challenges of multiple co-occurring invaders (Kuebbing, Nuñez & Simberloff 2013). Yet, differences in impacts of single versus multiple invaders seem to be idiosyncratic. For example, a greenhouse study reported that co-occurring invasive shrubs exacerbated the negative impacts on the understory herbaceous community (Kuebbing *et al.* 2016). On contrary, a field survey showed that co-occurring invasive shrubs had no larger impact on the forest community when compared to a single invading species (Mahla & Mlambo 2019). The results of our meta-analysis show that, overall, invasion caused by one shrub species is more detrimental than invasion by multiple co-occurring invaders in forest understories (Figure 2.4b). We speculate that diffuse competition (Goldberg 1987) might drive this pattern, indicating that competition among invaders would decrease the overall strength of impacts. However, we highlight these results should be taken with caution, given the small sample size of studies reporting multiple invaders. Still, early detection and removal of known impactful invaders, before widespread expansion, are important measures particularly when resources are limited.

2.6 Conclusions

We highlight that our meta-analysis, as many others (e.g., Pyšek *et al.* 2008; Sorte *et al.* 2013; Ibáñez *et al.* 2021), heavily represents the northern hemisphere, and in our case, temperate forests in particular, reflecting a systemic uneven distribution of research resources (Pyšek *et al.* 2008). To a certain extent, these results will still apply

to other forested systems. Our meta-analysis showed that invasive shrub performance did not vary across mechanisms of invasion. Yet, invasive effects were particularly detrimental under low biotic resistance, and marginally significant when caused by high invasive propagule pressure. Increases in light availability were the main abiotic factor associated with higher invasive performance, confirming the link between disturbance, especially anthropogenic disturbances, and invasive success. Impact was also associated with particular invasive species rather than diversity of invaders. These results can now be used to inform management of forest invasions, in particular, we recommend to:

- Manage to ensure a functionally diverse native community.

- Target landscape management actions to decrease invasive species propagule pressure while expanding native species dispersal sources.

- Avoid management techniques that degrade or diminish canopy cover.

- Focus on areas where high impact dominant invaders are present.

- Monitor post-management actions as the removal of a dominant invader might facilitate the establishment of subsequent invaders.

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2.8 Figures
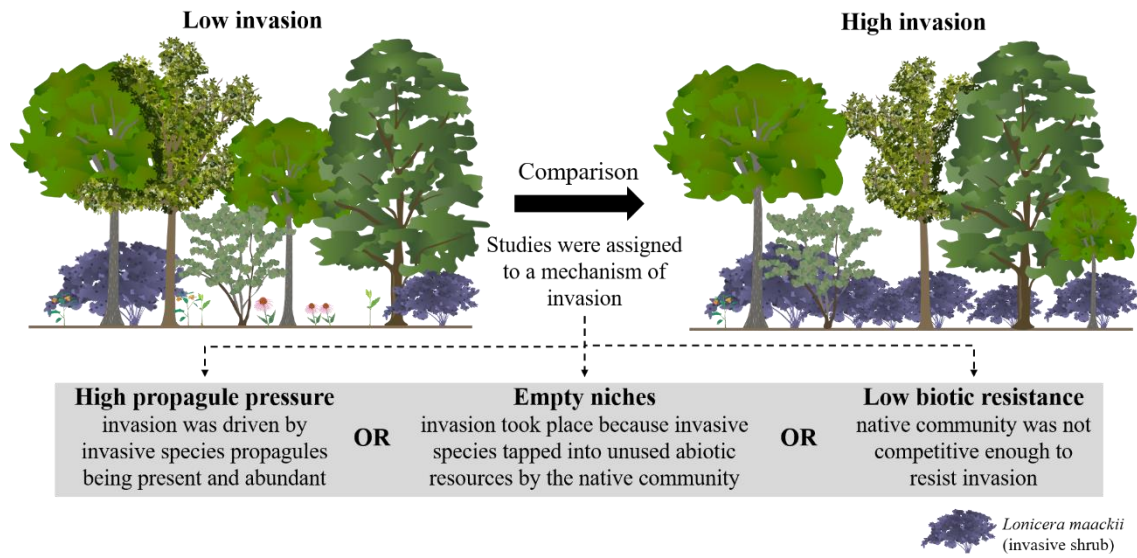
Figure 2.1: Conceptual figure. Graphical representation of the comparisons made in these analyses between low (left) and high (right) levels of invasive shrub abundance. Effect sizes of invasive and native performance, and resources (light, water, nutrients) were estimated between these two levels of invasion. Figure symbols were obtained through the Integration and Application Network (ian.umces.edu/media-library).
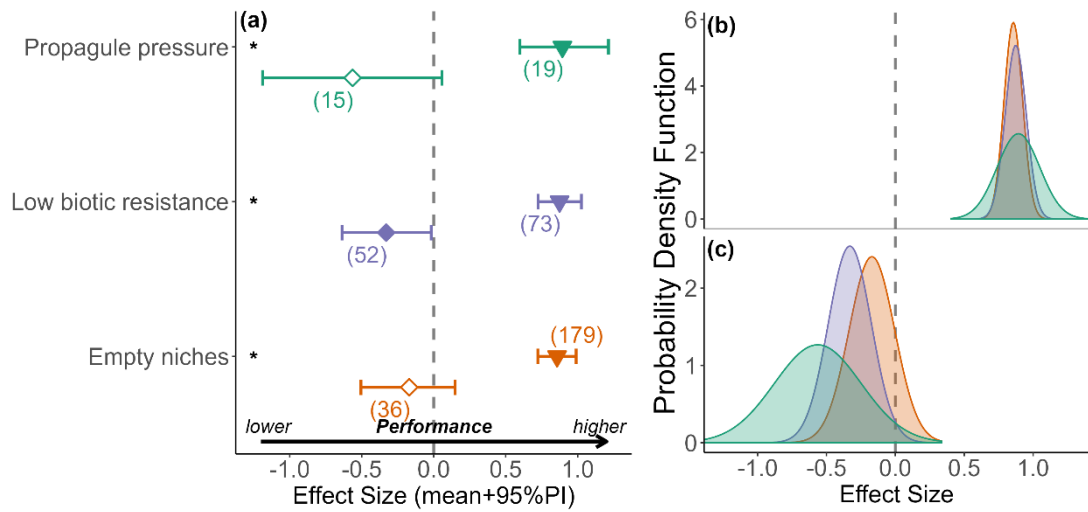
Figure 2.2: Invasive shrub success and mechanisms of invasion. (a) Results of the analysis of invasive shrub (▼) and native plant community (◆) performance (Effect Size) as a function of the mechanism of invasion (propagule pressure-green, low biotic resistance-purple, empty niches-orange). Predicted intervals [PI] that do not cross zero are statically significant (solid symbols). Numbers in parentheses indicate the number of observations. Statistically significant differences between invasive and native performance are indicated by asterisks (*; PI do not overlap). The graphs on the right show the probability density function of (b) invasive species and (c) native community performances by mechanism.
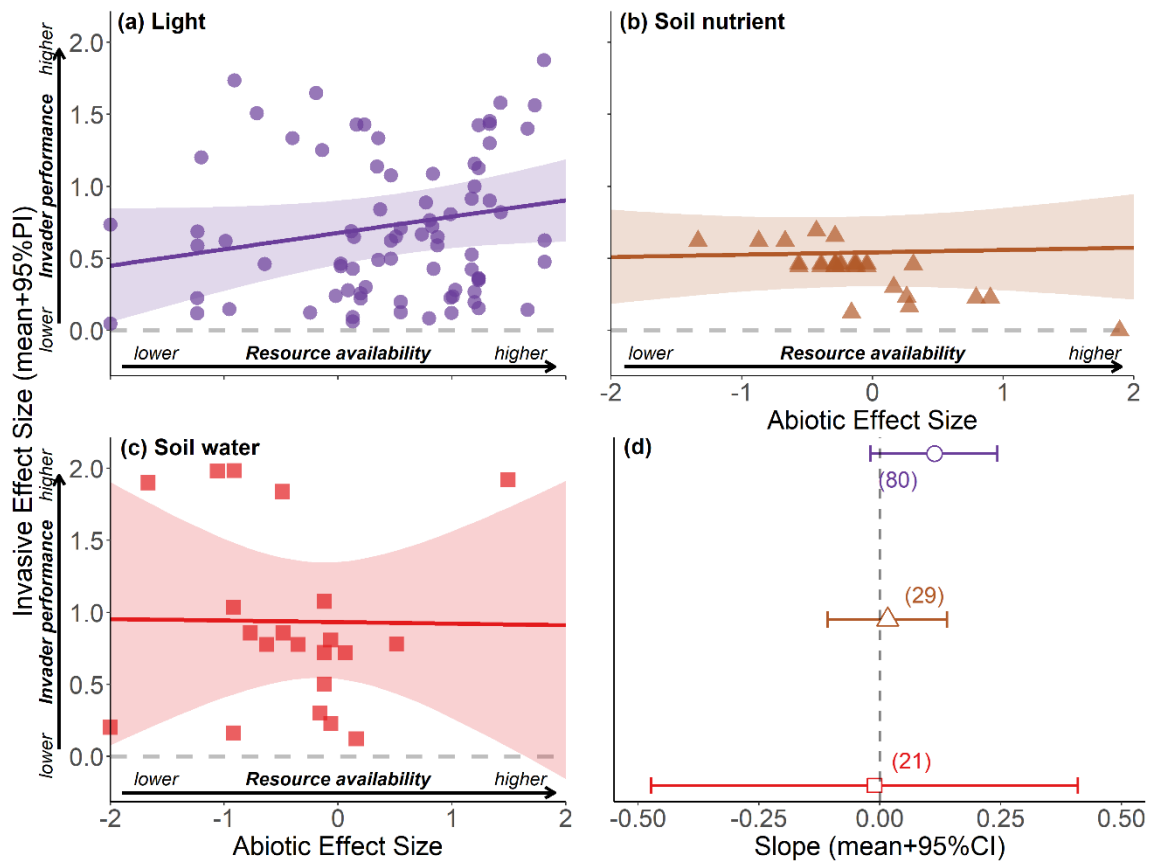
Figure 2.3: Effects of limiting resources on invasion success. Model results of invasive species performance as a function of resource availability partitioned into (a) light (● purple), (b) soil nutrient (▲ brown), and (c) soil water (■ red). Points are estimated effect sizes for each observation. Solid line indicates predicted mean effect size per category with associated 95 % predicted interval [PI] as shaded areas. (d) Slope parameters (mean and 95 % CI, credible interval). Numbers in parentheses indicate the number of observations.
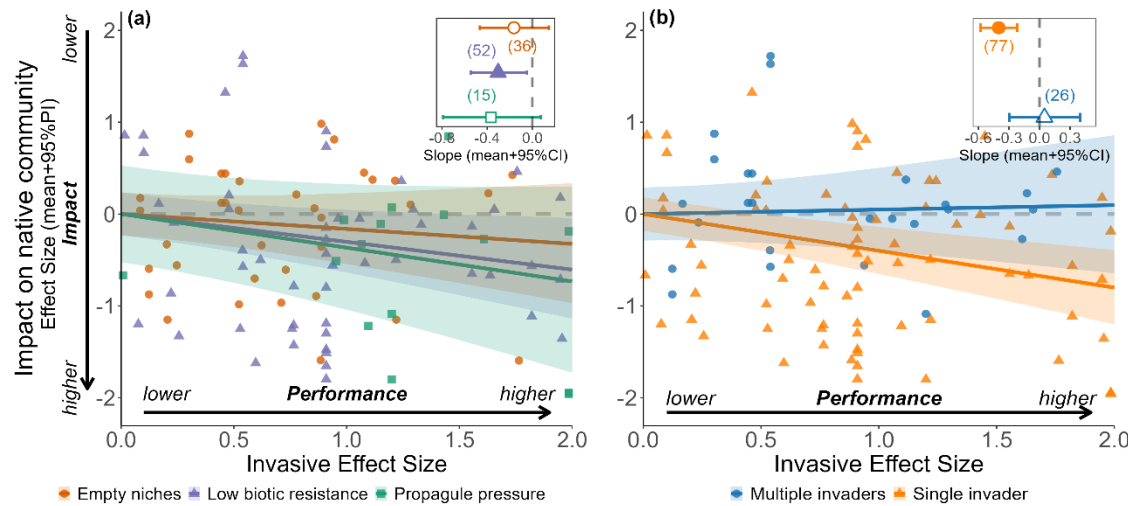
Figure 2.4: Invasive shrub impact on the native community. Analysis of native community performance as a function of invasive shrub performance partitioned into (a) the mechanisms of invasion, and (b) single vs. multiple invasive shrubs. Points in the main graphs are estimated effect sizes for each observation. Solid line indicates predicted mean effect size per category with associated 95 % predicted interval [PI] for each category. Inset graphs show the slope parameters (mean and 95 % CI, credible interval), and CIs that do not cross zero are statically significant (solid symbols). Numbers in parentheses indicate the number of observations.

2.9 Supporting Information

Text S 2.1: Extra details on data extraction, manipulation, and analysis.

Data extraction, and manipulation

Although we were unable to perform independent parallel screening of all articles, both authors revised 40 articles during the 'eligibility' stage (for all stages, check Figure S 2.1). Our classification and data collection agreed in 96% of the cases. Therefore, for the remaining articles, Laís Petri was responsible for their classification to guarantee consistency in assigning the mechanisms of invasion across all 124 articles. We used expert judgment to classify articles into one of the three mechanisms of invasion (i.e., propagule pressure, empty niches, or low biotic resistance) based on the information included in each article. Our classifications are an interpretation of the most likely mechanism driving invasion rather than the documentation of actual mechanisms, which is rarely done. We also highlight that the metrics (i.e., plant performance [List S2.1 and List S2.2], and abiotic features [List S2.3]) used to quantify effect sizes are proxies for the strength of mechanisms, not mechanisms themselves. Our classification is openly available to anyone for interpretation since we are providing the data we gathered.

We categorized an invasion as driven by empty niches when, for instance, invasive species explored forest edges (i.e., a proxy for higher light availability) or forest gaps more efficiently than understories in forest interiors or under intact canopies, or they performed better after disturbance (mainly human-induced disturbance) events or changes in disturbance regimes that released or decreased abiotic resources. We characterized shrub invasion driven by low biotic resistance when, for example, invasive species performed more successfully in primary forests, worse under natural disturbance regimes, or escaped herbivory (mainly deer). Finally, we classified invasion

as driven by propagule pressure when, for example, invasive species propagules were more abundant in forest understories closer to areas affected by anthropogenic activities, or invasive species increased in abundance over years. The temporal component of increases in invasion abundance was only categorized as propagule pressure when all other two mechanisms were eliminated as potential means by which invasion took place.

We extracted an extensive list of variables from each included research article (List S2.3). We recorded data on the following response variables: invasive species performance (List S2.2), native community performance (List S2.3), and/or native community abiotic features (List S2.3). We further aggregated the abiotic features into three broad categories of resource availability: light, soil nutrients, and soil water. To align the directionality of all responses, we changed the sign of the estimated effect size (ES) for a small number of the abiotic feature categories ($n_{categories} = 7$, $n_{observations} = 23$). This decision was made because their effect reflected the opposite response. For example, we changed the signs of ES estimated based on canopy cover values as a small percent cover value actually reflects high light availability reaching the forest understory through the canopy.

We additionally collected information on the plant species' Latin names and common names along with species origin (i.e., country or continent of origin). When the latter information was missing, we used online databases (CABI 2022; IUCN 2022; IUCN/ISSG 2022) to fill the gaps. We standardized invasive species taxonomy by using Taxonomic Name Resolution Service (TNRS; Boyle et al. 2013). We further classified the data entries as invaded by multiple invasive shrub species or not. Even if the performance data were reported separately for each invasive shrub species, leading to

multiple data entries for a particular study, we considered the forest community as one invaded by multiple shrub species.

We extracted geographic and climatic variables from each study site, and when missing, this information was complemented with online sources. In cases where the study site geographic coordinates were absent in the original article, we added the coordinates of the nearest city. We also recorded information on forest community type (e.g., temperate, tropical, sub-tropical, etc.), type of forest concerning its history of human exploration (e.g., natural primary, natural secondary, planted, etc.), study type (i.e., field experiment, greenhouse, or observational), and occurrence and type of disturbance. We broadly categorized disturbance as natural (e.g., storms), human-induced (e.g., grazing activities, mining, vegetation removal, among others), or both when the forest had experienced natural and human-induced disturbances. Finally, we appended information on global ecoregions by (The Nature Conservancy 2009) based on the geographic coordinates of each observation.

Data analysis – Effect size (ES) estimations

To estimate variability around ES, we ran simulations where the performance or resource availability at each level of invasion, *P* or *R,* was estimated from a normal distribution with reported mean and SD, *P, R ~ Normal* (*mean, SD*) (Code S 2.1). We then calculated ES mean and variance from these simulations. In our data, 34 % (n = 74) of the observations did not include any variance metric. If using standard approaches such as Hedges' *g*, these observations would be excluded, decreasing our sample size. For observations where performance or resource variation was not reported, we estimated ES directly and treated missing ES variances as latent variables to be estimated. We estimated latent variances (*ESvar*) as a function of the largest variance observed among ES calculations (*ESvarL*), *ESvar ~* Normal (*ESvarL, 1*)

bounded to be positive. We opted for this approach because it is the most conservative, it assigns large, but realistic, values to the variance estimate (Batson & Burton 2016). Values of ES not different from zero (i.e., credible intervals overlap with zero) indicate there was no difference in plant performance metric or resource availability between high and low levels of invasion.

Data analysis – Disturbance effects on performance across mechanisms of invasion

We carried out additional analysis to understand whether invasive species and native community performance responded differently to disturbance depending on the mechanism of invasion. We used a hierarchical approach to analyze the calculated values of ES, mean (ES), and SD (σ) as a function of the presence/absence of disturbance and disturbance type nested within mechanism. Study random effects (SRE) were also included. For observation *i*:

$$invESm_i \sim Normal\ (E_i, \sigma_i^2 + invESvar_i)$$
$$E_i = ES1_{mechanism(i),disturbance(i),type(i)} + SRE_i$$

Next, the parameter ES1 was then estimated for each combination of mechanism and disturbance (presence/absence) as

$$ES1_{mechanism(i),disturbance(i),type(i)} \sim Normal(ES2_{mechanism,disturbance}, \sigma_{mechanism,disturbance})$$

. We estimated the parameters ES1 and ES2 from non-informative prior distributions, ES1[*], ES2[*] ~ Normal (0, 0.1), while variance from random effects, SRE_i ~ Normal (0, σ_*^2), was estimated as σ^* ~ Uniform (0, 1).

For all mixed-effect models, analyses were run in OpenBUGS (Thomas *et al.* 2006) through R (R Core Team 2022) by using the 'R2OpenBUGS' (Sturtz, Ligges & Gelman 2005) and 'mcmcplots' (Curtis 2018) packages. We ran the all models with three chains, for 75,000 iterations. Only the last 50,000 iterations, after convergence, were used to estimate parameter posterior means and variances.

Text S 2.2: Parameters from analyses.

Analysis of invasive species performance by mechanism of invasion:

Metric	Mean	SD	2.50%	97.50%
propagule pressure	0.894038	0.155493	0.59840	1.2140
empty niches	0.857002	0.067512	0.72330	0.9894
low biotic resistance	0.874477	0.076426	0.72610	1.0260
variance propagule pressure	0.197154	0.164496	0.01225	0.6160
variance empty niches	0.202369	0.030351	0.15070	0.2689
variance biotic resistance	0.068208	0.026379	0.03167	0.1328
variance random effect	0.178415	0.040152	0.10940	0.2665

Analysis of invasive species performance as a function of resource availability by abiotic category:

Metric	Mean	SD	2.50%	97.50%
intercept light availability	0.676969	0.090384	0.50060	0.85640
intercept nutrient availability	0.542676	0.113878	0.32370	0.76520
intercept water availability	0.932631	0.169529	0.60840	1.27900
slope light availability	0.113482	0.066709	-0.01909	0.24380
slope nutrient availability	0.016438	0.063249	-0.10790	0.13890
slope water availability	-0.01079	0.224305	-0.47320	0.41010
variance light	0.148924	0.035918	0.09234	0.23210
variance nutrient	0.000653	0.000659	2.56E-05	0.00238
variance water	0.224389	0.166247	0.04806	0.65810
variance random effect	0.127182	0.063711	0.03280	0.27700

Analysis of native community performance by mechanism of invasion:

Metric	Mean	SD	2.50%	97.50%
propagule pressure	-0.56316	0.314909	-1.18900	0.05820
empty niches	-0.17003	0.165779	-0.505300	0.14920
low biotic resistance	-0.33025	0.156836	-0.636700	-0.01711
variance propagule pressure	0.98687	0.597194	0.326597	2.52800
variance empty niches	0.34407	0.131390	0.161500	0.66570
variance biotic resistance	0.45080	0.150024	0.230900	0.81040
variance random effect	0.20695	0.111536	0.035030	0.46910

Analysis of native community performance as a function of invasive species performance by mechanism of invasion:

Metric	Mean	SD	2.50%	97.50%
slope of propagule pressure	-0.36688	0.216560	-0.7895	0.0766

Metric	Mean	SD	2.50%	97.50%
slope of empty niches	-0.16289	0.153959	-0.4642	0.1467
slope of low biotic resistance	-0.30262	0.125386	-0.5436	-0.0476
variance of propagule pressure	0.990844	0.597700	0.3298	2.5150
variance of empty niches	0.371706	0.147422	0.1613	0.7263
variance of low biotic resistance	0.534934	0.156497	0.2934	0.9018
variance of random effects	0.181568	0.109127	0.0200	0.4404

Analysis of native community performance as a function of invasive species performance by single vs multiple invaders:

Metric	Mean	SD	2.50%	97.50%
slope multiple invaders	0.048417	0.176135	-0.2943	0.4008
slope single invader	-0.40036	0.091855	-0.5795	-0.2176
variance multiple invaders	0.496034	0.172554	0.2597	0.9221
variance single invader	0.476103	0.122392	0.2727	0.7504
variance random effect	0.106839	0.080298	0.0066	0.3069

Analysis of invasive species performance or native community performance by categorical variables:

- **Global ecoregions**

Type	Metric	Mean	SD	2.50%	97.50%
invader	Boreal Forests/Taiga	1.090840	1.688964	-2.378	4.573
invader	Deserts and Xeric Shrublands	0.800489	0.242549	0.3232	1.281
invader	Flooded Grasslands and Savannas	1.193136	1.727143	-2.338	4.737
invader	Mediterranean Forests, Woodlands and Scrub	1.021293	0.385492	0.2577	1.782
invader	Montane Grasslands and Shrublands	0.649896	1.549017	-2.608	3.863
invader	Temperate Broadleaf and Mixed Forests	0.843901	0.066027	0.7150	0.974
invader	Temperate Conifer Forests	0.636911	0.301673	0.0351	1.213
invader	Temperate Grasslands, Savannas and Shrublands	0.982369	0.290748	0.3930	1.543
invader	Tropical and Subtropical Dry Broadleaf Forests	1.286735	1.074946	-1.0330	3.534
invader	Tropical and Subtropical Grasslands, Savannas and Shrublands	1.133756	0.325324	0.4773	1.762
invader	Tropical and Subtropical Moist Broadleaf Forests	0.823303	0.159595	0.5083	1.137
invader	variance Boreal Forests/Taiga	4.138555	2.929417	0.1077	9.623

Type	Metric	Mean	SD	2.50%	97.50%
invader	variance Deserts and Xeric Shrublands	0.218837	0.261702	0.0060	0.887
invader	variance Flooded Grasslands and Savannas	4.401393	2.894022	0.1733	9.664
invader	variance Mediterranean Forests, Woodlands and Scrub	0.736785	0.532074	0.2310	2.116
invader	variance Montane Grasslands and Shrublands	4.117346	2.921353	0.1177	9.621
invader	variance Temperate Broadleaf and Mixed Forests	0.163969	0.027254	0.1187	0.224
invader	variance Temperate Conifer Forests	0.232967	0.605184	0.0016	1.689
invader	variance Temperate Grasslands, Savannas and Shrublands	0.262294	0.271271	0.0508	0.944
invader	variance Tropical and Subtropical Dry Broadleaf Forests	2.995353	2.747496	0.0468	9.318
invader	variance Tropical and Subtropical Grasslands, Savannas and Shrublands	0.147954	0.215091	0.0176	0.637
invader	variance Tropical and Subtropical Moist Broadleaf Forests	0.208693	0.073476	0.1046	0.387
invader	variance random effects	0.171315	0.041736	0.1003	0.264
native community	Deserts and Xeric Shrublands	-0.31764	0.488724	-1.2970	0.660
native community	Montane Grasslands and Shrublands	-0.52284	2.345822	-5.3120	4.281
native community	Temperate Broadleaf and Mixed Forests	-0.43532	0.125594	-0.6820	-0.187
native community	Temperate Conifer Forests	-0.23653	1.508535	-3.3900	2.923
native community	Temperate Grasslands, Savannas and Shrublands	0.159549	0.577921	-1.0380	1.297
native community	Tropical and Subtropical Moist Broadleaf Forests	-0.09646	0.322757	-0.7241	0.566
native community	variance Deserts and Xeric Shrublands	1.383140	1.28735	0.2312	5.167
native community	variance Montane Grasslands and Shrublands	4.991535	2.886295	0.2401	9.743
native community	variance Temperate Broadleaf and Mixed Forests	0.531225	0.117134	0.3439	0.799
native community	variance Temperate Conifer Forests	3.970730	2.928023	0.0890	9.601
native community	variance Temperate Grasslands, Savannas and Shrublands	1.039228	1.395946	0.0220	5.393
native community	variance Tropical and Subtropical Moist Broadleaf Forests	0.363497	0.641235	0.0042	1.975

Type	Metric	Mean	SD	2.50%	97.50%
native community	variance random effects	0.19283	0.109153	0.0328	0.455

- **Forest community**

Type	Metric	Mean	SD	2.50%	97.50%
invader	broadleaf	1.002753	0.273282	0.4575	1.539
invader	conifer	0.652739	0.402433	-0.1555	1.445
invader	deciduous	0.794476	0.083542	0.6305	0.958
invader	deciduous floodplain	0.750562	1.400618	-2.2140	3.724
invader	dry	0.915517	0.297364	0.3151	1.495
invader	evergreen	1.087045	0.179141	0.7345	1.439
invader	floodplain	0.854951	0.231758	0.3940	1.315
invader	mixed	0.857643	0.142887	0.577	1.14
invader	riparian	1.720756	1.13088	-0.6778	4.091
invader	savanna	1.278841	0.410022	0.4743	2.072
invader	semi-deciduous	0.819385	0.234411	0.3553	1.283
invader	semi-dry	1.160196	0.454299	0.2487	2.039
invader	shrubland	0.438659	0.722233	-1.034	1.961
invader	variance broadleaf	0.475854	0.459742	0.0568	1.635
invader	variance conifer	0.744754	0.832034	0.1335	2.999
invader	variance deciduous	0.147754	0.03247	0.0958	0.222
invader	variance deciduous floodplain	3.524858	2.960771	0.0358	9.528
invader	variance dry	0.395911	0.432966	0.0191	1.53
invader	variance evergreen	0.17784	0.087402	0.0717	0.398
invader	variance floodplain	0.174973	0.239823	0.0033	0.788
invader	variance mixed	0.261500	0.081523	0.1444	0.459
invader	variance riparian	3.068760	2.768185	0.0534	9.339
invader	variance savanna	0.418547	0.869604	0.0011	2.878
invader	variance semi-deciduous	0.057005	0.064735	0.0073	0.218
invader	variance semi-dry	0.420296	0.555993	0.0108	1.853
invader	variance shrubland	2.262409	2.144461	0.2424	8.396
invader	variance random effects	0.173032	0.045271	0.0963	0.273
native community	broadleaf	-0.93448	0.686322	-2.4200	0.464
native community	conifer	-0.30840	2.595827	-5.5860	4.984
native community	deciduous	-0.21754	0.163565	-0.5336	0.112
native community	dry	-0.48791	0.833511	-2.1820	1.349
native community	evergreen	-0.90049	0.363472	-1.6220	-0.177
native community	floodplain	-0.38824	0.405795	-1.2010	0.419
native community	mixed	-0.36650	0.236565	-0.8418	0.102
native community	riparian	-1.59604	2.269685	-6.2650	3.094

Type	Metric	Mean	SD	2.50%	97.50%
native community	savanna	0.099142	1.657927	-3.3310	3.52
native community	semi-deciduous	0.45837	1.042968	-1.6920	2.571
native community	shrubland	-0.64024	2.281462	-5.3450	4.061
native community	woodland	-0.13172	2.275115	-4.8490	4.571
native community	variance broadleaf	1.488107	2.028841	0.0341	7.876
native community	variance conifer	5.013213	2.878941	0.2658	9.752
native community	variance deciduous	0.505962	0.144355	0.2896	0.849
native community	variance dry	2.205367	2.407462	0.0312	8.771
native community	variance evergreen	0.992413	0.711657	0.3123	2.837
native community	variance floodplain	1.288232	1.026515	0.2988	4.135
native community	variance mixed	0.265247	0.212004	0.0701	0.805
native community	variance riparian	5.014978	2.882664	0.2590	9.749
native community	variance savanna	4.082142	2.936265	0.1008	9.625
native community	variance semi-deciduous	2.773389	2.584340	0.0485	9.113
native community	variance shrubland	5.007276	2.884286	0.2530	9.747
native community	variance woodland	5.003006	2.885897	0.2601	9.747
native community	variance random effects	0.155977	0.100061	0.0196	0.405

- **Forest type**

Type	Metric	Mean	SD	2.50%	97.50%
invader	natural	0.880562	0.090603	0.7028	1.059
invader	natural primary	1.053444	0.334795	0.3786	1.701
invader	natural secondary	0.926218	0.080190	0.7683	1.083
invader	natural secondary with invaded canopy	1.752548	2.628976	-3.5990	7.113
invader	plantation	0.679251	0.351232	-0.0134	1.377
invader	plantation and natural	0.843546	2.290117	-3.8630	5.571
invader	restoration (planted)	0.641713	0.705528	-0.8990	2.082
invader	variance natural	0.207113	0.051667	0.1259	0.326
invader	variance natural primary	0.266901	0.268705	0.0089	0.961
invader	variance natural secondary	0.205517	0.042795	0.1361	0.302
invader	variance natural secondary with invaded canopy	4.986659	2.891141	0.2421	9.752

Type	Metric	Mean	SD	2.50%	97.50%
invader	variance plantation	0.674240	0.692650	0.1331	2.480
invader	variance plantation and natural	5.004336	2.886814	0.2510	9.750
invader	variance restoration (planted)	1.668211	2.135109	0.0422	8.190
invader	variance random effects	0.130913	0.045958	0.0514	0.231
native community	natural	-0.19890	0.205137	-0.6049	0.208
native community	natural secondary	-0.29317	0.159284	-0.6074	0.021
native community	natural secondary with invaded canopy	-1.59578	2.274643	-6.2870	3.094
native community	plantation	-1.03598	0.498216	-2.0660	-0.035
native community	restoration (planted)	-0.12256	2.269723	-4.8330	4.558
native community	variance natural	0.527763	0.251433	0.2092	1.161
native community	variance natural secondary	0.659930	0.166688	0.4015	1.049
native community	variance natural secondary with invaded canopy	4.991829	2.888892	0.2468	9.753
native community	variance plantation	0.904532	1.431228	0.0315	5.638
native community	variance restoration (planted)	4.985198	2.892909	0.2421	9.75
native community	variance random effects	0.160765	0.110450	0.0142	0.432

- **Study type**

Type	Metric	Mean	SD	2.50%	97.50%
invader	field experiment	0.763016	0.099913	0.5664	0.958
invader	greenhouse	0.709579	0.202037	0.3090	1.104
invader	observational	0.941316	0.062789	0.8187	1.065
invader	variance field experiment	0.270866	0.059683	0.1752	0.408
invader	variance greenhouse	0.212098	0.097790	0.0926	0.460
invader	variance observational	0.122185	0.022644	0.0848	0.173
invader	variance random effects	0.155953	0.037915	0.0912	0.239
native community	field experiment	-0.32310	0.214353	-0.7474	0.098
native community	greenhouse	0.457881	1.050971	-1.7160	2.571
native community	observational	-0.39400	0.118232	-0.6236	-0.158
native community	variance field experiment	0.782612	0.286459	0.3872	1.485
native community	variance greenhouse	2.788497	2.590272	0.0531	9.126
native community	variance observational	0.443824	0.103872	0.2768	0.681
native community	variance random effects	0.164046	0.097678	0.0198	0.395

- **Disturbance**

Type	Metric	Mean	SD	2.50%	97.50%
invader	absent	0.708289	0.177816	0.3574	1.059
invader	present	0.854226	0.059594	0.7378	0.971
invader	variance absent	0.226381	0.104986	0.0935	0.490
invader	variance present	0.187950	0.031321	0.1351	0.257
invader	variance random effects	0.124492	0.040710	0.0568	0.216
native community	absent	0.002332	0.275765	-0.5427	0.553
native community	present	-0.33688	0.122150	-0.5754	-0.093
native community	variance absent	0.206917	0.278293	0.0199	0.881
native community	variance present	0.568487	0.119971	0.3749	0.841
native community	variance random effects	0.164257	0.100089	0.0223	0.409

- **Disturbance type**

Type	Metric	Mean	SD	2.50%	97.50%
invader	natural	0.97809	0.189754	0.6052	1.3500
invader	human-induced	0.85040	0.068651	0.7164	0.9857
invader	natural and human-induced	0.68954	0.405847	-0.1255	1.5100
invader	variance natural	0.34917	0.141299	0.1619	0.6969
invader	variance human-induced	0.10880	0.026515	0.0671	0.1702
invader	variance natural and human-induced	0.60253	1.036357	0.0058	3.658
invader	variance random effects	0.16733	0.046860	0.0890	0.2721
native community	natural	-0.35484	0.884905	-2.1860	1.5320
native community	human-induced	-0.33943	0.135048	-0.5971	-0.0661
native community	natural and human-induced	-0.35231	0.330646	-1.0090	0.2973
native community	variance natural	2.89184	2.499930	0.1432	9.1030
native community	variance human-induced	0.53206	0.132034	0.3240	0.8376
native community	variance natural and human-induced	1.17131	0.653588	0.4311	2.8520
native community	variance random effects	0.15847	0.117563	0.0101	0.4520

Hierarchical analysis of invasive species performance or native community performance of disturbance and disturbance type nested under mechanism of invasion:

Type	Metric	Mean	SD	2.50%	97.50%
invasive	propagule pressure	0.912392	0.836264	-0.7830	2.580
invasive	empty niches	0.886719	0.454149	-0.0802	1.828
invasive	low biotic resistance	0.805722	0.454412	-0.1588	1.747

Type	Metric	Mean	SD	2.50%	97.50%
invasive	propagule pressure, disturbance present	0.958708	0.503337	-0.0717	1.997
invasive	empty niches, disturbance present	0.872467	0.238361	0.3810	1.377
invasive	empty niches, disturbance absent	0.936932	0.124975	0.6919	1.184
invasive	low biotic resistance, disturbance present	0.817295	0.256226	0.2687	1.326
invasive	low biotic resistance, disturbance absent	0.826224	0.122229	0.5872	1.069
invasive	propagule pressure, disturbance present, natural	1.088698	0.384072	0.3425	1.864
invasive	propagule pressure, disturbance present, human	0.869185	0.191729	0.4949	1.256
invasive	empty niches, disturbance present, natural	0.946842	0.197030	0.5732	1.349
invasive	empty niches, disturbance present, human	0.800325	0.089290	0.6258	0.975
invasive	empty niches, disturbance present, both	0.833033	0.318915	0.1654	1.478
invasive	empty niches, disturbance present, not reported	0.886167	0.253253	0.3788	1.409
invasive	empty niches, disturbance absent, absent	0.936932	0.124975	0.6919	1.184
invasive	low biotic resistance, disturbance present, natural	0.812293	0.241685	0.3235	1.289
invasive	low biotic resistance, disturbance present, human	0.918527	0.107534	0.7079	1.131
invasive	low biotic resistance, disturbance present, both	0.685017	0.307302	0.0381	1.252
invasive	low biotic resistance, disturbance present, not reported	0.846323	0.316303	0.1933	1.479
invasive	low biotic resistance, disturbance absent, absent	0.826224	0.122229	0.5872	1.069
invasive	variance propagule pressure	0.496680	0.288286	0.0249	0.973
invasive	variance empty niches	0.386996	0.293373	0.0087	0.958
invasive	variance biotic resistance	0.384829	0.292149	0.0083	0.957
invasive	variance propagule pressure, disturbance	0.423076	0.290057	0.0137	0.963
invasive	variance empty niches, disturbance	0.214904	0.235288	0.0033	0.863
invasive	variance low biotic resistance, disturbance	0.242690	0.245521	0.0040	0.888
invasive	variance random effect	0.184013	0.041993	0.1122	0.277
native community	propagule pressure	-0.53604	0.314006	-1.1420	0.093
native community	empty niches	-0.18665	0.520604	-1.2470	0.872
native community	low biotic resistance	-0.39864	0.518514	-1.4520	0.668

Type	Metric	Mean	SD	2.50%	97.50%
native community	propagule pressure, disturbance present	-0.53604	0.314006	-1.1420	0.093
native community	empty niches, disturbance present	-0.16253	0.370117	-0.8926	0.602
native community	empty niches, disturbance absent	-0.21519	0.318149	-0.8520	0.407
native community	low biotic resistance, disturbance present	-0.33445	0.406893	-1.1710	0.486
native community	low biotic resistance, disturbance absent	-0.47864	0.248607	-0.9653	0.014
native community	propagule pressure, disturbance absent	-0.53604	0.314006	-1.1420	0.093
native community	empty niches, disturbance present, natural	0.017819	0.465293	-0.8514	0.996
native community	empty niches, disturbance present, human	-0.29289	0.193018	-0.6766	0.085
native community	empty niches, disturbance present, both	-0.16994	0.382621	-0.9257	0.600
native community	empty niches, disturbance present, not reported	-0.21519	0.318149	-0.8520	0.407
native community	low biotic resistance, disturbance present, human	-0.20339	0.225567	-0.6389	0.244
native community	low biotic resistance, disturbance present, both	-0.38694	0.302695	-0.9940	0.198
native community	low biotic resistance, disturbance present, not reported	-0.47864	0.248607	-0.9653	0.014
native community	variance empty niches	0.417716	0.291058	0.0131	0.963
native community	variance biotic resistance	0.424094	0.289628	0.0139	0.963
native community	variance empty niches, disturbance	0.365101	0.280448	0.0100	0.948
native community	variance low biotic resistance, disturbance	0.384037	0.287365	0.0106	0.956
native community	variance random effect	0.226976	0.124921	0.0380	0.523

List S2.1: List of all the variables extracted from each article and associated metadata of file "Data.csv" available in https://doi.org/10.5061/dryad.msbcc2g33.

StudyIDOriginal: each unique number corresponds to an article reference listed in *List S4* below;

ObsIDOriginal: unique ID attributed to each article when data was extracted;

Lat_m: latitude in degrees where the data was collected;

Long_m: longitude in degrees where the data was collected;

Continent: the continent where the data was collected;

Country: the country where the data was collected;

Province_Region: province, region, state, or county where the data was collected;

City: city (or the nearest city to the study site) where the data was collected;

OlsonEtAl2001_GlobalEcoregions: global ecoregions defined by (Olson *et al.* 2001). The shapefile "tnc_terr_ecoregions" was organized by The Nature Conservancy (2009; https://geospatial.tnc.org/datasets/b1636d640ede4d6ca8f5e369f2dc368b/about). The metadata for the shapefile source of this information can be found here;

Elevation_m: elevation in meters, of where the data was collected (if this information was provided by the authors) or the "City" reported in a previous column;

Precipitation_mm: or rainfall (mm), total annual precipitation where the data was collected. When this information was not reported in the paper, the value corresponds to the city's respective value. In the latter case, the information was collected from this website;

JanuaryTemp_C: mean January temperature in degrees Celsius. When this information was not reported in the paper, the value corresponds to the city's respective value. In the latter case, the information was collected from this website;

JulyTemp_C: mean July temperature in degrees Celsius. When this information was not reported in the paper, the value corresponds to the city's respective value. In the latter case, the information was collected from this website;

MeanAnnualTemp_C: mean annual temperature in degrees Celsius. When this information was not reported in the paper, the value corresponds to the city's respective value. In the latter case, the information was collected from this website;

ForestCommunity: defines the forest community type. This information was either extracted from the paper when it was specifically mentioned or inferred by the location and vegetation composition;

TypeOfForest: defines the forest type with regard to history of exploration and/or current use (e.g., natural primary, natural secondary, planted, etc.). Not always this information was mentioned by the authors, or could be extrapolated from the site description;

TypeOfStudy: specifies the general method of data collection (i.e., field experiment, greenhouse, or observational);

Disturbance: defines whether the forest community experienced or not disturbance history, or whether disturbance was not mentioned at all. Greenhouse studies were filled with an NA for this category;

NatureOfDisturbance: dummy variable to characterize the disturbance type in numbers. The categories are: 1 = natural; 2 = human; 3 = natural and human; NA = when disturbance was not reported or NA in the previous column; not_reported = when disturbance was indicated that existed but no specifics were given;

YearOfDisturbance: year that the disturbance ceased; interval of years it happened; or if it was ongoing when data was collected;

YearOfDataMeasurement: defines the year or the interval of years that the data was collected. When not reported, the data of the article publication was included instead;

YearOfDataMeasurement_reported: specifies whether the article reported the year of data collection ("yes") or not ("no");

AccInvasiveSpecies: invasive species Latin name(s) standardized through the Taxonomic Name Resolution Service (TNRS; Boyle *et al.* 2013);

CommInvasiveSpecies: common name for each invasive species as reported by the paper, or collected in online databases [http://www.iucngisd.org/gisd/; https://www.cabi.org/isc; http://issg.org/database/species/List.asp; https://www.iucnredlist.org/] when this information was missing;

InvasiveSpeciesOrigin: invasive species country/continent of origin as reported by the paper, or collected in online databases [http://www.iucngisd.org/gisd/; https://www.cabi.org/isc; http://issg.org/database/species/List.asp; https://www.iucnredlist.org/] when this information was missing;

MultipleInvader: multiple shrub invasive species present in the system (1) or not (0);

Mechanism: mechanism by which invasion took place. The mechanisms are: (1) propagule pressure (i.e., invasion was driven by invasive species propagules being present and abundant); (2) empty niches (i.e., invasion took place because invasive species tapped into unused abiotic resources by the native plant community); and (3) low biotic resistance (i.e., native community was not competitive enough to resist invasion);

NcontInv: sample size of invader response control (low invasion);

NtreatInv: sample size of invader response treatment (high invasion);

TypeOfResponse: defines the performance metric;

UnitOfResponse: specifies the unit of the performance metric defined in the previous column;

TypeOfMeasuredVariability: unit of variance metric reported associated with the mean performance value. The categories are SD, SE, and upper maximum value;

InvContmean: mean value of invader performance metric when forest understory was under low invasion levels;

InvContsd: variance value associated with the mean value of invader performance metric (previous column) when the community is under low invasion levels reported;

InvTreatmean: mean value of invader performance metric when forest understory was under high invasion levels;

InvTreatsd: variance value associated with the mean value of invader performance metric (previous column) when the community is under high invasion levels;

NativeResponse_CATEGORY: native community metrics in broad categories;

NativeResponse_SUBCATEGORY: specifies/details the subcategories within each broad category;

NativeCommunity: when biotic response, specifies whether the native response is at the community level (1) or species level (0). Here, observations with abiotic response are filled with "NA".

NcontNat: sample size for the native response control when understory was at low invasion levels;

NtreatNat: sample size for the native response treatment when understory was at high invasion levels;

TypeOfTreatment: defines the native response metric;

UnitOfTreatment: specifies the unit of the native response metric defined in the previous column;

TypeOfMeasuredVariability_Response: unit of variance metric reported associated with the mean native response value. The categories are SD, SE, and upper maximum value;

NatContmean: mean value of native response metric when forest understory was under low invasion levels;

NatContsd: variance value associated with the mean value of native response metric (previous column) when the community is under low invasion levels;

NatTreatmean: mean value of native response metric when forest understory was under high invasion levels;

NatTreatsd: variance value associated with the mean value of native response metric (previous column) when the community is under high invasion levels;

SourceFromPapers: figure, table, or text section from where the data was extracted.

List S2.2: List of invasive species performance metrics extracted from selected articles. Units are in parenthesis.

Abundance (number of seedlings; number of seeds; number of stems; number of seedlings; %)

Basal area ($m^2.ha^{-1}$; $cm^2.200m^{-2}$, $m^2.400m^{-2}$)

Basal diameter (mm)

Biomass [aboveground, belowground, total] (g; $g.seedling^{-1}$; $kg.m^{-2}$; $cm^2.g^{-1}$; $g.plant^{-1}.year^{-1}$)

Chlorophyll content (%)

Cover (%)

Crown width (cm)

Density (number of individuals or stems or $seedlings.area^{-1}$)

Fecundity ($fruits.shrub^{-1}$; $seeds.shrub^{-1}$)

Frequency [total, vegetative shoots] (%; number of occurrences; %, number of $patches.gap^{-1}$)

Germination (%; $seedlings.m^{-2}$)

Growth rate [height, stem] ($cm.year^{-1}$; $mm.year^{-1}$)

Height (cm)

Importance value (unitless)

Leaf area (cm^2)

Number of branches (counts)

Number of leaves (counts; number of $leaves.stem^{-1}$; number of $leaves.plant^{-1}$)

Photosynthetic rate (mmol $CO_2.g^{-1}.s^{-1}$)

Potential to spread (number of pollen grains)

Qualitative assessment of shrub density (score)

Relative aboveground NPP (total aboveground NPP.shrub $density^{-1}$)

Relative biomass [total, leaf, stem] (cm2.g-1; leaf or stem biomass.total aboveground $biomass^{-1}$; total aboveground biomass.total aboveground NPP^{-1})

Relative growth (circumference growth.intial $growth.^{-1}$; $cm.cm^{-1}.day^{-1}$)

Relative growth rate [aboveground, diameter, stem] ((final dry weight – estimated initial dry weight).estimated initial dry $weight^{-1}$; $10^{-2}cm.(cm.week^{-1})^{-1}$; $mm.year^{-1}$; $mm.cm^{-1}.day^{-1}$)

Relative leaf area ($cm^2.g^{-1}$)

Relative mass [leaf, root, stem] ($g.g^{-1}$)

Relative production rate ($g.g^{-1}.year^{-1}$)

Reproductive effort [fruit set] (%; proportion)

Reproductive effort [mass of seed, dry pericarp, fruit] (g)

Reproductive effort [production of flower, fruit, inflorescence, infructescence, seed] (number of $flowers.stem^{-1}$; number of $flowers.shoot^{-1}$; number of $flowers.node^{-1}$; number of $fruits.shoot^{-1}$; number of $fruits.node^{-1}$; number of inflorescences.main $branch^{-1}$; number of $infructescence.stem^{-1}$)

Richness (number of species)

Shoot length (cm)

Specific leaf area ($cm^2.g^{-1}$)

Stem NPP (total stem NPP.total residual stem NPP^{-1})

Survival (%; $plants.plot^{-1}$; number of individuals)

Water use efficiency (unitless)

List S2.3: List of metrics of the native community abiotic features and performance extracted from selected articles. Units are in parenthesis.

Abiotic features
Canopy height variability (log of standard deviation)
CO_2 concentration (µmol.mol^{-1})
Depth of debris (cm)
Depth of sediments deposited (cm)
Depth of soil mottling (cm)
Distance from edge (m)
Distance from river (m)
Light availability (%, light available.total light^{-1}; photosynthetic photon flux density; lux.100; mmol.m^{-2}.s^{-1}; µmol.m^{-2}.s^{-1}; mol.m^{-2}.day^{-1})
Light heterogeneity (light standard deviation, 0.9 quantile)
Litter biomass (kg.m^{-2})
Mean water potential (MPa)
Rock index (unitless)
Soil bulk density (g.cm^3)
Soil moisture (%)
Soil nutrient availability (ppm, %, mg.kg^{-1}; µgN.g^{-1}.month^{-1})
Soil pH (pH)
Standing litter biomass (m^2)
Water depth (m)
Water flow pick (m^{-3}.s^{-1})
Water flow velocity (m.s^{-1})
Water surface flow permanence (%)
Water table depth (m)

Biotic variables
Abundance (number of seedlings; number of individuals)
Ash decline (index i.e., total basal area of trees with compromised health.total stand basal area^{-1})
Basal area (m^2.ha^{-1})
Biomass (g)
Chlorophyll content (unitless)
Fruit set (%)
Germination (%; seedlings.m^{-2})
Growth rate (cm.year^{-1}; cm.week^{-1}; mm.year^{-1})
Height (cm)
Leaf area (cm^2)
Leaf C:N (ratio)
Relative frequency (unitless)
Richness or richness density (number of species; number of species.plot^{-1}; number of species.m^{-2}; number of species.25 m^{-2})
Specific leaf area (cm^2.g^{-1})
Survival (%)

List S2.4: Complete references of the articles included in this meta-analysis.

Abrams, M. D., and S. E. Johnson. (2012) Long-term impacts of deer exclosures on mixed-oak forest composition at the Valley Forge National Historical Park, Pennsylvania, USA. *Journal of the Torrey Botanical Society,* **139**, 167-180.

Akatov, V. V., T. V. Akatova, and A. E. Shadzhe. (2012) Species richness of tree and shrub layers in riparian forests of the Western Caucasus dominated by alien species. *Russian Journal of Ecology,* **43**, 294-301.

Allen, R. B. (1991) A preliminary assessment of the establishment and persistence of *Berberis-darwinii* Hook, a naturalized shrub in secondary vegetation near Dunedin, New-Zealand. *New Zealand Journal of Botany,* **29**, 353-360.

Auge, H., and R. Brandl. (1997) Seedling recruitment in the invasive clonal shrub, *Mahonia aquifolium* Pursh (Nutt). *Oecologia,* **110**, 205-211.

Awanyo, L., E. M. Attuah, and M. McCarron. (2011) Rehabilitation of forest-savannas in Ghana: The impacts of land use, shade, and invasive species on tree recruitment. *Applied Geography,* **31**, 181-190.

Bartuszevige, A. M., R. L. Hrenko, and D. L. Gorchov. (2007) Effects of leaf litter on establishment, growth and survival of invasive plant seedlings in a deciduous forest. *American Midland Naturalist*, **158**, 472-477.

Birken, A. S., and D. J. Cooper. (2006) Processes of *Tamarix* invasion and floodplain development along the lower Green River, Utah. *Ecological Applications,* 16**, 1103-1120.

Boever, C. J., M. D. Dixon, W. C. Johnson, M. L. Scott, and T. P. Malloy. (2019) Effects of a large flood on woody vegetation along the regulated Missouri River, USA. *Ecohydrology,* **12**.

Bowles, M. L., K. A. Jacobs, and J. L. Mengler. (2007) Long-term changes in an oak forest's woody understory and herb layer with repeated burning. *Journal of the Torrey Botanical Society,* **134**, 223-237.

Bowles, M. L., and J. L. McBride. (1998) Vegetation composition, structure, and chronological change in a decadent midwestern North American savanna remnant. *Natural Areas Journal,* **18**, 14-27.

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Bradburn, B. N., W. M. Aust, C. A. Dolloff, D. Cumbia, and J. Creighton. (2010) Evaluation of riparian forests established by the Conservation Reserve Enhancement Program (CREP) in Virginia. *Journal of Soil and Water Conservation,* **65**, 105-112.

Brooks, W. R., and R. C. Jordan. (2013) Propagule pressure and native species richness effects drive invasibility in tropical dry forest seedling layers. *Perspectives in Plant Ecology Evolution and Systematics,* **15**, 162-170.

Brown, K. A., J. C. Ingram, D. F. B. Flynn, R. Razafindrazaka, and V. Jeannoda. (2009) Protected Areas Safeguard Tree and Shrub Communities from Degradation and Invasion: A Case Study in Eastern Madagascar. *Environmental Management,* **44**, 136-148.

Brym, Z. T., D. Allen, and I. Ibanez. (2014) Community control on growth and survival of an exotic shrub. *Biological Invasions,* **16**, 2529-2541.

Burnham, K. M., and T. D. Lee. (2010) Canopy gaps facilitate establishment, growth, and reproduction of invasive *Frangula alnus* in a *Tsuga canadensis* dominated forest. *Biological Invasions,* **12**, 1509-1520.

Busch, D. E., and S. D. Smith. (1995). Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern us. *Ecological Monographs,* **65**, 347-370.

Cabin, R. J., S. G. Weller, D. H. Lorence, S. Cordell, and L. J. Hadway. (2002) Effects of microsite, water, weeding, and direct seeding on the regeneration of native and alien species within a Hawaiian dry forest preserve. *Biological Conservation,* **104**, 181-190.

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Cassidy, T. M., J. H. Fownes, and R. A. Harrington. (2004) Nitrogen limits an invasive perennial shrub in forest understory. *Biological Invasions,* **6**, 113-121.

Cavallero, L., and E. Raffaele. (2010) Fire enhances the 'competition-free' space of an invader shrub: *Rosa rubiginosa* in northwestern Patagonia. *Biological Invasions,* **12**, 3395-3404.

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Table S 2.1: List of all invasive shrub species, ordered by the scientific name. Scientific names were harmonized according to Taxonomic Resolution Service (TNRS; Boyle *et al.* 2013). Species marked with an asterisk (*) are considered shade-tolerant based on (Martin, Canham & Marks 2009; IUCN/ISSG 2022).

Family	Scientific Name	Author
Fabaceae	*Acacia dealbata*	Link
Fabaceae	*Amorpha fruticosa*	L.
Primulaceae	*Ardisia elliptica* *	Thunb.
Berberidaceae	*Berberis darwinii* *	Hook.
Berberidaceae	*Berberis thunbergii* *	DC.
Urticaceae	*Boehmeria macrophylla*	Hornem.
Urticaceae	*Boehmeria penduliflora*	Wedd. ex D.G. Long
Phyllanthaceae	*Breynia retusa*	(Dennst.) Alston
Fabaceae	*Caragana arborescens*	Lam.
Asteraceae	*Chromolaena odorata*	(L.) R.M. King & H. Rob.
Asteraceae	*Chrysanthemoides monilifera* *	(L.) Norl.
Melastomataceae	*Clidemia hirta* *	(L.) D. Don
Fabaceae	*Cytisus scoparius*	(L.) Link
Thymelaeaceae	*Daphne laureola*	L.
Fabaceae	*Desmodium incanum*	(Sw.) DC.
Elaeagnaceae	*Elaeagnus angustifolia* *	L.
Elaeagnaceae	*Elaeagnus umbellata* *	Thunb.
Celastraceae	*Euonymus alatus* *	(Thunb.) Siebold
Celastraceae	*Euonymus europaeus*	L.
Rhamnaceae	*Frangula alnus* *	Mill.
Asparagaceae	*Furcraea foetida*	(L.) Haw.
Malpighiaceae	*Hiptage benghalensis*	(L.) Kurz
Aquifoliaceae	*Ilex aquifolium* *	L.
Crassulaceae	*Kalanchoe pinnata*	(Lam.) Pers.
Verbenaceae	*Lantana camara*	L.
Oleaceae	*Ligustrum obtusifolium* *	Siebold & Zucc.
Oleaceae	*Ligustrum sinense* *	Lour.
Oleaceae	*Ligustrum vulgare* *	L.
Caprifoliaceae	*Lonicera* *	L.
Caprifoliaceae	*Lonicera maackii* *	(Rupr.) Maxim.
Caprifoliaceae	*Lonicera tatarica* *	L.
Berberidaceae	*Mahonia aquifolium*	(Pursh) Nutt.
Piperaceae	*Piper aduncum*	L.
Rosaceae	*Prunus laurocerasus* *	L.
Rosaceae	*Prunus serotina* *	Ehrh.
Rosaceae	*Pyrus calleryana*	Decne.
Rhamnaceae	*Rhamnus cathartica* *	L.
Rosaceae	*Rosa multiflora*	Thunb.
Rosaceae	*Rosa rubiginosa*	L.
Rosaceae	*Rubus alceifolius*	Poir.
Rosaceae	*Rubus ellipticus*	Sm.

Family	Scientific Name	Author
Rosaceae	*Rubus fruticosus*	L.
Rosaceae	*Rubus laciniatus*	Willd.
Rosaceae	*Rubus phoenicolasius*	Maxim.
Rosaceae	*Rubus ulmifolius*	Schott
Anacardiaceae	*Schinus terebinthifolius* *	Raddi
Asteraceae	*Senecio inaequidens* *	DC.
Asteraceae	*Senecio pterophorus* *	DC.
Solanaceae	*Solanum auriculatum*	Aiton
Solanaceae	*Solanum capsicoides*	All.
Solanaceae	*Solanum jamaicense*	Mill.
Solanaceae	*Solanum mauritianum*	Scop.
Solanaceae	*Solanum torvum*	Sw.
Rubiaceae	*Spermacoce exilis*	(L.O. Williams) C.D. Adams
Verbenaceae	*Stachytarpheta indica*	(L.) Vahl
Tamaricaceae	*Tamarix*	L.
Tamaricaceae	*Tamarix chinensis*	Lour.
Tamaricaceae	*Tamarix ramosissima*	Ledeb.

Table S 2.2: PRISMA-EcoEvo v.10 (O'Dea *et al.* 2021) with checklist of reported items in this paper.

Checklist item	Sub-item#	Sub-item description	Reported?	Notes
Title and abstract	1.1	Identify the review as a systematic review, meta-analysis, or both	Yes	The term is explicitly stated in both title and meta-analysis
	1.2	Summarise the aims and scope of the review	Yes	Topic 2 of the abstract
	1.3	Describe the data set	Yes	Title and topic 2 of the Abstract
	1.4	State the results of the primary outcome	Yes	Topic 3 of the Abstract
	1.5	State conclusions	Yes	Topic 4 of the Abstract
	1.6	State limitations	No	They are in the Conclusion
Aims and questions	2.1	Provide a rationale for the review	Yes	Introduction
	2.2	Reference any previous reviews or meta-analyses on the topic	NA: see 'Notes' for why	To the best of our knowledge, this is the first meta-analysis focused on shrub invasion of forests
	2.3	State the aims and scope of the review (including its generality)	Yes	Last paragraph of the Introduction, 'Systematic search and data extraction' in the Materials and Methods, and SM
	2.4	State the primary questions the review addresses (e.g. which moderators were tested)	Yes	Last paragraph of the Introduction, L224-227 in the Materials and Methods
	2.5	Describe whether effect sizes were derived from experimental and/or observational comparisons	Yes	This is a variable ('TypeOfStudy') collected across all studies included. Data is publicly available here: https://datadryad.org/stash/dataset/doi:10.5061/dryad.msbcc2g33
Review registration	3.1	Register review aims, hypotheses (if applicable), and methods in a time-stamped and publicly accessible archive and provide a link to the registration in the methods section of the manuscript. Ideally registration occurs before the search, but it can be done at any stage before data analysis.	No	
	3.2	Describe deviations from the registered aims and methods	NA: see 'Notes' for why	Aims were kept the same throughout the study.
	3.3	Justify deviations from the registered aims and methods	NA: see 'Notes' for why	See topic 3.2
Eligibility criteria	4.1	Report the specific criteria used for including or excluding studies when screening titles and/or abstracts, and full texts,	Yes	Systematic search and data extraction' in the Materials and Methods, and 'Data extraction, and manipulation' and 'Figure S 2.1' in the SM.

Checklist item	Sub-item#	Sub-item description	Reported?	Notes
		according to the aims of the systematic review (e.g. study design, taxa, data availability)		
	4.2	Justify criteria, if necessary (i.e. not obvious from aims and scope)	Yes	Systematic search and data extraction' in the Materials and Methods, and 'Data extraction, and manipulation' and 'Figure S 2.1' in the SM.
Finding studies	5.1	Define the type of search (e.g. comprehensive search, representative sample)	Yes	'Systematic search and data extraction' in the Materials and Methods
	5.2	State what sources of information were sought (e.g. published and unpublished studies, personal communications)	Yes	'Systematic search and data extraction' in the Materials and Methods
	5.3	Include, for each database searched, the exact search strings used, with keyword combinations and Boolean operators	Yes	'Systematic search and data extraction' in the Materials and Methods
	5.4	Provide enough information to repeat the equivalent search (if possible), including the timespan covered (start and end dates)	Yes	Systematic search and data extraction' in the Materials and Methods
Study selection	6.1	Describe how studies were selected for inclusion at each stage of the screening process (e.g. use of decision trees, screening software)	Yes	Systematic search and data extraction' in the Materials and Methods, and detailed explanation present in Text S1 in the SM
	6.2	Report the number of people involved and how they contributed (e.g. independent parallel screening)	Yes	As reported in Text S1 in the SM
Data collection process	7.1	Describe where in the reports data were collected from (e.g. text or figures)	Yes	This is a variable ('SourceFromPapers') collected across all studies included. Data is publicly available here: https://datadryad.org/stash/dataset/doi:10.5061/dryad.msbcc2g33
	7.2	Describe how data were collected (e.g. software used to digitize figures, external data sources)	Yes	'Systematic search and data extraction' in the Materials and Methods
	7.3	Describe moderator variables that were constructed from collected data (e.g. number of generations calculated from years and average generation time)	Yes	List S 2.1 in the SM

Checklist item	Sub-item#	Sub-item description	Reported?	Notes
	7.4	Report how missing or ambiguous information was dealt with during data collection (e.g. authors of original studies were contacted for missing descriptive statistics, and/or effect sizes were calculated from test statistics)	Yes	Data analysis' in the Materials and Method
	7.5	Report who collected data	Yes	Text S1 in the SM
	7.6	State the number of extractions that were checked for accuracy by co-authors	Yes	Text S1 in the SM
Data items	8.1	Describe the key data sought from each study	Yes	List S1 in the SM
	8.2	Describe items that do not appear in the main results, or which could not be extracted due to insufficient information	Yes	All cells of the main data file that have missing data were filled with NAs
	8.3	Describe main assumptions or simplifications that were made (e.g. categorising both 'length' and 'mass' as 'morphology')	Yes	Text S1, List S2, and List S3 in the SM
	8.4	Describe the type of replication unit (e.g. individuals, broods, study sites)	No	But generally replication units were vegetation plots
Assessment of individual study quality	9.1	Describe whether the quality of studies included in the systematic review or meta-analysis was assessed (e.g. blinded data collection, reporting quality, experimental *versus* observational)	Yes	This is a variable ('TypeOfStudy') collected across all studies included.
	9.2	Describe how information about study quality was incorporated into analyses (e.g. meta-regression and/or sensitivity analysis)	Yes	Study random effects were incorporated in the models. Effects sizes were explored as a function of climatic variables. And model residuals were explored as a function of six core covariates.
Effect size measures	10.1	Describe effect size(s) used	Yes	Effect size calculations' in the Materials and Methods
	10.2	Provide a reference to the equation of each calculated effect size (e.g. standardised mean difference, log response ratio) and (if applicable) its sampling variance	Yes	Effect size calculations' in the Materials and Methods

Checklist item	Sub-item#	Sub-item description	Reported?	Notes
	10.3	If no reference exists, derive the equations for each effect size and state the assumed sampling distribution(s)	NA: a reference for the effect size and its sampling variance was available, so no derivation was required	
Missing data	11.1	Describe any steps taken to deal with missing data during analysis (e.g. imputation, complete case, subset analysis)	Yes	Data analysis' in the Material and Methods
	11.2	Justify the decisions made to deal with missing data	Yes	Data analysis' in the Material and Methods
Meta-analytic model description	12.1	Describe the models used for synthesis of effect sizes	Yes	Data analysis' in the Material and Methods, and code that contains models is publicly available
	12.2	The most common approach in ecology and evolution will be a random-effects model, often with a hierarchical/multilevel structure. If other types of models are chosen (e.g. common/fixed effects model, unweighted model), provide justification for this choice	NA: only (weighted) random-effects models were used	Data analysis' in the Material and Methods
Software	13.1	Describe the statistical platform used for inference (e.g. R)	Yes	In the Materials and Methods
	13.2	Describe the packages used to run models	Yes	In the Materials and Methods, and in the publicly available code
	13.3	Describe the functions used to run models	Yes	In the Materials and Methods, and in the publicly available code
	13.4	Describe any arguments that differed from the default settings	NA: see 'Notes' for why	Models were run in OpenBUGS through R which gave us flexiliblity on how to build models without a pre-set function
	13.5	Describe the version numbers of all software used	Yes	In the Materials and Methods
Non-independence	14.1	Describe the types of non-independence encountered (e.g. phylogenetic, spatial, multiple measurements over time)	Yes	56.5 % of the studies articles generated more than one observation
	14.2	Describe how non-independence has been handled	Yes	Study random effects were added to the models
	14.3	Justify decisions made		Adding study random effects is a standard way of dealing with non-independency across effect sizes

Checklist item	Sub-item#	Sub-item description	Reported?	Notes
Meta-regression and model selection	15.1	Provide a rationale for the inclusion of moderators (covariates) that were evaluated in meta-regression models	Yes	Covariates were not included because both effect sizes and models' residuals did not vary as a function of, respectively, climatic variables and six core covariates. Therefore, their inclusion in the model as a met-regression was not justifiable.
	15.2	Justify the number of parameters estimated in models, in relation to the number of effect sizes and studies (e.g. interaction terms were not included due to insufficient sample sizes)	N/A	Number of parameters in the model was smaller than number of effect sizes.
	15.3	Describe any process of model selection	Yes	Simplest models' structure were kept as neither climatic variables nor core covariates helped to decrease unexplained variability.
Publication bias and sensitivity analyses	16.1	Describe assessments of the risk of bias due to missing results (e.g. publication, time-lag, and taxonomic biases)	Yes	Differences in sample size between native and invasive ES, the majority of the studies coming from North America, particularly, United States. Visual investigation of bias via Funnel plots are presented in Figure S 2.2, and map in Figure S 2.4
	16.2	Describe any steps taken to investigate the effects of such biases (if present)	Yes	
	16.3	Describe any other analyses of robustness of the results, e.g. due to effect size choice, weighting or analytical model assumptions, inclusion or exclusion of subsets of the data, or the inclusion of alternative moderator variables in meta-regressions	Yes	Egger's regression test was performed.
Clarification of post hoc analyses	17.1	When hypotheses were formulated after data analysis, this should be acknowledged.	NA: there are no hypotheses that were formed after data collection	
Metadata, data, and code	18.1	Share metadata (i.e. data descriptions)	Yes	Both data and reproducible code are publicly available.
	18.2	Share data required to reproduce the results presented in the manuscript	Yes	Both data and reproducible code are publicly available.
	18.3	Share additional data, including information that was not presented in the manuscript (e.g. raw data used to calculate effect sizes, descriptions of where data were located in papers)	Yes	Both data and reproducible code are publicly available.

Checklist item	Sub-item#	Sub-item description	Reported?	Notes
	18.4	Share analysis scripts (or, if a software package with graphical user interface (GUI) was used, then describe full model specification and fully specify choices)	Yes	Both data and reproducible code are publicly available.
Results of study selection process	19.1	Report the number of studies screened	Yes	Figure S 2.1 in the SM.
	19.2	Report the number of studies excluded at each stage of screening	Yes	Figure S 2.1 in the SM.
	19.3	Report brief reasons for exclusion from the full text stage	Yes	Figure S 2.1 in the SM.
	19.4	Present a Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA)-like flowchart (www.prisma-statement.org).	Yes	Figure S 2.1 in the SM.
Sample sizes and study characteristics	20.1	Report the number of studies and effect sizes for data included in meta-analyses	Yes	Results
	20.2	Report the number of studies and effect sizes for subsets of data included in meta-regressions	Yes	Results
	20.3	Provide a summary of key characteristics for reported outcomes (either in text or figures; e.g. one quarter of effect sizes reported for vertebrates and the rest invertebrates)	Yes	Results
	20.4	Provide a summary of limitations of included moderators (e.g. collinearity and overlap between moderators)	N/A	Covariates were not included in the models as explained above.
	20.5	Provide a summary of characteristics related to individual study quality (risk of bias)	Yes	Results and supplementary material
Meta-analysis	21.1	Provide a quantitative synthesis of results across studies, including estimates for the mean effect size, with confidence/credible intervals	Yes	
Heterogeneity	22.1	Report indicators of heterogeneity in the estimated effect (e.g. I^2, tau^2 and other variance components)	Yes	Text S2 in the SM.
Meta-regression	23.1	Provide estimates of meta-regression slopes (i.e. regression coefficients) and confidence/credible intervals	Yes	All graphs represent mean effect sizes and respective credible or predictive intervals. All parameter

Checklist item	Sub-item#	Sub-item description	Reported?	Notes
				values from the analyses are reported in Text S2
	23.2	Include estimates and confidence/credible intervals for all moderator variables that were assessed (i.e. complete reporting)	No	Covariates were not included in the models as explained above.
	23.3	Report interactions, if they were included	NA: no interactions were included	
	23.4	Describe outcomes from model selection, if done (e.g. R2 and AIC)	Yes	Simplest models' structure were kept as neither climatic variables nor core covariates helped to decrease unexplained variability.
Outcomes of publication bias and sensitivity analyses	24.1	Provide results for the assessments of the risks of bias (e.g. Egger's regression, funnel plots)	Yes	Funnel plots are presented in Figure S 2.2.
	24.2	Provide results for the robustness of the review's results (e.g. subgroup analyses, meta-regression of study quality, results from alternative methods of analysis, and temporal trends)	Yes	Figures S 2.3, S 2.5-S 2.13.
Discussion	25.1	Summarise the main findings in terms of the magnitude of effect	Yes	
	25.2	Summarise the main findings in terms of the precision of effects (e.g. size of confidence intervals, statistical significance)	Yes	
	25.3	Summarise the main findings in terms of their heterogeneity	Yes	
	25.4	Summarise the main findings in terms of their biological/practical relevance	Yes	
	25.5	Compare results with previous reviews on the topic, if available	Yes	
	25.6	Consider limitations and their influence on the generality of conclusions, such as gaps in the available evidence (e.g. taxonomic and geographical research biases)	Yes	Single vs. multiple invader problem is discussed in the Dicussion. Geographical research biases are briefly discussed in the Conclusion
Contributions and funding	26.1	Provide names, affiliations, and funding sources of all co-authors	Yes	
	26.2	List the contributions of each co-author	Yes	
	26.3	Provide contact details for the corresponding author	Yes	

Checklist item	Sub-item#	Sub-item description	Reported?	Notes
	26.4	Disclose any conflicts of interest	NA: there were no conflicts of interest	
References	27.1	Provide a reference list of all studies included in the systematic review or meta-analysis	Yes	
	27.2	List included studies as referenced sources (e.g. rather than listing them in a table or supplement)	No	The complete references of the articles included in our meta-analysis are reported in the List S4 in the SM.

Table S 2.3: Egger's test results. Results of Egger's test performed on estimated effect sizes (ES) for invasive species and native community performance, and abiotic effect size. *: statistically significant result as confidence interval does not include zero.

ES type	Intercept	Confidence interval	t	p
Invasive species	12.4	6.42—18.5*	4.07	0.0000642
Native community	-9.13	-26—7.74	-1.08	0.285
Abiotic	1.28	-4.87—7.43	0.412	0.681

Figure S 2.1: PRISMA flowchart. PRISMA flowchart (http://www.prisma-statement.org/) with the selection criteria and the number of articles included or excluded at each step.

| Criteria for inclusion | Excluded |

Identification

Initial pool of records using terms:'invasi* OR invade* OR alien OR exotic OR ruderal OR weed OR non-native OR nonnative OR introduced OR naturaliz* OR nonindigenous OR non-indigenous' AND 'shrub OR scrub OR bush OR brush OR "woody plant*"' AND 'forest OR forests"
(n = 3,389)

Books and book sections (n = 113)
Review or comments (n = 157)
Retractions (n = 2)

Screening

Title and abstract were screened to ensure the study's system was a forest and the invasive species was a shrub. Records with non-clear definitions of those were kept for the next stage.
(n = 3,117)

Related to paleoecology (n = 65)
Not a forest system AND invasive shrub (n = 2,320)

Eligibility

Full texts were assessed for eligibility:
1) Study was conducted in a forest system and investigated invasive shrub; AND
2) Study reports two levels of invasion; AND
3) Study provide information on associated native community performance or abiotic; feature of the native community when under the two levels of invasion.
(n = 797)

Study did not meet all the eligibility criteria (n = 632)
Study reported the presence and absence of the invader (n = 33)
Full text was inaccessible (n = 8)

Included

Studies included in the quantitative synthesis and had the data extracted
(n = 124)

Figure S 2.2: Funnel plots. Funnel plots of estimated effect sizes (ES) for invasive species and native community performance, and abiotic effect size.
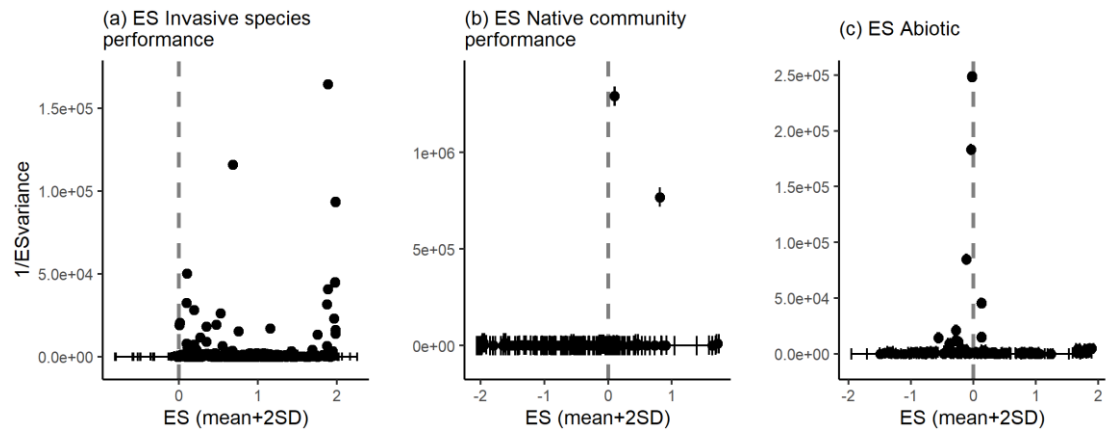
Figure S 2.3: Invasive shrub and native community performance as a functions of covariates. Mean effect size (ES) with 95% credible interval of invasive species (purple circles) and native community (pink diamonds) performance as a function of different categorical variables extracted from articles: (a) study type, (b) global ecoregion [60], (c) forest community, (d) forest type, (e) presence and type (f) of disturbance. Credible intervals that do not cross zero are statically significant and denoted with solid dots, and hollow dots represent non-significant ES.
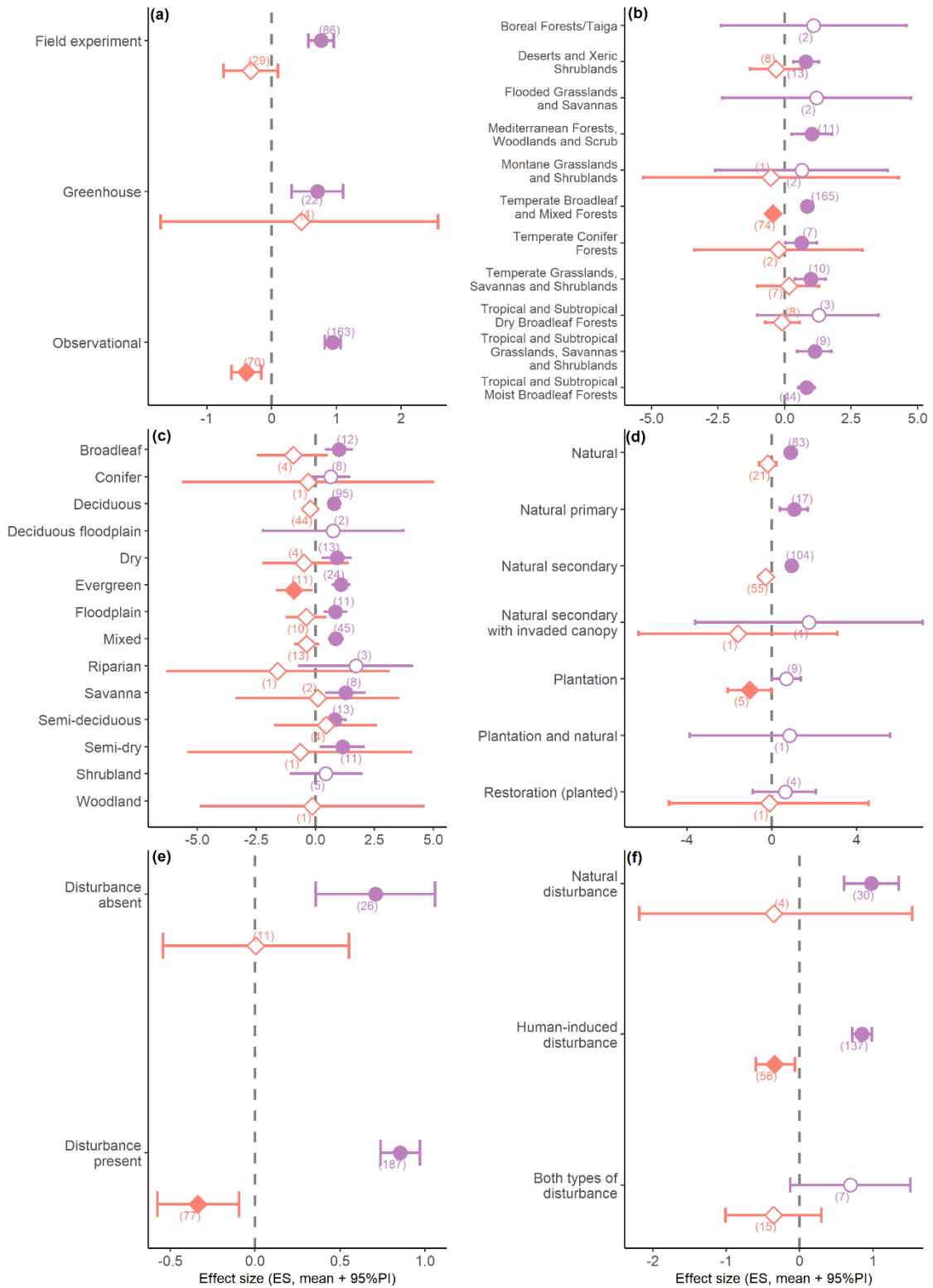
Figure S 2.4: World map of unique study sites included in the meta-analysis.

World map of study sites included in the meta-analysis
(124 studies from 24 countries)
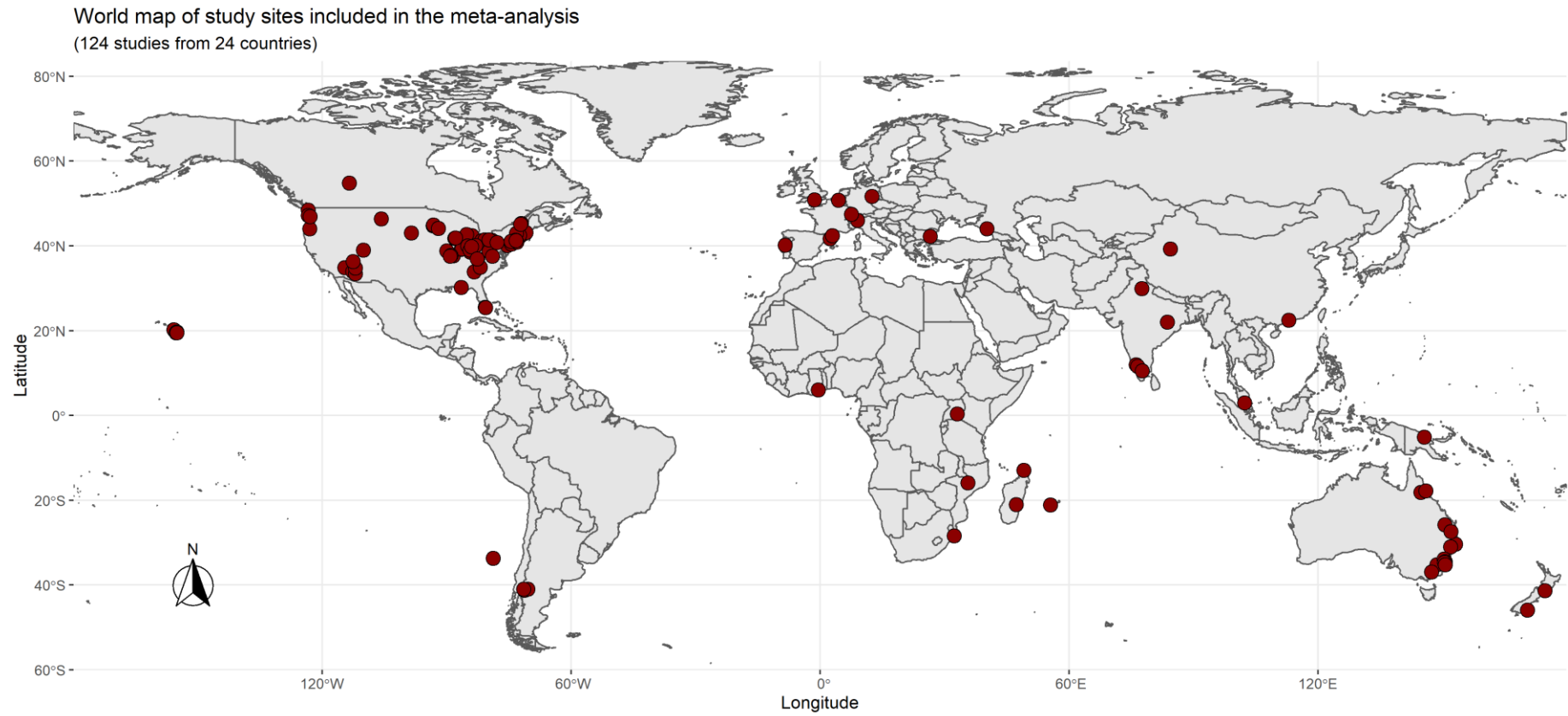
Figure S 2.5: Disturbance and invasive shrubs and native community performance. Mean effect size (ES) with 95% credible interval (CI) of invasive species (purple circles) and native community (pink diamonds) performance as a function of disturbance and disturbance type nested within mechanism of invasion. Data points with a single observation represent the observed ES value with respective calculated CI.
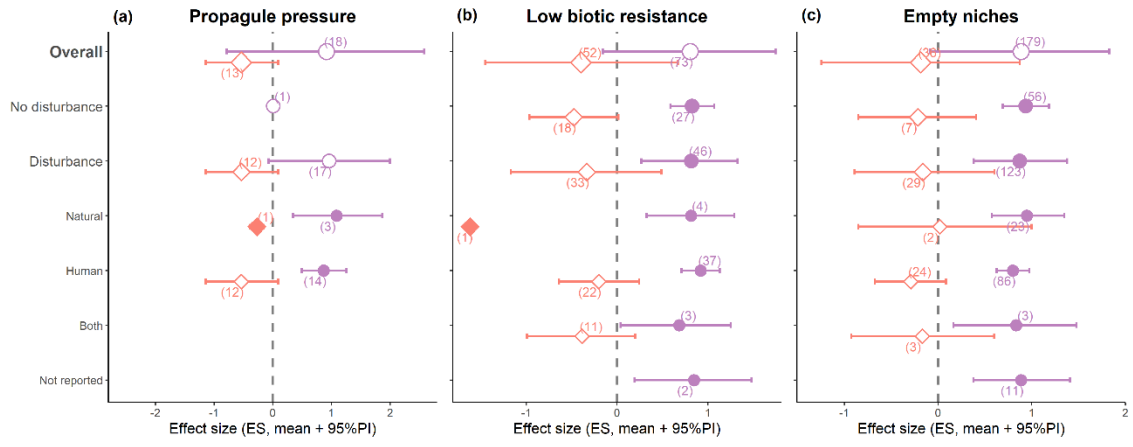
Figure S 2.6: Association between the estimated effect size of invasive species performance and recorded metrics.
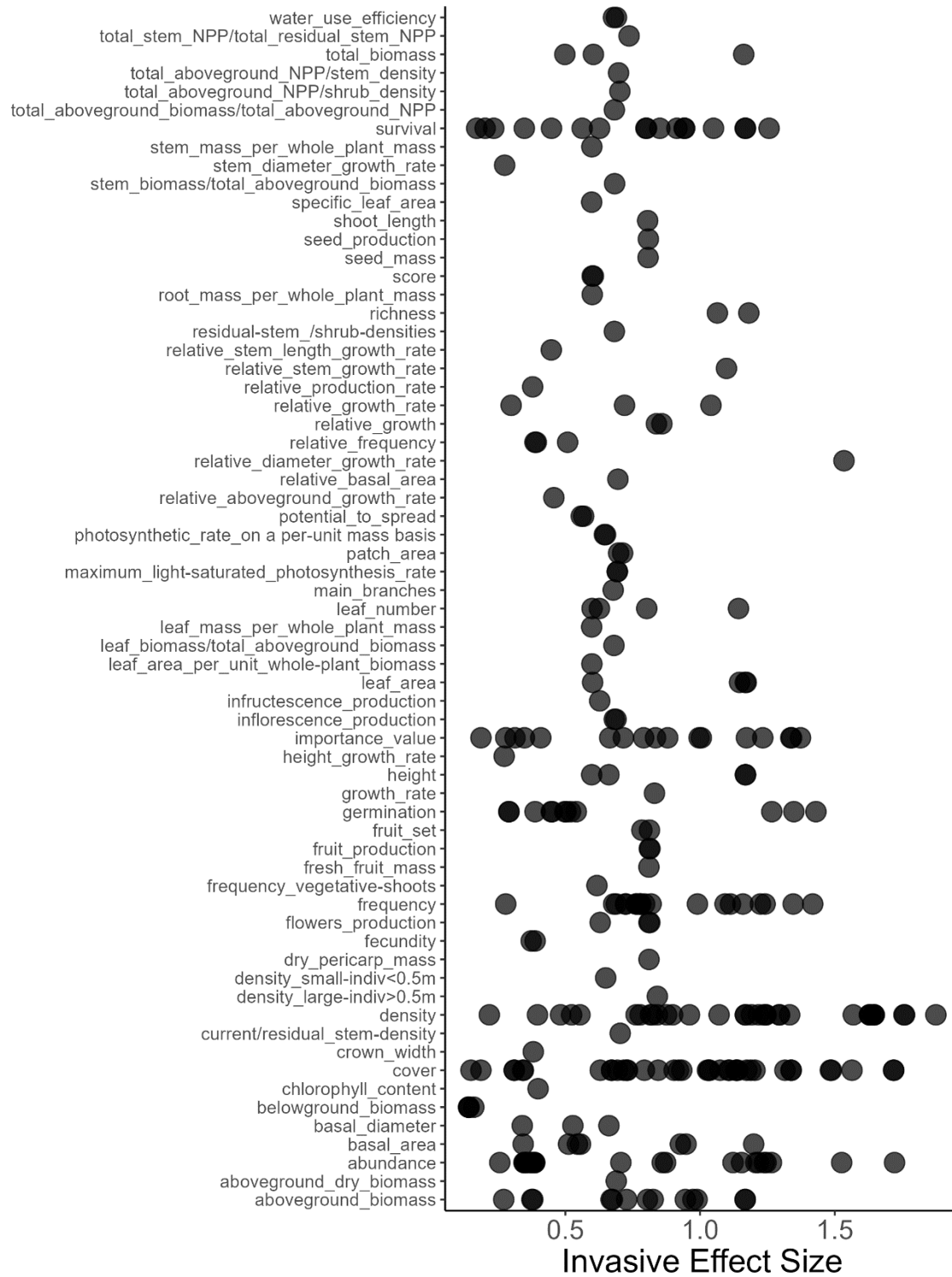
Figure S 2.7: Association between the estimated effect size of native community performance and recorded metrics.
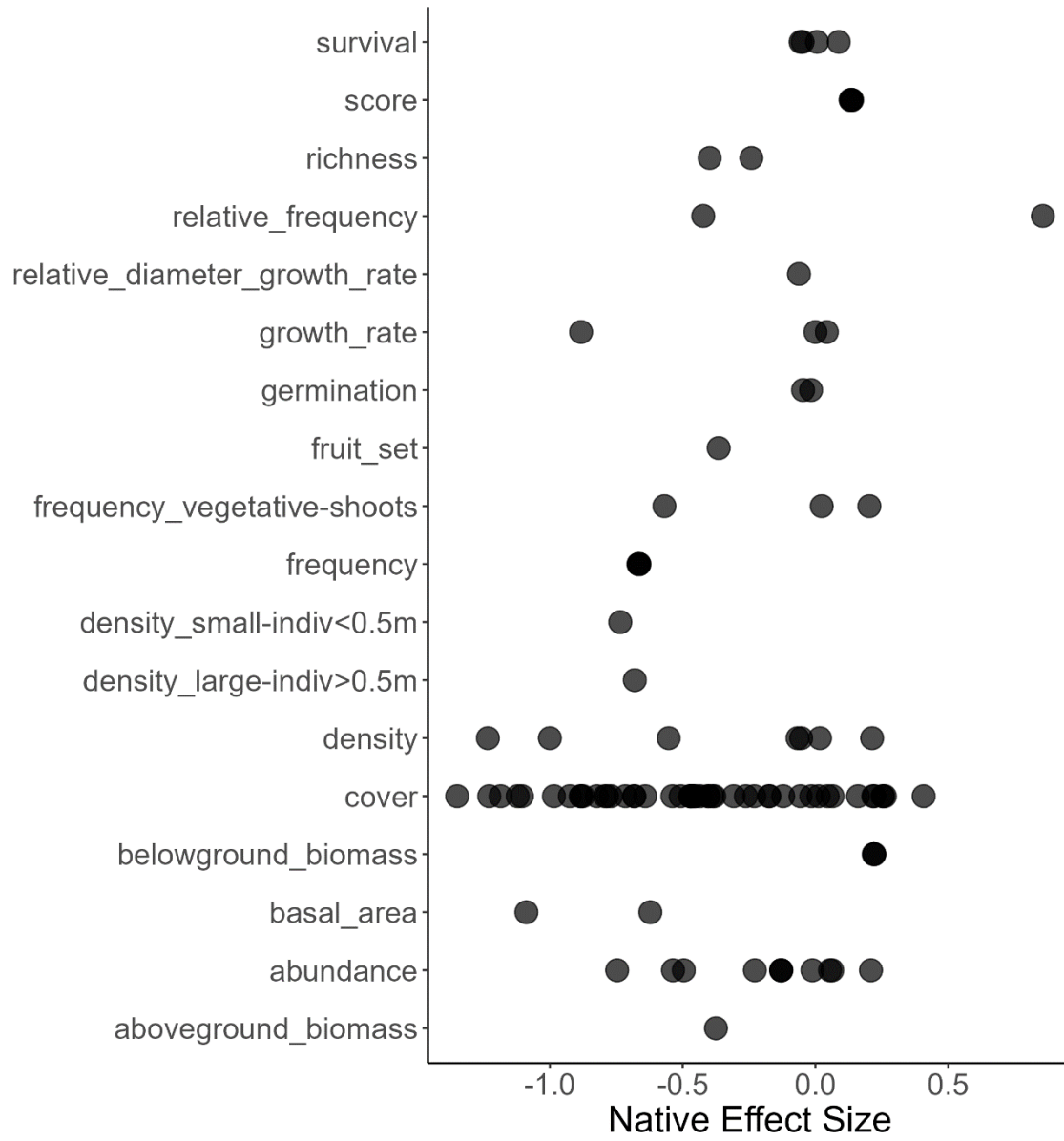
Figure S 2.8: Association between the estimated abiotic effect size and recorded metrics.
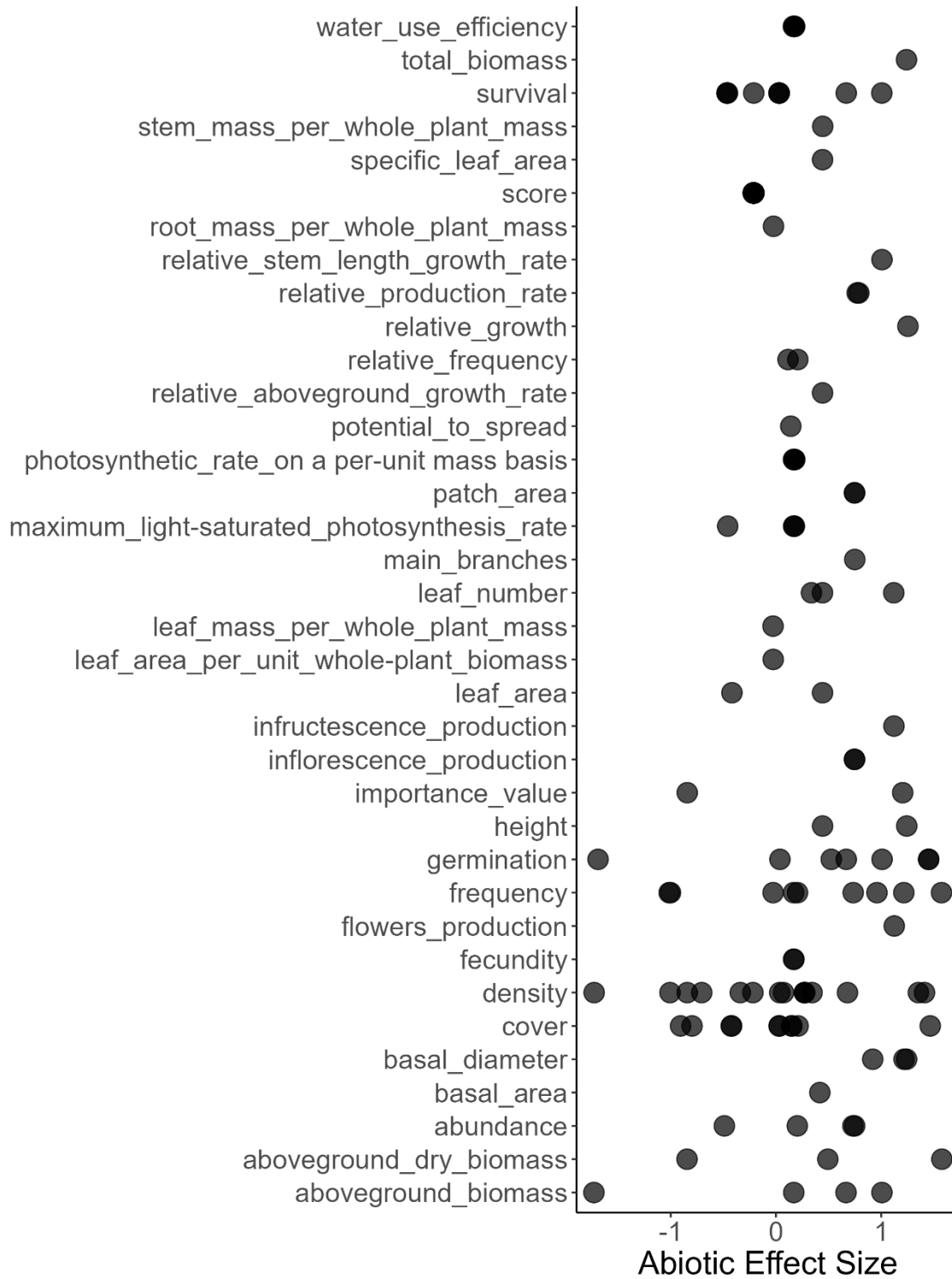
Figure S 2.9: Correlation values between the estimated effect size of invasive species performance and climatic variables or year of data collection.
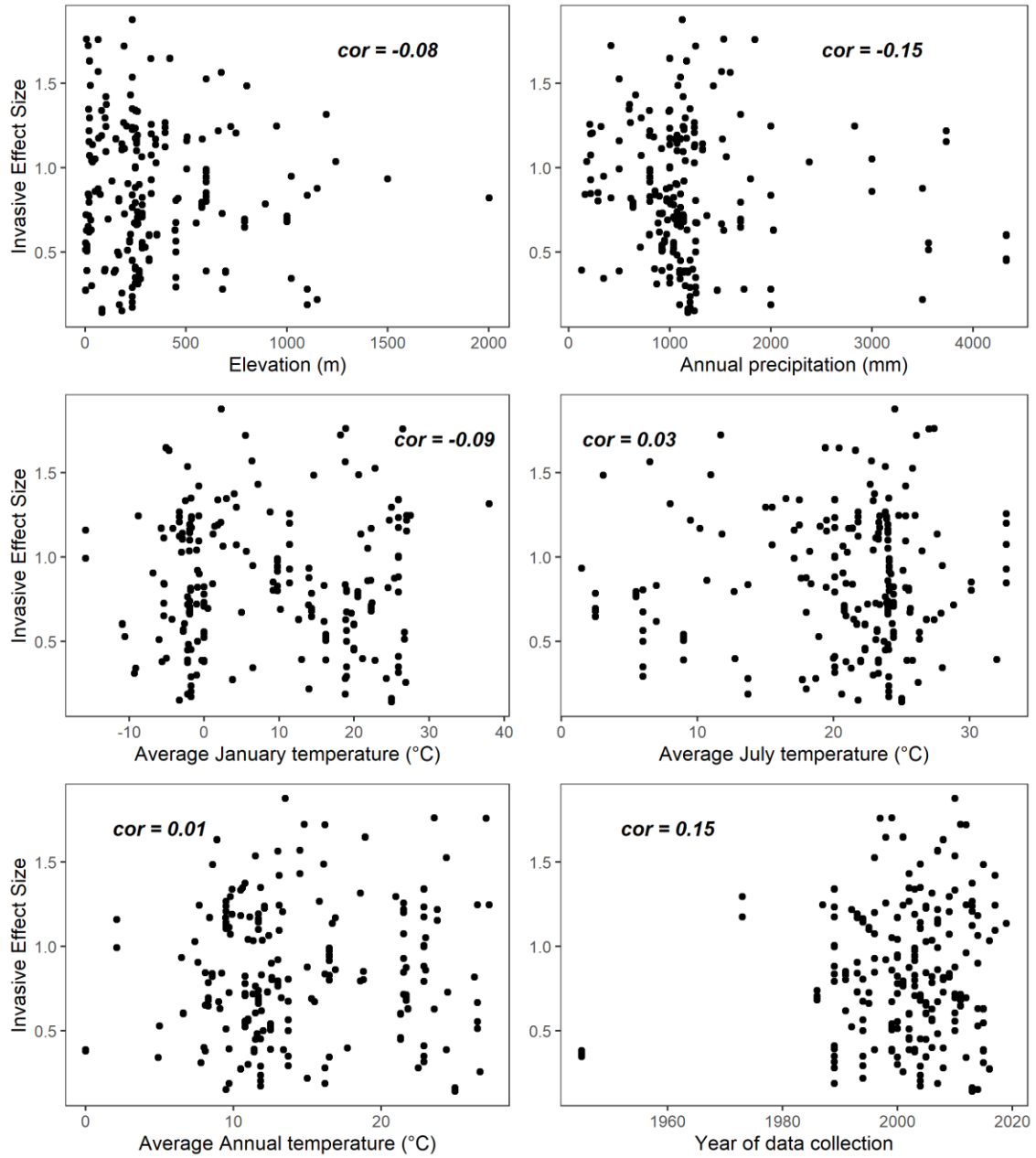
Figure S 2.10: Correlation values between the estimated effect size of native community performance and climatic variables or year of data collection.
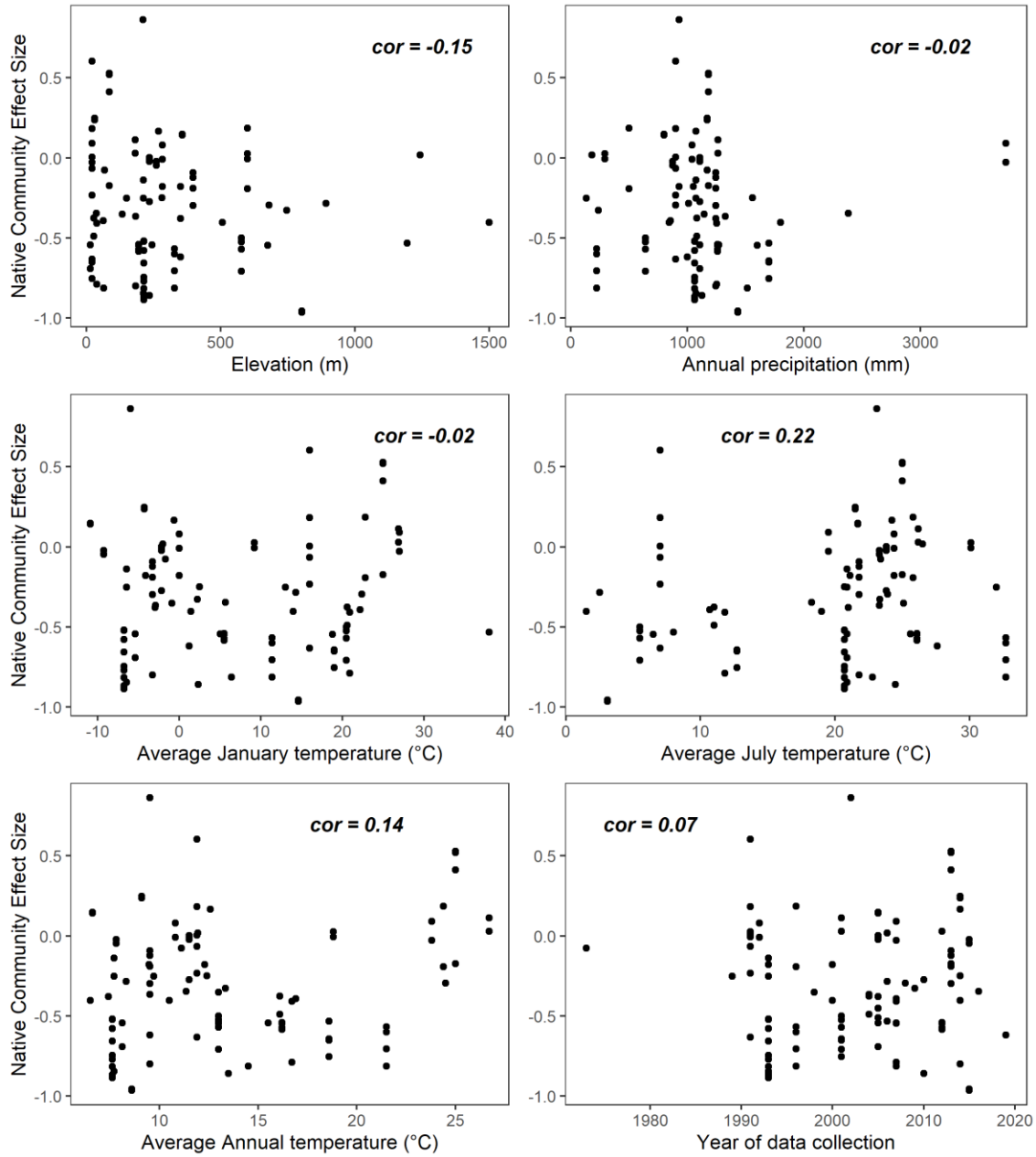
Figure S 2.11: Correlation values between the estimated abiotic effect size and climatic variables or year of data collection.
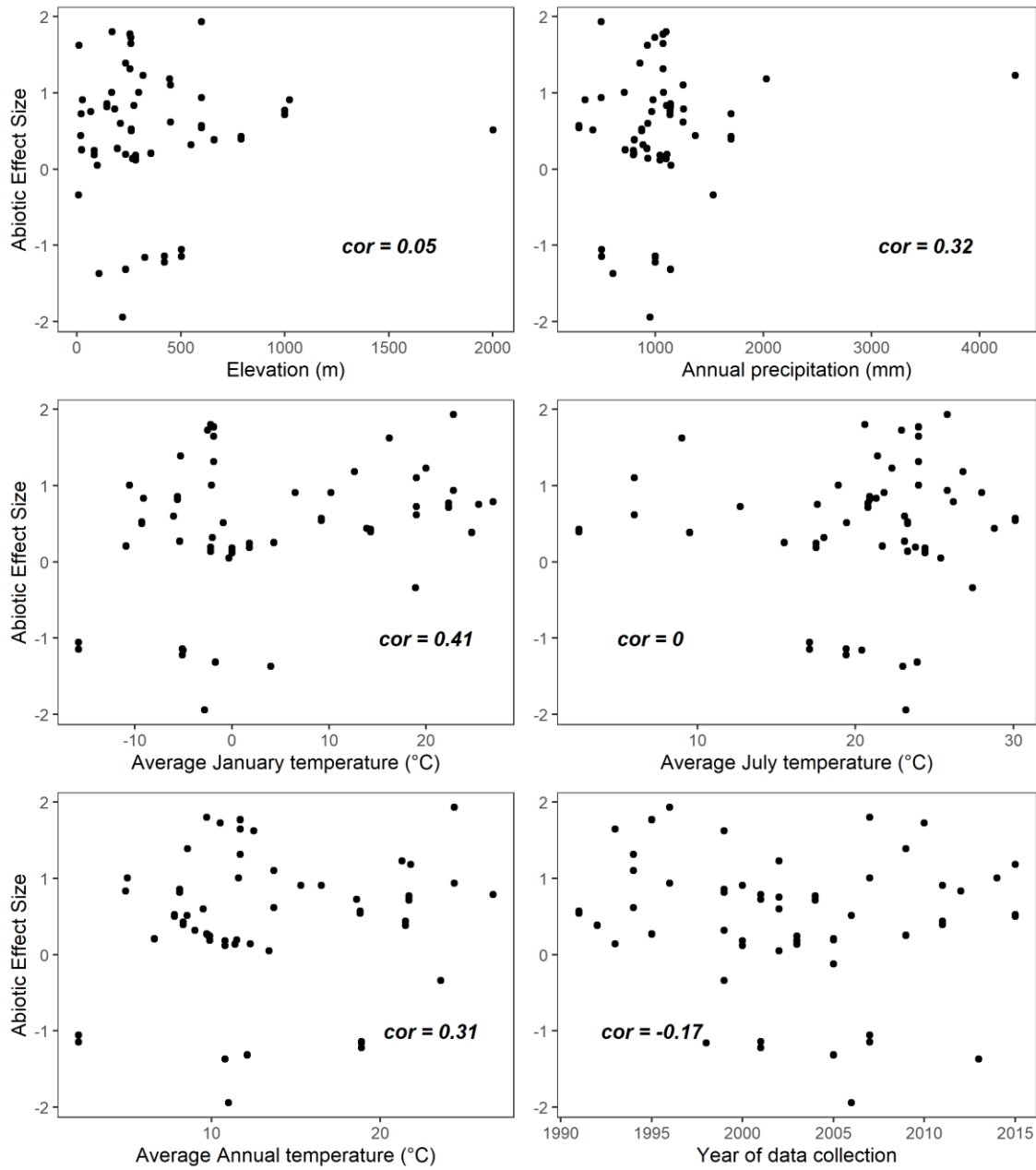
Figure S 2.12: Residuals from model that investigates invasion performance as a function of mechanism of invasion (Q1, Equation 3) as a function of covariates. Global ecoregion: A - Boreal Forests/Taiga, B - Deserts and Xeric Shrublands, C - Flooded Grasslands and Savannas, D - Mediterranean Forests, Woodlands and Scrub, E - Montane Grasslands and Shrublands, F - Temperate Broadleaf and Mixed Forests, G - Temperate Conifer Forests, H - Temperate Grasslands, Savannas and Shrublands, I - Tropical and Subtropical Dry Broadleaf Forests, J - Tropical and Subtropical Grasslands, Savannas and Shrublands, K - Tropical and Subtropical Moist Broadleaf Forests. Forest Community: AA - broadleaf, BB - conifer, CC - deciduous, DD – deciduous floodplain mixed, EE - dry, FF - evergreen, GG - floodplain, HH - mixed, II - riparian, JJ - savanna, KK – semi-deciduous, LL – semi-dry, MM - shrubland. Forest type: AAA - natural, BBB – natural primary, CCC – natural secondary, DDD – natural secondary with invaded canopy, EEE - plantation, FFF – plantation and natural, GGG – restoration (planted).
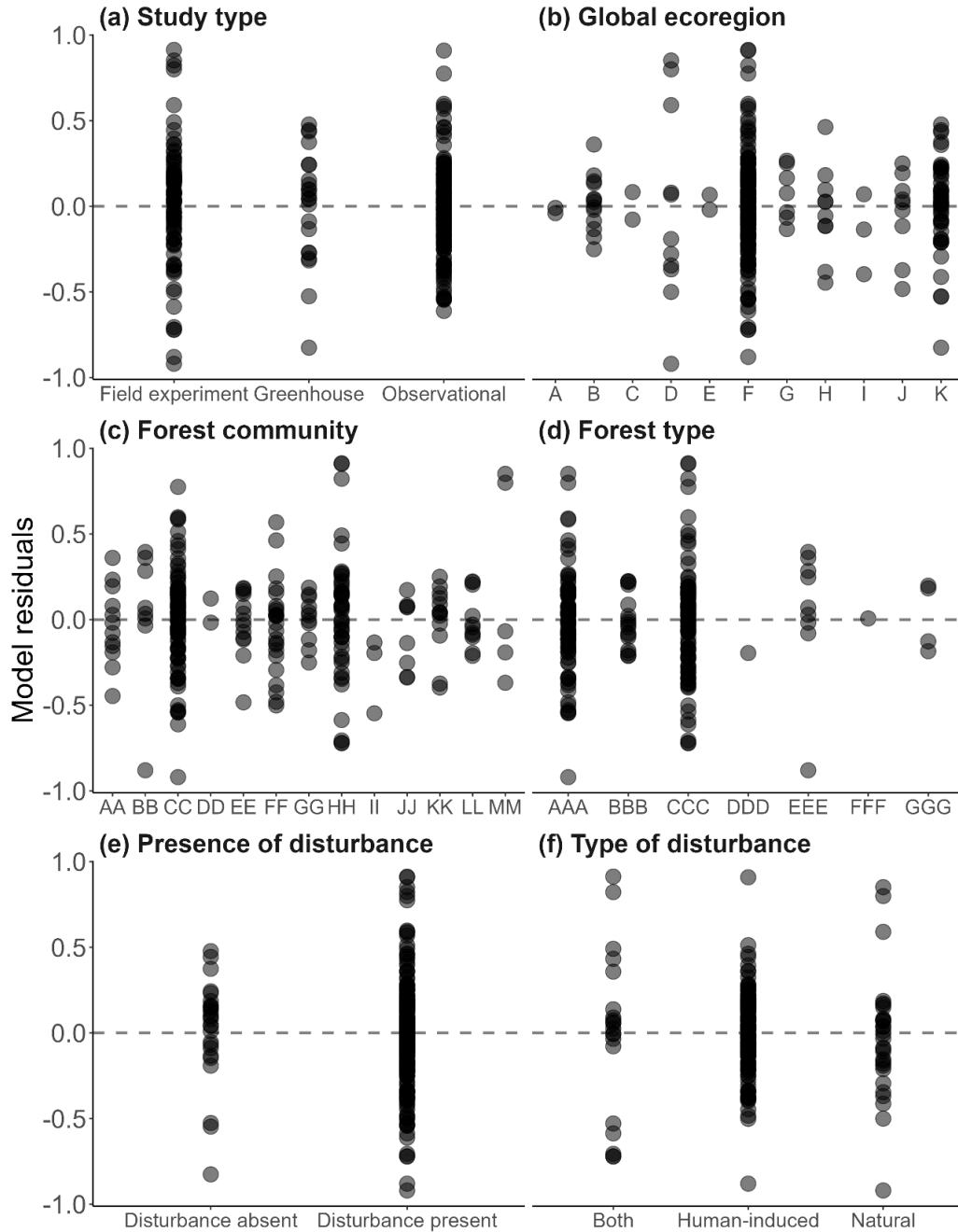
Figure S 2.13: Residuals from model that investigates native community performance as a function of mechanism of invasion (Q1, equivalent of Equation 3) as a function of covariates. Global ecoregion: A - Deserts and Xeric Shrublands, B - Montane Grasslands and Shrublands, C - Temperate Broadleaf and Mixed Forests, D - Temperate Conifer Forests, E - Temperate Grasslands, Savannas and Shrublands, F - Tropical and Subtropical Moist Broadleaf Forests. Forest Community: AA - broadleaf, BB - conifer, CC – deciduous, DD - deciduous floodplain mixed, EE - dry, FF - evergreen, GG - floodplain, HH - mixed, II - riparian, JJ - savanna, KK – semi-deciduous, LL – semi-dry, MM - shrubland, NN - woodland. Forest type: AAA - natural, BBB – natural secondary, CCC – natural secondary with invaded canopy, DDD - plantation, EEE – restoration (planted).
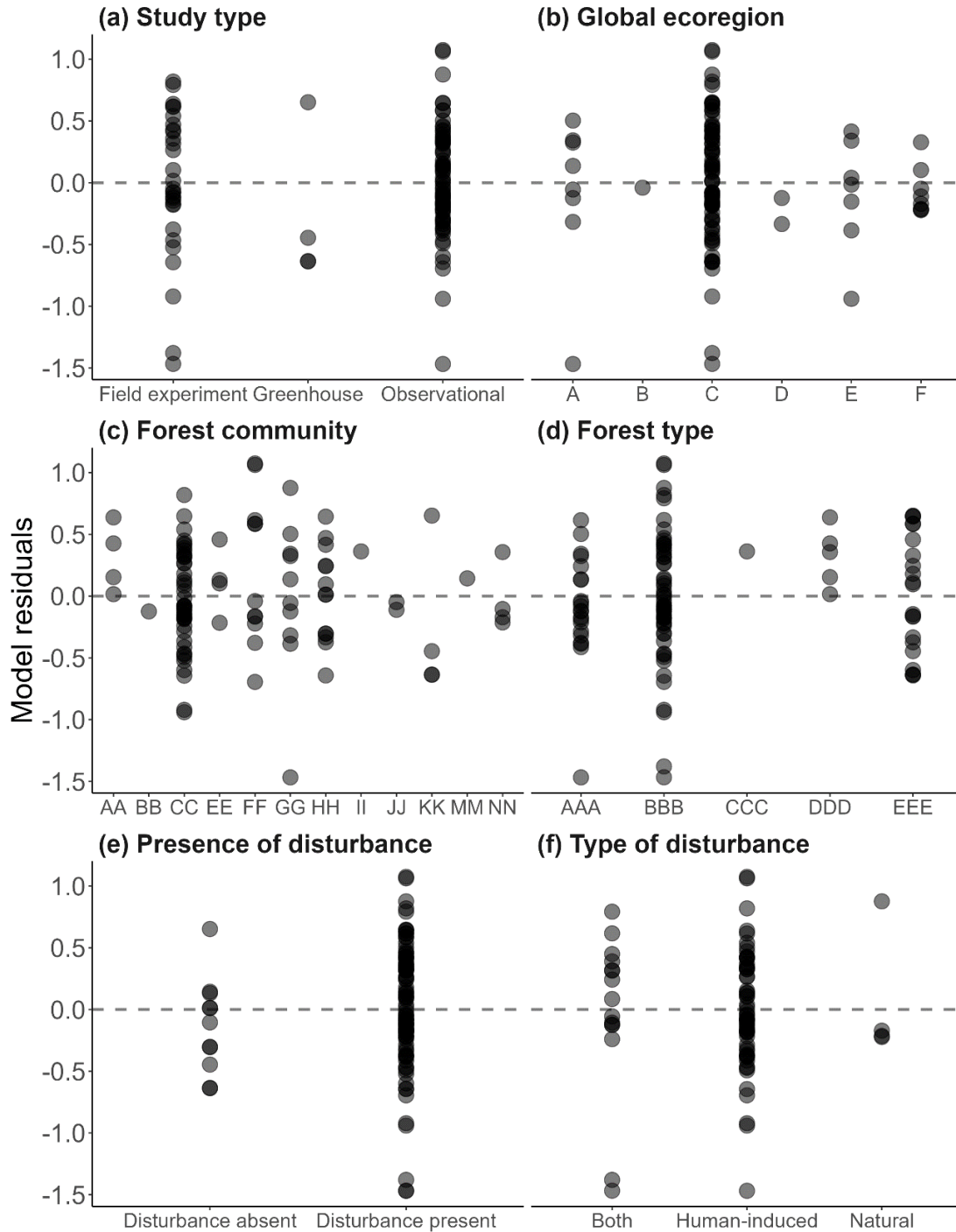
Figure S 2.14: Residuals from model that investigates which abiotic conditions invasive shrubs are taking advantage of in forests understories (Q2, Equation 5) as a function of covariates. Global ecoregion: A - Boreal Forests/Taiga, B - Deserts and Xeric Shrublands, C - Flooded Grasslands and Savannas, D - Mediterranean Forests, Woodlands and Scrub, E - Temperate Broadleaf and Mixed Forests, F - Temperate Conifer Forests, G - Temperate Grasslands, Savannas and Shrublands, H - Tropical and Subtropical Grasslands, Savannas and Shrublands, I - Tropical and Subtropical Moist Broadleaf Forests. Forest Community: AA - broadleaf, BB - conifer, CC - deciduous, DD – deciduous floodplain mixed, EE - dry, FF - evergreen, GG - floodplain, HH - mixed, II – riparian, JJ - savanna, KK – semi-deciduous. Forest type: AAA - natural, BBB – natural primary, CCC – natural secondary, DDD - plantation.
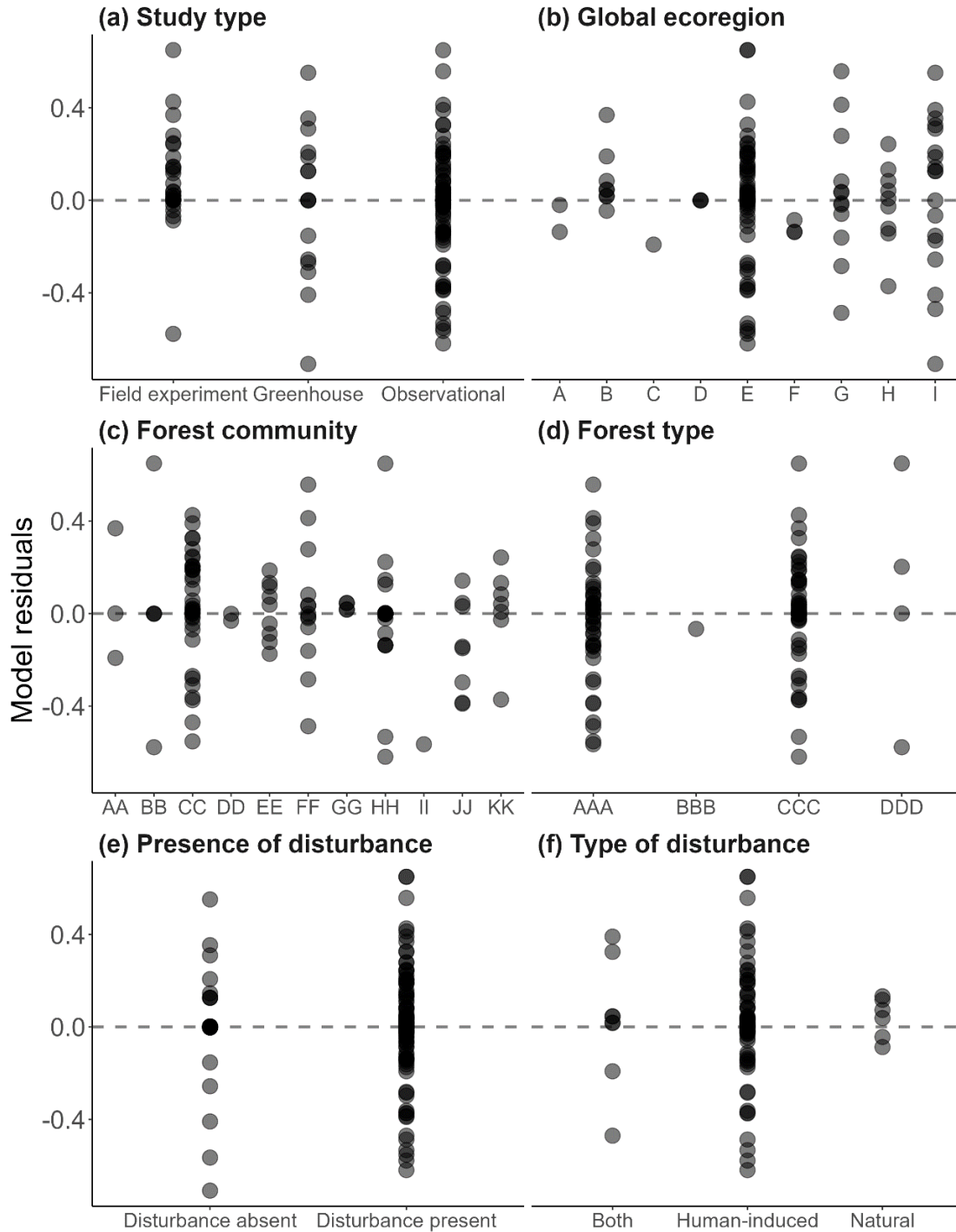
Figure S 2.15: Residuals from model that investigates if impact of invasion on the native community is associated with invasive performance and dependent on the invasion mechanism (Q3, Equation 7) as a function of covariates. Global ecoregion: A - Deserts and Xeric Shrublands, B - Montane Grasslands and Shrublands, C - Temperate Broadleaf and Mixed Forests, D - Temperate Conifer Forests, E - Temperate Grasslands, Savannas and Shrublands, F - Tropical and Subtropical Moist Broadleaf Forests. Forest Community: AA - broadleaf, BB - conifer, CC - deciduous, DD - dry, EE - evergreen, FF - floodplain, GG - mixed, HH - riparian, II - savanna, JJ – semi-deciduous, KK - shrubland, LL - woodland. Forest type: AAA - natural, BBB – natural secondary, CCC – natural secondary with invaded canopy, DDD - plantation, EEE – restoration (planted).
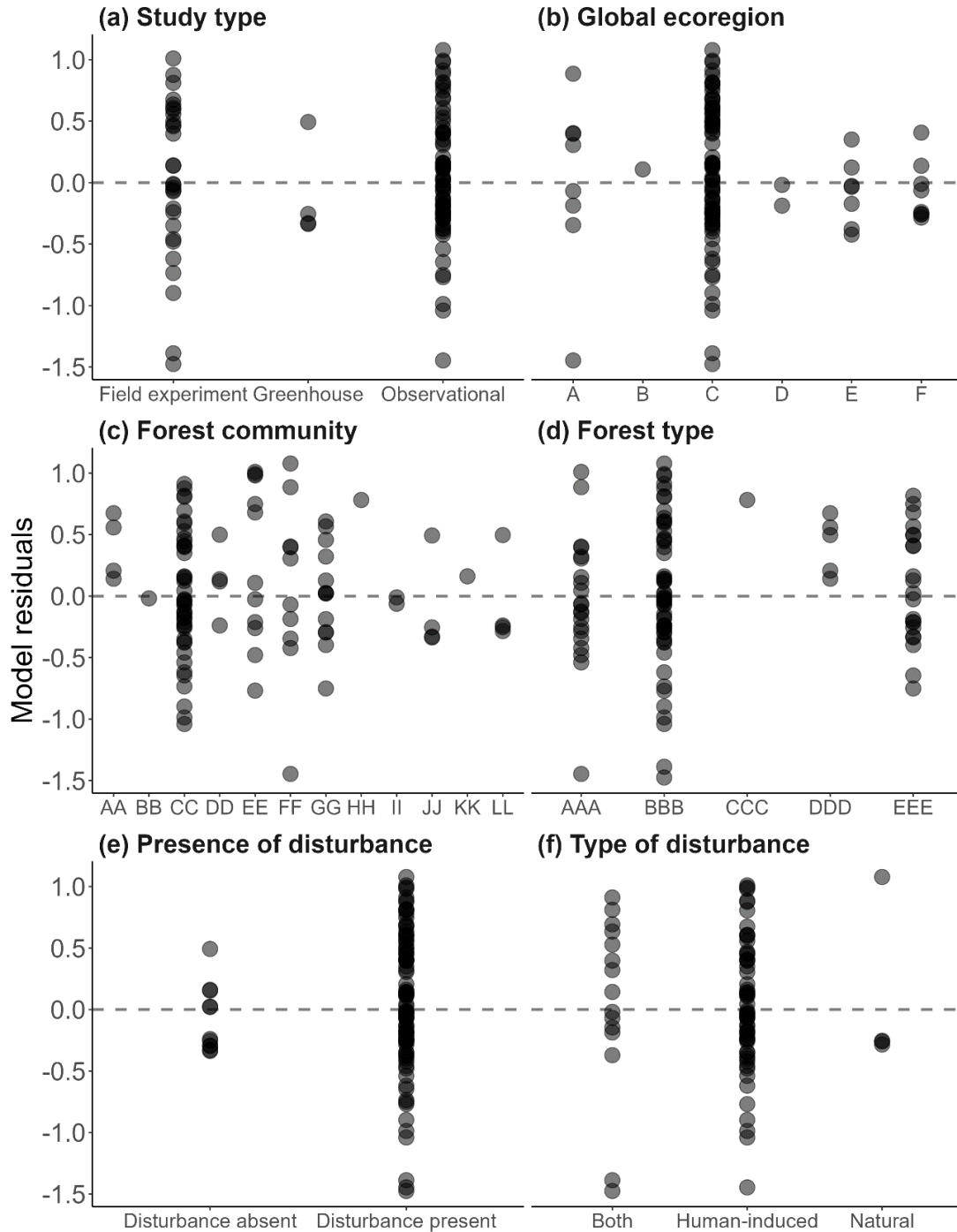
Figure S 2.16: Residuals from model that investigates if impact of invasion on the native community is associated with invasive performance and dependent on single or multiple invading species (Q3, equivalent of Equation 7) as a function of covariates. Global ecoregion: A - Deserts and Xeric Shrublands, B - Montane Grasslands and Shrublands, C - Temperate Broadleaf and Mixed Forests, D - Temperate Conifer Forests, E - Temperate Grasslands, Savannas and Shrublands, F - Tropical and Subtropical Moist Broadleaf. Forest Community: AA - broadleaf, BB - conifer, CC - deciduous, DD - dry, EE - evergreen, FF - floodplain, GG - mixed, HH – riparian, II - savanna, JJ – semi-deciduous, KK - shrubland, LL - woodland. Forest type: AAA – natural, BBB – natural secondary, CCC – natural secondary with invaded canopy, DDD - plantation, EEE – restoration (planted).
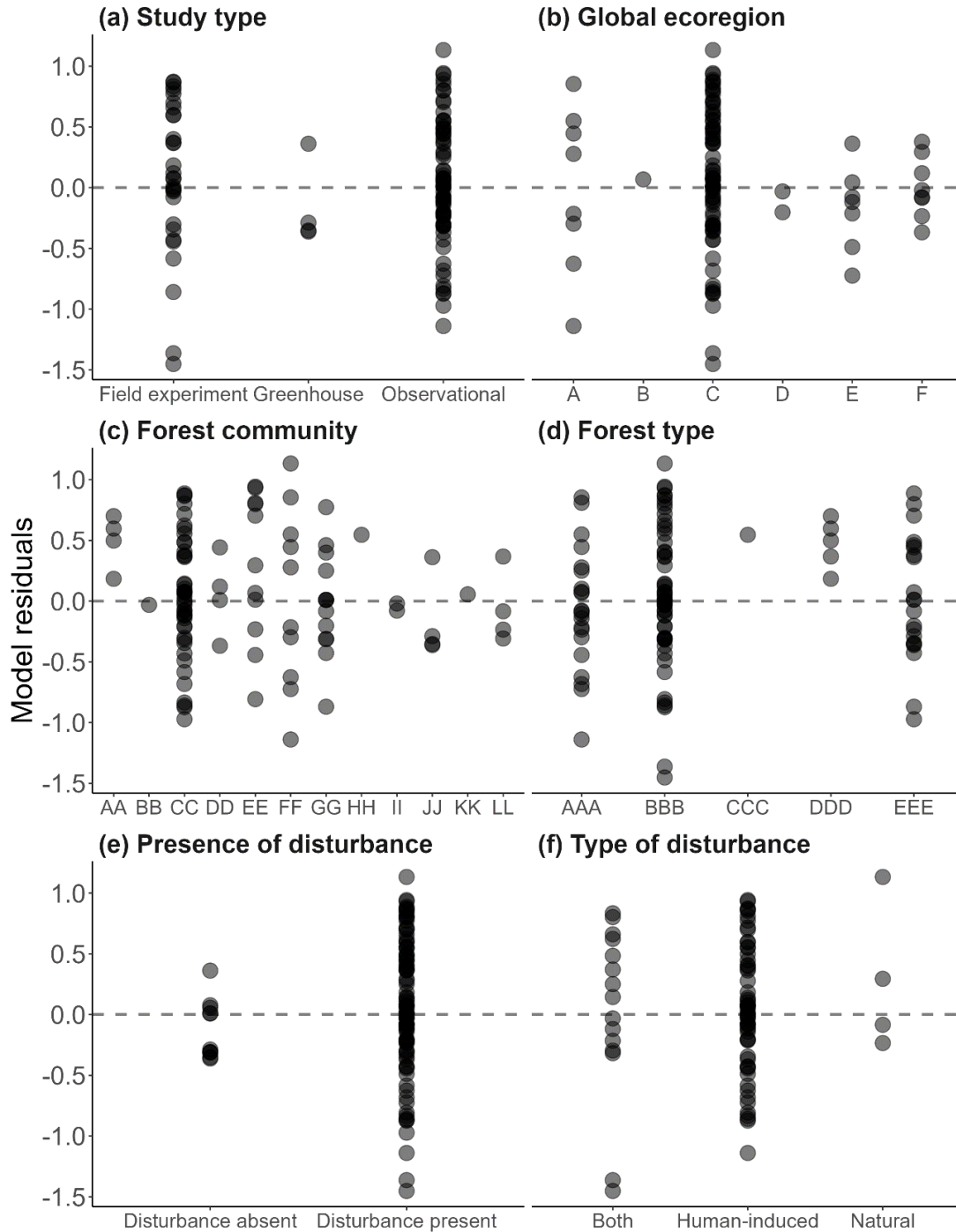
Code S 2.1: Code of models to simulate effect sizes (ES) in OpenBUGS. The code for analysis can be found in https://github.com/laispetri/ShrubInvasionInForests_Meta-analysis.

ES estimate: invasive species performance (full analysis)
```
model{

for(i in 1:J) { #J = number of observations with variance

TC[i] <- Invconttau[i]*NcontInv[i]
TI[i] <- Invtreattau[i]*NtreatInv[i]

Control[i]~dnorm(InvContmean[i], TC[i])C(0,)
Treat[i]~dnorm(InvTreatmean[i], TI[i])C(0,)

aveESInv[i]<-(Treat[i]-Control[i])/((Treat[i]+Control[i])/2)
}
}
```
ES estimate: native community performance
```
model{

for(i in 1:J) { #J = number of observations with variance

TC[i] <- max(0.0001,Natconttau[i])*NcontNat[i]
TI[i] <- max(Nattreattau[i],0.0001)*NtreatNat[i]

Control[i]~dnorm(NatContmean[i], TC[i])C(0,)
Treat[i]~dnorm(NatTreatmean[i], TI[i])C(0,)

aveESNat[i]<-(Treat[i]-Control[i])/((Treat[i]+Control[i])/2)
}
}
```
ES estimate: abiotic resources
```
model{

for(i in 1:J = ) { # J = number of observations with variance

TC[i] <- max(0.0001,Natconttau[i])*NcontNatA[i]
TI[i] <- max(Nattreattau[i], 0.0001)*NtreatNatA[i]

Control[i]~dnorm(NatContmeanA[i], TC[i])C(0,)
Treat[i]~dnorm(NatTreatmeanA[i], TI[i])C(0,)

aveESNat[i]<-(Treat[i]-Control[i])/((Treat[i]+Control[i])/2)
}
}
```

2.9.1 References

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Chapter 3 Successful Recovery of Native Plants After Invasive Removal in Forest Understories is Driven by Native Richness, High SLA Species, and Low Drought Stress, Rather Than Restoration Treatments

3.1 Abstract

Temperate forest understories hold the majority of the diversity present in these ecosystems and play an essential role in the recruitment and establishment of native trees. However, the long-term persistence of healthy forest understories is threatened by the impacts of invasive plants. As a result, a common practice is the removal of the agent of invasion. However, we know little about the success of these practices and a lack understanding of what shapes the recovery of the native community post-invasive species removal. In a multi-year field experiment, we investigated whether (Q1) native seeding after invasive plant removal would enhance native community recovery, (Q2) what the characteristics of the recovering community are, and (Q3) under which environmental conditions recovery rates are faster. After an initial removal of invasives, we seeded native species to manipulate assembly history and mimic restoration practices and removed invasive species annually in half of the treatments in a full-factorial design. We collected data on plant species composition and abundance (i.e., species level percent cover), which we linked to leaf trait data, and to environmental conditions (i.e., light and soil water availability) in the three subsequent summers. Our results show that native community recovery rates were independent of seeding additions or frequency of invasive plant removal. The fastest rates of recovery were associated with high native species richness, native communities with higher values of specific leaf area (SLA), and low drought stress years. Our

results suggest that restoration practices post-invasive plant removal should be tailored to enhance natural dispersal or artificial addition if the resident community is species-poor, of native species with traits compatible with high resource availability, such as species with high SLA. In addition to the importance of the native community characteristics, our results underscore the need for assessing environmental conditions, favoring management practices during years of low drought stress to maximize native community recovery.

3.2 Introduction

Native plant species recruitment is essential for maintaining healthy forest ecosystems (Clark *et al.* 1999). However, forested lands in human-modified landscapes are often subjected to multiple novel stressors, i.e., fragmentation, pollution, and introduced species (Vilà & Ibáñez 2011). Among these stressors, invasive species have the potential to interfere with native plant recruitment (Link *et al.* 2018). Under those conditions, removing the invasive species is a common management practice (Kettenring & Adams 2011), but the potential lack of native propagules and site degradation associated with human activities could hinder the system's recovery (Smith, Kelly & Finch 2006; Schuster, Wragg & Reich 2018). In this context, the same invasive species, or others, might be well positioned to establish and fully benefit from the temporary weak competitive interactions associated with plant removal (Pearson *et al.* 2016). Promoting an early arrival of native species, i.e., priority effects, could then prevent re-invasion and boost the recovery of the native community (Fukami, Mordecai & Ostling 2016; Byun, de Blois & Brisson 2018). However, there is little empirical evidence that priority effects would be sufficient to restore forest understories after invasive plant management (Fukami, Mordecai & Ostling 2016; Weidlich *et al.* 2021). Furthermore, there is little knowledge about what features of the native community may affect its recovery post invasive plant removal. Still, understanding

these mechanisms is critical for ensuring successful restoration of a healthy understory. To address this knowledge gap, we leveraged data from a multi-year field experiment where we removed invasive plants and seeded native species mimicking restoration practices. We then tested if priority effects could be a successful mechanism of forest recovery and assessed the features of the native community that led to faster recovery.

Natural forest regeneration is a critical stage for maintaining forest composition and function (Grubb 1977; Clark *et al.* 1999; Green, Harms & Connell 2014). However, natural regeneration can be negatively impacted by novel stressors associated with rapidly changing climate, modified landscapes, and new species assemblages (Dyderski & Jagodzinski 2018; Vasquez-Grandon, Donoso & Gerding 2018). Global warming has resulted in increasingly dry conditions, which are likely to decrease the establishment and survival of tree recruits (Walck *et al.* 2011; Ibáñez, Katz & Lee 2017; Petrie *et al.* 2017; Clark *et al.* 2021). Forest fragmentation reduces seed availability and changes microclimate conditions into less favorable environments for establishment (Haddad *et al.* 2015; Smith *et al.* 2019). In addition, novel species assemblages resulting from the introduction of plant species (Seebens *et al.* 2017), can lead to competitive imbalances that suppress native plant recruitment via competition (Link *et al.* 2018). Over time, these stressors may hamper forests' long-term existence (Ward, Williams & Linske 2018). Giving native species the advantage from early arrival via seed additions could be an effective pathway to recover plant communities after invasive species removal. However, the conditions under which sowing would successfully contribute to the recovery of the native community remain unclear.

The characteristics of early establishing plant species may play a vital role in determining the success of recovery efforts in forests. In active restoration practices, growth form and plant

functional traits of added species are particularly important factors to consider (Ostertag *et al.* 2015). For example, there is growing evidence that tree planting and naturally regenerated forests are ineffective in promoting understory regeneration (Aubin, Messier & Bouchard 2008; Kremer & Bauhus 2020). Shrubs and herbaceous plants are, however, the growth forms that most contribute to plant diversity in temperate forests (Spicer, Mellor & Carson 2020), and their addition in restoration plans are critical for ensuring biodiversity and ecosystem function (Hupperts *et al.* 2019). In addition to growth forms, understanding plant functional traits can help predict plant growth rates and resource use efficiency (Ostertag *et al.* 2015). For example, species with acquisitive traits, like higher specific leaf area (SLA: area/dry mass), tend to have faster growth rates, making them ideal for early establishment when resources are abundant (Dahlgren *et al.* 2006). However, these species may also be more susceptible to drought stress, which could end up stalling the recovery process if conditions are not optimal (Greenwood *et al.* 2017; Wellstein *et al.* 2017). By considering growth forms and leaf traits, restoration practitioners can select native species that are better adapted to the environmental conditions of the restoration site, increasing the likelihood of successful restoration outcomes (Laughlin *et al.* 2017).

Forest understories are highly competitive environments for limiting resources, such as water and light (Landuyt *et al.* 2019). Resource availability governs the spatial distribution of species from the available species pool that can thrive under or tolerate specific abiotic conditions (Cavender-Bares *et al.* 2009; HilleRisLambers *et al.* 2012). Disturbance events, like the management of invasive species, lead to both pulses of resources that early arrivals would have access to and a low competitive environment (Fukami 2015; Sarneel, Kardol & Nilsson 2016). Priority effects, may, therefore, have long-lasting impacts on community assemblage if

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the species that first colonize a site are highly competitive and establish a strong dominance over the late arrivals. But, even if early arrival species lose their competitive edge as the environment changes, early establishment of native species may still work by 'buying time' for other native species better adapted to the new environment (Margulies, Bauer & Ibáñez 2017).

Despite the possible benefit of promoting priority effects to ensure forest community recovery after invasive species removal, this mechanism has been studied primarily in temperate grasslands and controlled settings (Weidlich *et al.* 2021). Consequentially, the potential of sowing as a restoration tool in forests remains unknown. To address this knowledge gap, we investigated the role of priority effects in the community assembly of temperate forests under restoration, by deliberately giving native plant species the advantage of arriving first after removing invasive plants. Specifically, we aimed to answer: (Q1) could seed additions be a successful practice driving community assembly after invasive plant removal? (Q2) What are the characteristics of the native plant community associated with faster recovery, in terms of coverage percentage? Lastly, (Q3) how is the recovery of the native community affected by environmental conditions, specifically, light and soil water availability? Answers to these questions will inform both the mechanisms of community assembly after disturbance and the effectiveness of common restoration practices implemented after invasive plant removal.

3.3 Methods

To answer our research questions, we carried out a multi-year field experiment in which we removed all invasive plants of all growth forms (i.e., herbaceous, woody, and lianas; for complete list of species and respective growth forms see Table S 3.1), once or multiple times, and seeded the plots with two different native species seed mix. During the growing season for three years following the implementation of the treatments, we collected data on the vegetation

and on key environmental variables. We then used an autoregressive model to analyze these data and answer our research questions.

3.3.1 Study locations

We carried out this study in four forests in southeastern Michigan, USA (for detailed coordinates of forest locations refer to Table S 3.2). All forests are characterized by temperate broadleaf species common in dry-mesic southern forests (Kost *et al.* 2007). Climate is similar across all four forests. Climate data based on based on measurements taken from 1991 to 2020 (Arguez *et al.* 2010) for the region indicates that the mean annual temperature is 8.7°C, with a minimum mean temperature in January of -5.4°C and a maximum in July of 22°C. The average annual rainfall is 822 mm.

3.3.2 Field experimental set-up

In the summer of 2019, in each forest, we selected two to four sites and at each site, we set up three sets of 3x2 m plots in areas occupied by invasive species. Each plot was divided into six 1 m^2 subplots where treatments were applied in a full factorial design (Figure 3.1). Late that first summer (August to October), we recorded invasive species identity at the subplot level (for a list of the invasive plant species recorded see Table S 3.1), and then we clipped all invasive species stems at the soil surface level (roots were not removed to avoid additional disturbance). From 2020 to 2022, in half of the subplots, we clipped invasive species monthly over the growing season (from June to August), i.e., one-year vs. multi-year invasive species removal; the other half of the subplots were left unclipped.

To identify whether priority effects are the mechanism driving community assembly, in mid-Fall of 2019 and 2020, we left one-third of the subplots untreated (control treatment), and to

a third of the subplots we added a native forb seed mix (forbs added treatment; density of 1.5 g

of seeds/m^2), to another third we added a mixture of forb and grass seeds (mixture added

treatment; density of 1.5 g and 2.4 g of seeds/ m^2 of forbs and grass, respectively) (Figure 3.1).

Refer to Table S 3.3 for the complete list of seeded forbs and grass species. All seed mixes were

purchased from Michigan Wildflower Farm. The grass mix contained cool and warm season

grasses to span as much of the growing season as possible. We used a mixture of forbs and

grasses because native grasses usually establish faster than forbs, which need 2 to 3 years after

seeding to achieve higher cover percentages. In total, we surveyed 216 1 m^2 subplots (4 forests x

3-4 sites per forest x 3 plots per site x 6 subplots), with 36 m^2 subplots per removal (one-year and

multi-year) and seeding (control, forbs added, and mixture added) combination.

3.3.3 Plant data

In 2019, before implementing treatments, we collected data on the percent cover of native

and invasive plants. After treatments, in 2020 to 2022, at each 1 m^2 subplot we collected monthly

data at the species level on percent cover (ocular estimation; precision to 1%, maximum of 100%

cover per subplot) over the growing season (June to August). We also recorded invasive species

density, and in the multi-year removal subplots, we estimated the biomass of clipped re-sprouts.

Clipped biomass was dried at 60°C until a constant weight was achieved. Data collection

spanned June, July, and August from 2020 to 2022 for the added forbs seed treatment, and from

2021 and 2022 for the added mixture seed treatment. We harmonized species names using

Taxonomic Name Resolution Service (Boyle *et al.* 2013) and assigned native status following

Reznicek *et al.* (2014). We obtained specific leaf area values from TRY database (Kattge, Díaz

& Lavorel 2011) and growth form from USDA PLANTS (USDA & NRCS 2022). We calculated

the community weighted mean of specific leaf area (SLA) using the 'FD' package (Laliberté *et*

al. 2014). For species without SLA values (18% of species), we assigned genus-level values. We aggregated the original growth form categories into three groups, 'graminoids', 'forbs', and 'woody', and determined the proportion of the total cover occupied by each group at the subplot level.

3.3.4 Environmental data

Each summer, we estimated light availability once the canopy had fully closed by taking canopy photos at the peak of greenness (July) in the center of each subplot using a fish-eye lens attached to a tripod-mounted smartphone at a height of 1.2 m. We analyzed the photos following the methods outlined by Bianchi *et al.* (2017). We measured soil moisture monthly from June to August each year using the Fieldscout TDR300 Soil Moisture Meter at the center of each subplot, but only used data from July, the driest month because water stress constrains growth. To calculate vapor pressure deficit (VPD) values between 2020 and 2022 at the forest level, we used hourly temperature (ºC) and relative humidity (%) data from HOBO U23 Pro v2 data loggers (Onset Computer Corp.) placed under the forest canopy at each forest. We then obtained daily averages and calculated the cumulative sum of VPD per year, although only two forests had available data from May to August. For VPD calculations, we utilized the package "pvldcurve" (Raesch 2020). We estimated soil nutrient availability by deploying ion-exchange resin capsules at each site (three-four sites at each forest), purchased and analyzed from UNIBEST. We performed all data wrangling using the family of packages "tidyverse" (Wickham *et al.* 2019) in R (R Core Team 2022).

3.3.5 Data analysis

To answer whether priority effects (sowing) and repeated invasive removal (two levels) affected community assembly after invasive removal we analyzed native percent cover (*Cover*) in August for each subplot (*i*) and year (*t*). Percent cover in year *t* was estimated as a function of cover the year before (i.e., autoregressive dependency, differentiated by growth form) for each sowing and removal combination. And to account for year-to-year variability in this dependency we estimated this effect for each year ($\beta_{treatment,t}$). We also included features of the native community and environmental conditions that could have contributed to recovery, i.e., native richness, SLA community weighted mean of the native community (CWM$_{SLA}$, estimated earlier in the June census), soil moisture and light measures taken at each summer:

$$Cover_{(i,t)} \sim Normal(C_{i,t}, \sigma^2)$$

Being the process model:

$$C_{i,t} = \beta_{treatment(i),t} * (w_1 * \%Graminoids_{t-1} + w_2 * \%Forbs_{t-1} + w_3 * \%Woody_{t-1})$$
$$+ \alpha_1 NativeRichness_{(i,t)} + \alpha_2 CWMSLA_{(i,t)} \quad + \alpha_3 Light_{(i,t)}$$
$$+ \alpha_4 SoilMoisture_{(i,t)}$$

Parameter β represents the rate of native recovery per seeding treatment and removal frequency, estimated for each year. Here, recovery is defined as the rate of increases in native species percent cover. Parameter ω are weights given to each growth form (graminoids, forbs, woody) to assess their specific contribution to recovery ($\sum w_k = 1$). Note that growth forms were not included in the 2020 analysis, in 2019 we only recorded overall native community cover and used that measurement. We estimated all parameters from non-informative prior distributions, $\alpha_*, \beta_* \sim Normal(0,100)$ and $\omega_* \sim Dirichlet(1)$, and variance $1/$ $\sigma^2 \sim Gamma(0.0001, 0.0001)$. We ran multiple iterations of the process models, which incorporated variables associated with the invasive community (i.e., percent cover, biomass,

density) and with soil nutrients, particularly soil nitrogen, phosphorus, and potassium, as explanatory variables. However, these variables did not improve model fit, leaving us with the model structure we show above.

We retrieved posterior distributions and parameters values after convergence, using at least 50,000 iterations with a thinning interval of 100. We ran the auto-regressive mixed-effects models in JAGS (Hornik *et al.* 2003) through R using "rjags" (Plummer 2022). To assess whether added seeds had differential effects across levels of native richness, we calculated an effect size (ES) of native cover across the treatments of seed addition. ES was calculated as $ES = (native\ cover_{seed\ addition} - native\ cover_{control})/|average|$, following Sorte *et al.* (2013); we did this calculation for the two levels of invasive removal. We also performed extensive exploratory data analysis of the model residuals to identify any associations with variables not included in the analysis (e.g., invasive species identity and initial cover, forest, plot, and year). To elucidate potential explanations for the observed variations across years, $\beta_{treatment,t}$, we conducted additional investigations into environmental conditions that could explain these differences, e.g., vapor pressure deficit (VPD). The modeling code can be found on Code S 3.1.

3.4 Results

The total percent cover of the native community within a plot varied from 0 (16 subplots in 2019, one subplot in 2020, and one in 2022) to 100 % (seven in 2021 and three in 2022). We recorded a total of 132 native species across all forests. At the subplot level and across years, light availability ranged from 5.83 % to 70.2 % of full sunlight, and soil moisture, measured as volumetric water content, ranged from 0 % to 43.4 %. We were only able to calculate complete vapor pressure deficit (VPD) values at two of our forests due to sensor failure, but year-to-year

variation in climatic conditions are similar across the study area (GLISA 2023). All parameter

values from the analyses are reported in Table S 3.4 and model fit in Figure S 3.2. Exploration of

residuals can be found in Figure S 3.3 and Figure S 3.4.

(Q1) *Could seed additions be a successful practice driving community assembly after*

invasive plant removal? Recovery rates of the native community were not significantly different

between control and seeded treatments (i.e., forbs added, or mixture added; Figure 2.2a).

Although multi-year removal subplots tended to have a higher recovery rate than one-year

removal subplots, these were not statistically different from one another except in the forbs

added treatment in 2021 (Figure 2.2a). The native community recovery rates were higher in 2021

for all treatments compared to the other two years (Figure 2.2a). Mean percent native cover

across years and treatments were not significantly different from each other as all confidence

intervals overlap, but richer forests (i.e., Forest 1, 2 and 3) tended to have a consistently higher

total native cover per treatment in 2021 and 2022 (Figure S 3.5). Growth form categories

contributed similarly to native community recovery (parameters ω, Figure 3.2b).

(Q2) *What characteristics of the native plant community are associated with faster*

recovery? Our analysis revealed that native richness was significantly and positively, associated

with recovery of the native community following invasive species management (Figure 3.3a).

This coefficient was the strongest of the variables considered. When analyzing sowing treatment

effect size (ES) as a function of native richness, we did not find any patterns, i.e., sowing did not

make a difference across all levels of native richness (Figure S 3.6). Recovery was also higher

among subplots with a higher community weighted mean of specific leaf area (SLA) values

(Figure 3.3a). To investigate further, we compared the SLA values of seeded species that

established versus those that failed to establish (i.e., species that were not recorded in any subplot

at any given time-point of the experiment). Although not significantly different (ranges overlap), our results indicate that those added forbs and grasses able to establish tended to have higher SLA values than the species that did not establish (Figure 3.4 a and b). And among the seeded species that established, those with higher SLA tended to establish in higher density (Figure 4C; linear regression, $\beta = 2.97$ [confidence intervals: 0.942–4.99], $p = 0.00849$).

(Q3) *How is the recovery of the native community affected by environmental conditions, specifically, light and soil water availability?* Subplots with higher available light (marginally significant) tended to also have higher native recovery rates (Figure 3.3a). Soil moisture availability at the subplot level did not have a significant effect on the native recovery rate (Figure 3.3a). However, in further exploration of environmental conditions that differed across years while our experiment was in place, 2021 had lower cumulative values of vapor pressure deficit (VPD) compared to the other years, indicating lower atmospheric water demand (Figure 3.3b). This effect of VPD would be represented in the variability of β parameters across years (Figure 3.2a).

3.5 Discussion

Invasive plants, along with other stressors, threaten the long-term persistence and function of forest ecosystems by negatively impacting forest regeneration and the maintenance of a healthy understory (Vilà & Ibáñez 2011). Despite extensive restoration efforts after invasive plant removal, successful native recovery is rarely achieved and re-invasion frequently occurs (Kettenring & Adams 2011). We examined native plant community assembly following the removal of invasive species and the addition of native propagules to better understand the recovery process (evaluated as increased coverage of native plants). We found that neither seed additions nor multi-year invasive removal speeded native community recovery; the fastest

recovery rates resulted from a combination of high native richness, a native community with relatively high SLA and low drought stress. Overall, our results provide valuable information to assess the viability of invasive removal practices and to guide the implementation of more effective restoration aimed at the recovery of temperate forest understories.

3.5.1 (Q1) *Could seed additions be a successful practice driving community assembly after invasive plant removal?*

Efforts to manage natural ecosystems dominated by invasive plants typically involve attempts to eradicate or reduce the abundance of targeted invasive species (D'Antonio *et al.* 2017). These removal practices generally restart community assembly by reducing plant density and increasing resource availability, leading to the assumption that priority effects, or the ability to establish first, could be the driving factor of community assembly (Fukami, Mordecai & Ostling 2016; Byun, de Blois & Brisson 2018). Due to the potential lack of native propagules as a consequence of fragmentation and degradation (Schuster, Wragg & Reich 2018), and from plant invasion further reducing the diversity in the seedbank (Collier, Vankat & Hughes 2002; Ward, Williams & Linske 2018), seeding practices are designed to supplement native propagules in sites under restoration (Copeland *et al.* 2019). However, our results show that, in these understory environments, native species recovery rates are similar between the control (i.e., no native seed addition) and treatment groups (added native seeds; Figure 3.2a; Figure S 3.5). This finding indicates that in our study system, the lack of native propagules is not stalling recovery. Our study supports evidence from a previous experiment in other invaded temperate deciduous forests, where the addition of native seeds resulted in comparable plant community composition to that observed in control plots after two years from the removal of a dominant invasive shrub (Moore, D'Amico & Trammell 2023). These temperate forests seem to be able to provide enough

native propagules to promote a rate of native community recovery that does not improve by artificial seed addition. In forests, studies are usually focused on tree planting (Kettenring & Adams 2011; Schuster, Wragg & Reich 2018; Castro *et al.* 2021) and on controlling invasion (e.g., Blumenthal, Jordan & Svenson 2003; Kettenring & Adams 2011; Bucharova & Krahulec 2020; Byun 2023), with little information on the actual recovery of native vegetation as we investigated in this study.

3.5.2 (Q2) *What characteristics of the native plant community are associated with faster recovery?*

Functionally diverse communities with complementary resource use strategies are better equipped to exploit available resources (Davis, Grime & Thompson 2000; Funk *et al.* 2008; Byun, de Blois & Brisson 2018). Theory predicts this because diverse communities are more likely to contain one or more particularly competitive species under a given set of environmental conditions (i.e., sampling effect). These competitive species decrease the amount of unused limiting resources when either diversity or richness, increases (Tilman 2001; Funk *et al.* 2008; Tilman, Isbell & Cowles 2014). Specifically in forest understories, a richer native community could be more likely to have strong native competitors that thrive in the shaded understory (Vojik & Boublik 2018; Gomez *et al.* 2019), while also including species which respond rapidly to pulses of resources that are often found after disturbance or invasive removal (Moles *et al.* 2012; Driscoll 2017). Our results show that the recovery of native understory plant communities was positively influenced by two key variables: native richness and community-level specific leaf area (SLA) (Figure 3.3a) – with native richness having the strongest positive association with recovery. Such a community feature is particularly relevant in the context of recently managed invaded forests, where the reduction of invader plant density leaves unutilized

resources over time and space. These unused resources could then be explored by richer native communities given the greater potential of interspecific complementarity, as discussed above.

The main goals of forest restoration include effective invasive plant removal while maximizing native plant establishment and survival rates (Kettenring & Adams 2011; Weidlich *et al.* 2020; Castro *et al.* 2021). Practices to aid native plant establishment often focus on the addition of specific growth forms, such as planting trees that will structure the canopy (Castro *et al.* 2021), or seeding understory herbs and graminoids (Moore, D'Amico & Trammell 2023). While growth forms provide an easy way to categorize plant species based on morphology (Gillison 2013), the variation in resource-use strategies within a morphological category should not be ignored. Resource-use strategies can be inferred from plant leaf traits, as described in the leaf economic spectrum (LES; Wright *et al.* 2004; Diaz *et al.* 2016). On one end of the LES, species with acquisitive leaves have high specific leaf area, N content, light demands, and maximum photosynthetic rates, but low investment in tissue per area (or specific leaf area), survival rates, and shorter life span (Wright *et al.* 2004; Diaz *et al.* 2016). On the other end, conservative species are shade-tolerant, investing heavily in leaf tissue, and have leaves with longer life span, and slower carbon processing rates (Wright *et al.* 2004; Diaz *et al.* 2016). The LES is a generalizable framework and holds across growth forms, plant functional groups, or biomes (Wright *et al.* 2004; Diaz *et al.* 2016). Our analysis shows that rates of native community recovery following invasive species removal were independent of growth form (Figure 3.2a) but dependent on overall native community leaf trait composition. Specifically, our results suggest that native communities with higher CWM_{SLA} were linked to faster recovery rates (Figure 3.3a), and that seeded species with higher specific leaf area (SLA) values were more likely to establish (Figure 3.4). Plants with higher SLA values are more adapted to high-resource environments

(Pérez-Harguindeguy *et al.* 2016; Maracahipes *et al.* 2018 but see Gommers *et al.* 2013; Liu *et al.* 2016) and disturbed areas, such as sites after management interventions (Ordonez & Olff 2013; Gong & Gao 2019; Ibáñez *et al.* 2021). Therefore, selecting plant species, if artificial seed addition is needed, based on their trait values can be an important tool to create more resistant native communities that could increase native coverage given site-specific characteristics (Laughlin *et al.* 2017), and can greatly improve restoration success to control invasive species (Ostertag *et al.* 2015).

3.5.3 (Q3) *How is the recovery of the native community affected by environmental conditions, specifically, light and soil water availability?*

In temperate broadleaf forests, understory growth is mainly limited by light availability (Axmanová *et al.* 2011; Landuyt *et al.* 2020). In these shaded environments, understory plants acquire most of their carbon before the canopy leafs out and after canopy leaf senescence (Jolly, Nemani & Running 2004; Lee & Ibáñez 2021), or when growing in forest gaps (Gravel *et al.* 2010). Our results support a positive response in recovery at higher light levels, matching the higher establishment of species with higher SLA. Species with higher SLA values characterize acquisitive leaves which are better equipped to rapidly obtain essential resources, such as enhanced ability to intercept light, which in turn leads to higher carbon fixation and faster growth (Wright *et al.* 2004). Our finding is also consistent with previous studies that have demonstrated strong correlations between both understory plant richness and cover, and light availability and heterogeneity in temperate forests (Dormann *et al.* 2020; Helbach *et al.* 2022). Although our invasive removal treatments did not directly affect the canopy structure, our experimental plots were established across sites with substantial variation in light availability within the canopy.

Furthermore, the removal of a dense shrub layer, as we performed through clipping, is known to enhance light availability to the forest floor (Kaye & Hone 2016).

While our analysis did not reveal a significant effect of soil moisture (based on measurements taken at one particular time each month), the year-to-year differences on recovery rate align with those in VPD values (Figure 3.2 and Figure 3.3). Plants regulate evapotranspiration rates based on the non-linear relationship between temperature and relative humidity, or VPD (McAdam & Brodribb 2015; Grossiord *et al.* 2020). This regulation directly affects photosynthesis rates: high temperatures in combination with low relative humidity (i.e., high VPD values) induce stomata closure, thereby suspending photosynthesis to avoid hydraulic failure (McAdam & Brodribb 2015; Novick *et al.* 2016). Together, these results suggest that to achieve higher and lasting recovery rates in the native community optimal growing conditions are essential. Years characterized by lower water stress levels in the warmest months in the growing season, such as 2021, play a disproportionately important role in promoting native plant recovery, particularly in sites with higher richness. This importance is supported by the sustained higher total native cover observed in Forests 1 and 3 in 2022 following the increase in cover experienced in 2021 (Figure S 3.5).

3.5.4 Dominant invader vs. invasive plant community

Current management practices for controlling or eradicating invasive species typically involve targeting a focal nuisance plant with significant impacts (D'Antonio *et al.* 2017). One example is garlic mustard (*Alliaria petiolata* (M. Bieb.) Cavara & Grande), a species that occurs in some of our studied forests, which is well known for its allelopathic effects and usually draws significant control efforts and resources from managers, practitioners, and landowners (Cipollini, Titus & Wagner 2012; Portales-Reyes *et al.* 2015; Blossey *et al.* 2021). We further investigated

whether the unexplained variability by our model's predictors could be attributed to the identity of the dominant invasive species. However, we found no clear associations which suggests that the management of invaders could shift from an invasive species-focus to a native community-level approach. Improving the ability of the native community to take advantage of the removal of an invasive species could, then, help prevent secondary invasions or the re-invasion by low abundance species already present at a site (Kuebbing, Nunez & Simberloff 2013; Pearson *et al.* 2016). Invasive species often have intrinsic advantages over co-occurring natives, e.g., larger carbon gain per leaf area, longer leaf lifespan, and extended leaf phenology (Fridley 2012; Heberling & Fridley 2013; Fridley & Craddock 2015). So, adopting a community-level approach where the richness and functionality of the native vegetation are evaluated before invasive removal could prevent reinvasion and ensure restoration success.

3.6 Conclusions

The scientific literature on invaded ecosystems primarily focuses on the agent of the impact: the invasive plants harming the native community (McGeoch *et al.* 2016; Ibáñez *et al.* 2021). Here, we switched the research focus from the invasive species to the affected community by studying mechanisms of community assembly of temperate forest understories. Specifically, we investigated the role of priority effects in structuring such communities, the features of this recently assembled community, and the environmental conditions aiding native community recovery. We performed our study after the management of invasive species in natural conditions, a specific applied setting, when restoration success is typically low (Kettenring & Adams 2011). Thus, our results could be beneficial to managers and practitioners on the ground by allowing them to tailor and adapt their current approaches to potentially increase native community recovery success in forested systems. Specifically, management of invaded forest

understories could be targeted to increase the native richness of the incoming community if native propagules are limited, choosing species with higher SLA or more acquisitive strategies to supplement local native propagules. Additionally, managers should consider assessing whether the environmental conditions are optimal for removal, particularly with respect to predicted drought levels.

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3.8 Figures
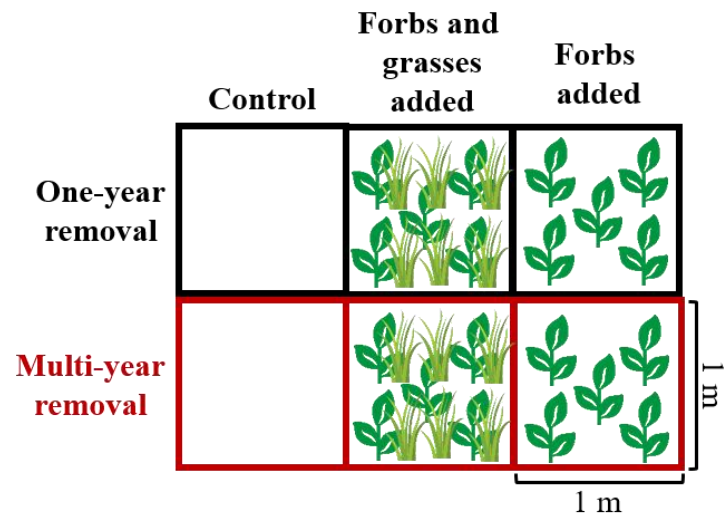
Figure 3.1: Experimental setup with a representation of all removal and seeding treatments used to investigate the role of priority effects in recovery of recently managed invaded forest understories. The actual location of each subplot within a plot was randomized and adjusted depending on its slope.
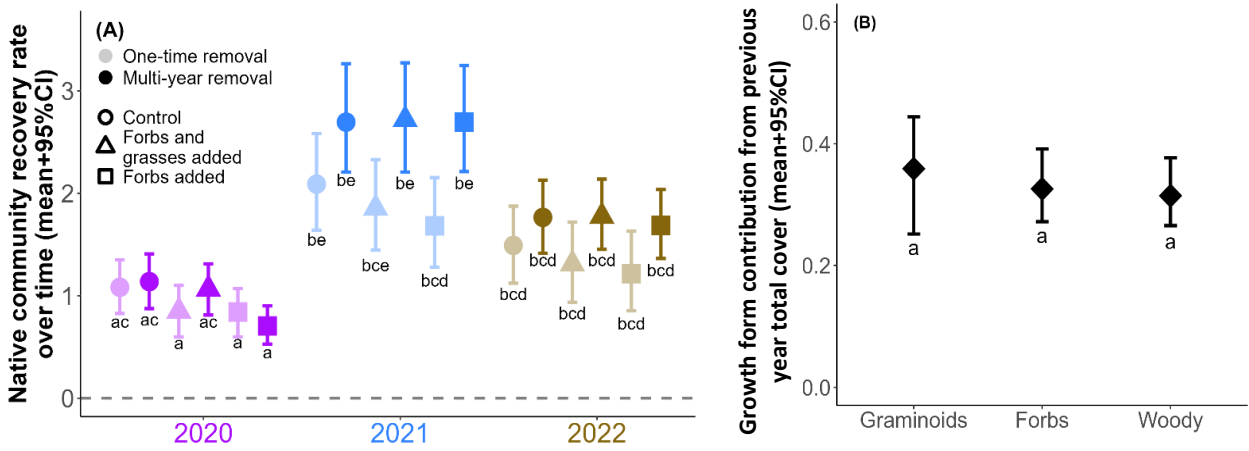
Figure 3.2: Treatment effects across years and growth form contribution to previous year total cover. (A) Native community cover recovery rates (β parameters) across years, seeding treatments, and removal frequencies. (B) Contribution of each growth form from previous year's cover (ω parameters). Parameters in which 95% credible intervals (CI) do not overlap with each other are considered statistically different from each other, i.e., different letters.
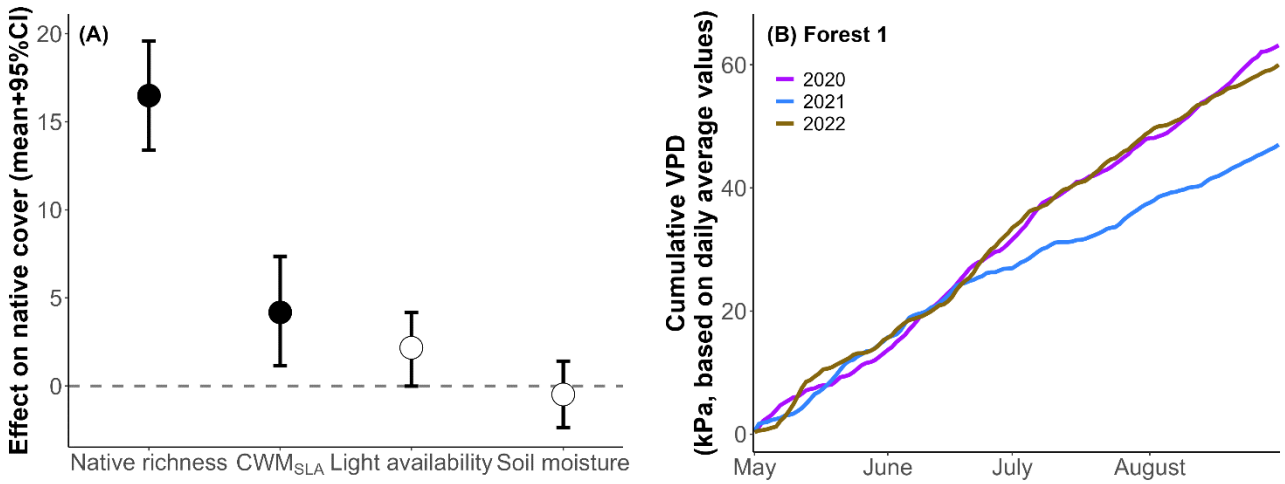
Figure 3.3: Covariate effects on native cover and cumulative vapor pressure deficit (VPD). (A) Posterior means and 95% CI of parameter values (standardized for comparisons) from the additional covariates included in the analysis. CWM_{SLA}: community weighted mean of specific leaf area. Credible intervals (CI) that do not cross zero are statically significant (solid symbols). (B) Cumulative vapor pressure deficit (VPD) from one of the environmental sensors.
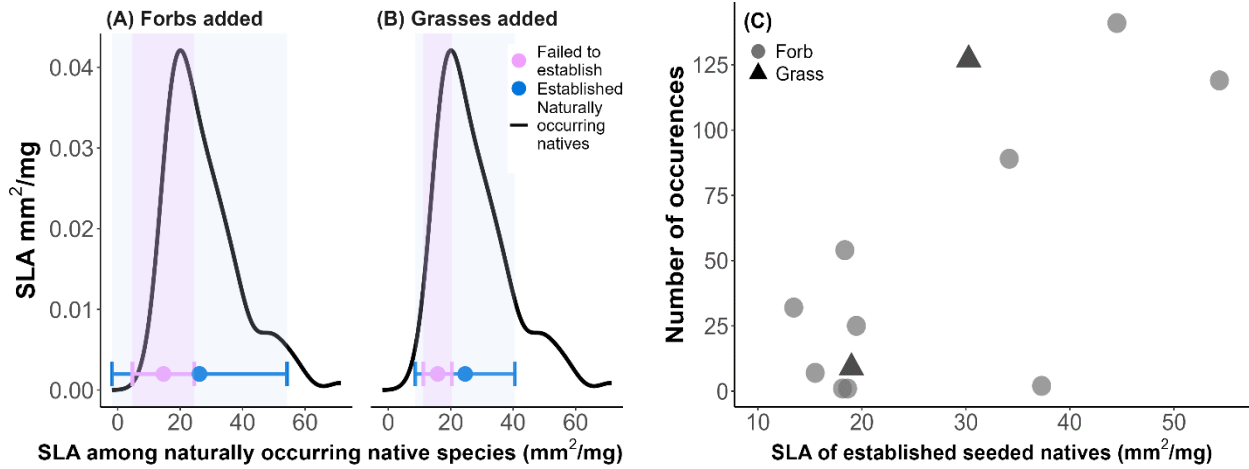
Figure 3.4: Specific leaf area (SLA) distribution of added forbs and grasses, and relationship between number of species occurrences and their respective SLA values. (A, B) Distribution of SLA values among naturally occurring native species (black line) and range of SLA values of seeded forbs (A) and seeded grasses (B) differentiated as a function of having successfully established or not (colors). (C) Relationship between established seeded native species and their SLA values (β = 2.97 [confidence intervals: 0.942–4.99], p = 0.00849).

3.9 Supporting information

Figure S 3.1: Map of the four study forests where 36 experimental plots are installed to investigated priority effects in invaded temperate forests. Refer to Table S 3.1 for location names and coordinates based on the numbers displayed here. Background 2020 land cover data has 30 meters resolution and was produced as part of the North American Land Change Monitoring System (NALCMS; http://www.cec.org/nalcms). Insert: main location of our study in North America.
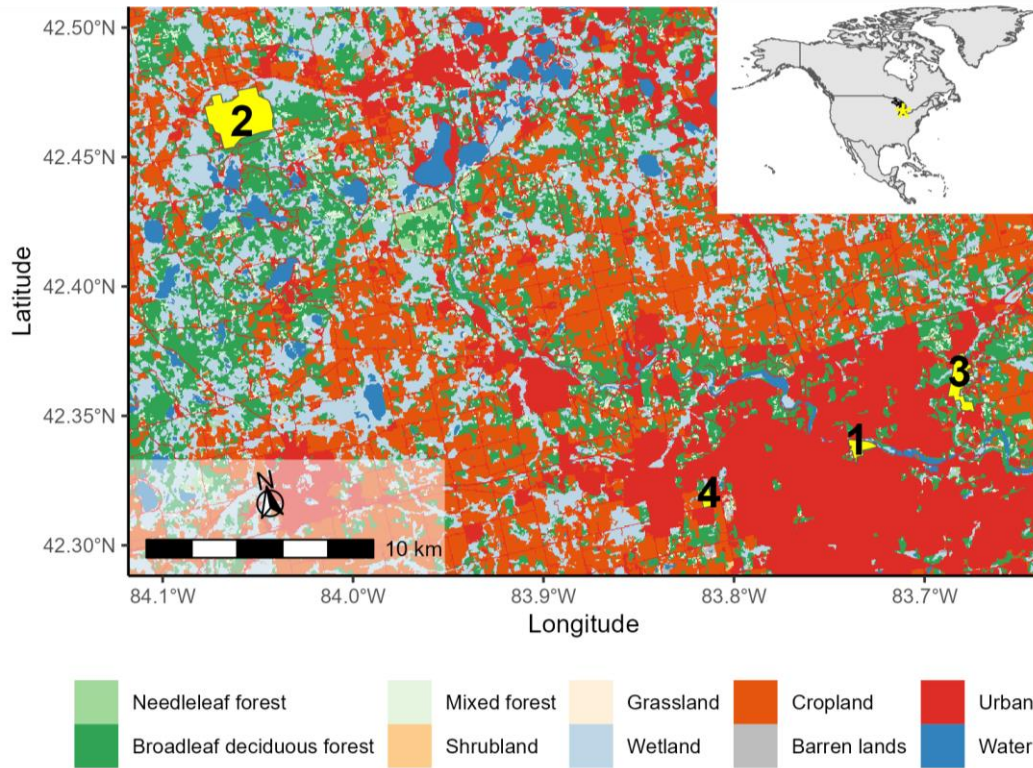
Table S 3.1: List of introduced plant species considered invasive in our experiment. Growth forms follows USDA PLANTS (USDA & NRCS 2022).

Scientific name	Common name	Growth form
Acer platanoides L.	Norway maple	Tree
Ailanthus altissima (Mill.) Swingle	Tree of heaven	Tree
Alliaria petiolata (M. Bieb.) Cavara & Grande	Garlic mustard	Forb/herb
Berberis thunbergii DC.	Barberry	Shrub
Cardamine impatiens L.	Bitter cress	Forb/herb
Catalpa speciosa Warder	Northern catalpa, cigar-tree	Tree
Celastrus orbiculatus Thunb.	Bittersweet	Vine
Chelidonium majus L.	Celandine	Forb/herb
Cirsium vulgare (Savi) Ten.	Bull thistle	Forb/herb
Convallaria majalis L.	Lily-of-the-valley	Forb/herb
Elaeagnus umbellata Thunb.	Autumn-olive	Shrub
Euonymus alatus (Thunb.) Siebold	Winged euonymus	Shrub
Frangula alnus Mill.	Glossy buckthorn	Tree, Shrub
Hesperis matronalis L.	Dame's rocket	Forb/herb
Ligustrum vulgare L.	Common privet	Shrub
Lonicera maackii (Rupr.) Herder	Amur honeysuckle	Shrub
Lonicera morrowii A. Gray	Morrow honeysuckle	Shrub
Lonicera x bella Zabel	Hybrid honeysuckle	Shrub
Philadelphus coronarius L.	Sweet mock-orange	Shrub
Rhamnus cathartica L.	Common buckthorn	Tree, Shrub
Rosa multiflora Murray	Multiflora rose	Vine, Subshrub
Taraxacum officinale F. H. Wigg.	Common dandelion	Forb/herb
Verbascum thapsus L.	Common mullein	Forb/herb
Wisteria sinensis (Sims) DC.	Wisteria	Vine

Table S 3.2: Local names and corresponding acronyms, plot numbers, and respective locations.

Local name	Forest#	Site	Plot #	Coordinate X (m)	Coordinate Y (m)
Nichols Arboretum	1	A	114	-83.7206	42.2800
Nichols Arboretum	1	A	116	-83.7204	42.2800
Nichols Arboretum	1	A	118	-83.7203	42.2796
Nichols Arboretum	1	B	124	-83.7225	42.2809
Nichols Arboretum	1	B	122	-83.7219	42.2821
Nichols Arboretum	1	B	120	-83.7228	42.2818
Nichols Arboretum	1	C	112	-83.7244	42.2805
Nichols Arboretum	1	C	126	-83.7243	42.2796
Nichols Arboretum	1	C	128	-83.7249	42.2807
Edwin S. George Reserve	2	A	153	-84.0163	42.4531
Edwin S. George Reserve	2	A	155	-84.0160	42.4531
Edwin S. George Reserve	2	A	157	-84.0157	42.4526
Edwin S. George Reserve	2	B	165	-84.0149	42.4574
Edwin S. George Reserve	2	B	167	-84.0153	42.4572
Edwin S. George Reserve	2	B	169	-84.0152	42.4577
Edwin S. George Reserve	2	C	159	-84.0109	42.4580
Edwin S. George Reserve	2	C	161	-84.0106	42.4583
Edwin S. George Reserve	2	C	163	-84.0102	42.4584
Edwin S. George Reserve	2	D	179	-84.0014	42.4662
Edwin S. George Reserve	2	D	110	-84.0018	42.4663
Edwin S. George Reserve	2	D	177	-84.0023	42.4663
Matthaei Botanical Gardens	3	A	175	-83.6574	42.3031
Matthaei Botanical Gardens	3	A	171	-83.6571	42.3038
Matthaei Botanical Gardens	3	A	173	-83.6572	42.30446
Matthaei Botanical Gardens	3	B	152	-83.6648	42.2970
Matthaei Botanical Gardens	3	B	148	-83.6652	42.2975
Matthaei Botanical Gardens	3	B	150	-83.6656	42.2968
Saginaw Forest	4	A	130	-83.805	42.2749
Saginaw Forest	4	A	132	-83.8050	42.2747
Saginaw Forest	4	A	134	-83.8046	42.2744
Saginaw Forest	4	B	136	-83.8090	42.2771
Saginaw Forest	4	B	140	-83.8087	42.2772
Saginaw Forest	4	B	158	-83.8079	42.2769
Saginaw Forest	4	C	146	-83.8080	42.2721
Saginaw Forest	4	C	144	-83.8085	42.2725
Saginaw Forest	4	C	142	-83.8072	42.2731

Table S 3.3: List of plant forbs and grasses used in the seed mixers applied in the treatments as described in the methods section. Table includes the requirement and tolerance for light and soil moisture (M = mesic; WM = wet mesic; D = extremely; DM = dry mesic) requirements from the seed source company. The seed sources are from the Great Lakes region.

Seed mix type	Scientific name	Common name	Light	Soil moisture
Forbs mix	*Achillea millefolium* L.	Yarrow, milfoil	Partial sun - sun	M-D
Forbs mix	*Allium cernuum* Roth	Nodding wild onion	Partial sun - sun	M-DM
Forbs mix	*Aquilegia canadensis* L.	Wild columbine	Partial sun - sun	M-D
Forbs mix	*Asclepias syriaca* L.	Common milkweed	Sun	WM-DM
Forbs mix	*Asclepias tuberosa* L.	Butterfly-weed	Partial sun - sun	M-D
Forbs mix	*Desmodium canadense* (L.) DC.	Showy tick-trefoil	Partial sun - sun	WM-DM
Forbs mix	*Ageratina altissima* (L.) R. M. King & H. Rob.	White snakeroot	Partial sun - sun	WM-DM
Forbs mix	*Monarda fistulosa* L.	Wild-bergamot	Partial sun - sun	WM-D
Forbs mix	*Penstemon digitalis* Nutt.	Foxglove beard-tongue	Partial sun - sun	M-DM
Forbs mix	*Penstemon hirsutus* (L.) Willd.	Hairy beard-tongue	Partial sun - sun	DM-D
Forbs mix	*Rudbeckia hirta* L.	Black-eyed susan	Partial sun - sun	M-D
Forbs mix	*Rudbeckia triloba* L.	Three-lobed coneflower	Partial sun - sun	WM-DM
Forbs mix	*Solidago rigida* L.	Stiff goldenrod	Partial sun - sun	WM-D
Forbs mix	*Symphyotrichum novae-angliae* (L.) G. L. Nesom	New england aster	Partial sun - sun	W-DM
Forbs mix	*Symphyotrichum oolentangiensis* (Riddell) G. L. Nesom	Sky-blue aster	Partial sun - sun	D
Forbs mix	*Thalictrum dioicum* L.	Early meadow rue	Partial sun	WM-D
Forbs mix	*Thalictrum dasycarpum* Fisch. & Avé-Lall.	Purple meadow rue	Partial sun - sun	WM-M
Grasses mix cool season	*Koeleria macrantha* (Ledeb.) Schult.	June Grass	Partial sun - sun	DM-D
Grasses mix cool season	*Elymus canadensis* L.	Canada wild-rye	Partial sun - sun	M-D
Grasses mix warm season	*Schizachyrium scoparium* (Michx.) Nash	Little Bluestem	Partial sun - sun	M-D
Grasses mix warm season	*Elymus hystrix* L.	Bottlebrush grass	Partial sun - sun	M-D

Table S 3.4: Model parameters values. Statistically significant differences across seeding and removal treatments over the three years are indicated with different letters (95%CI do not overlap), and statistically significant covariates are indicated in bold (95%CI do not overlap with zero.

PARAMETER$_{\text{TREATMENT COMBINATION, YEAR}}$	TREATMENT COMBINATION REMOVAL, SOWING	YEAR	MEAN	SD	2.5 % QUANTILE	97.5 % QUANTILE
$\beta_{1,1}$	one-time removal, control	2020	0.8182	0.9868	1.0772	1.1673ac
$\beta_{2,1}$	one-time removal, forbs and grasses added	2020	0.597	0.7628	0.843	0.9287a
$\beta_{3,1}$	one-time removal, forbs added	2020	0.6063	0.7625	0.8411	0.9229a
$\beta_{4,1}$	multi-year removal, control	2020	0.8592	1.0427	1.1282	1.2222ac
$\beta_{5,1}$	multi-year removal, forbs and grasses added	2020	0.8076	0.9728	1.0583	1.1403ac
$\beta_{6,1}$	multi-year removal, forbs added	2020	0.524	0.6397	0.7033	0.7685a
$\beta_{1,2}$	one-time removal, control	2021	1.6306	1.9337	2.0898	2.267be
$\beta_{2,2}$	one-time removal, forbs and grasses added	2021	1.4171	1.7203	1.8621	2.0309bce
$\beta_{3,2}$	one-time removal, forbs added	2021	1.2603	1.5322	1.6741	1.8284bcd
$\beta_{4,2}$	multi-year removal, control	2021	2.186	2.5289	2.6979	2.8892be
$\beta_{5,2}$	multi-year removal, forbs and grasses added	2021	2.1797	2.5422	2.735	2.9173be
$\beta_{6,2}$	multi-year removal, forbs added	2021	2.1617	2.5129	2.6933	2.8784be
$\beta_{1,3}$	one-time removal, control	2022	1.0915	1.3481	1.4863	1.6183bcd
$\beta_{2,3}$	one-time removal, forbs and grasses added	2022	0.9153	1.1686	1.3132	1.4527bcd
$\beta_{3,3}$	one-time removal, forbs added	2022	0.8347	1.0809	1.217	1.3727bcd
$\beta_{4,3}$	multi-year removal, control	2022	1.4344	1.6341	1.7617	1.8917bcd
$\beta_{5,3}$	multi-year removal, forbs and grasses added	2022	1.445	1.6625	1.781	1.894bcd
$\beta_{6,3}$	multi-year removal, forbs added	2022	1.35	1.5654	1.689	1.809bcd
α_1	native richness	NA	**1.6999**	**1.9675**	**2.1048**	**2.2421**
α_2	CWM$_{\text{SLA}}$	NA	**0.0319**	**0.0955**	**0.1305**	**0.1663**
α_3	light availability	NA	-0.0058	0.078	0.1241	0.1721
α_4	soil moisture	NA	-0.1973	-0.0916	-0.0396	0.017
σ^2	likelihood	NA	251.9674	269.6624	280.0435	290.5618
ω_1	graminoids	NA	0.2561	0.3267	0.3595	0.392
ω_2	forbs	NA	0.2699	0.3065	0.3256	0.3451
ω_3	woody	NA	0.2638	0.2959	0.3149	0.3344

Figure S 3.2: Model fit for native species cover (predicted vs observed) and R^2.

y = 1.000 x
R^2 = 0.91
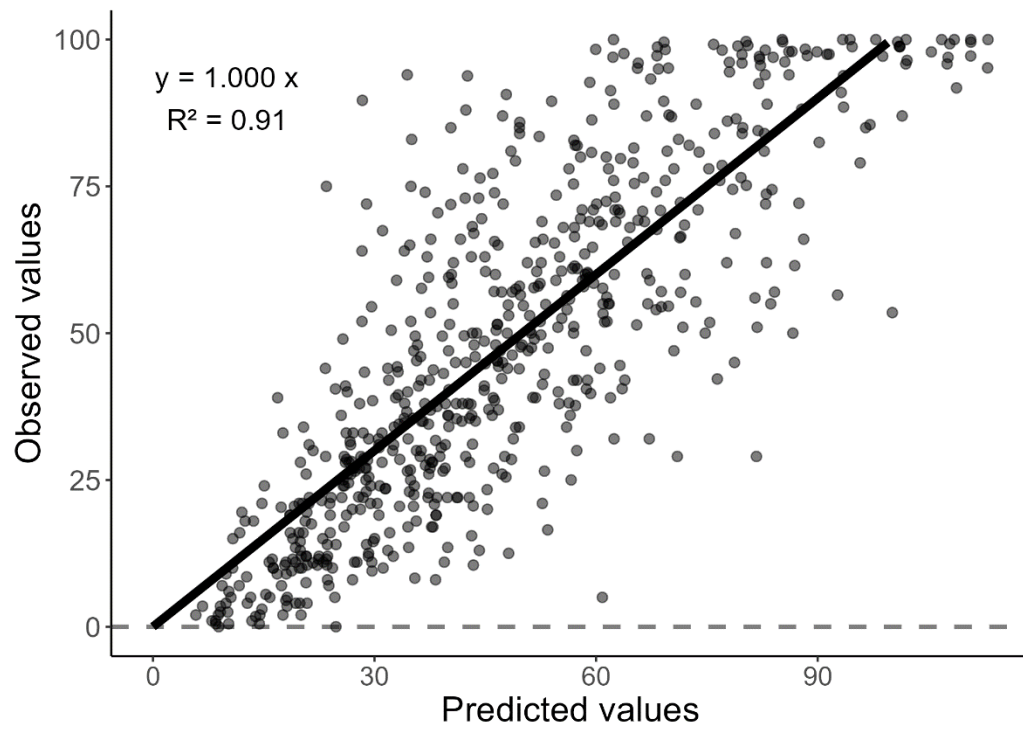
Figure S 3.3 Model residuals plotted against important predictors: (A) forests, (B) sites within forests, (C) year, and (D) cover of invasive species. Refer to Table S 3.2 above for forests acronyms.
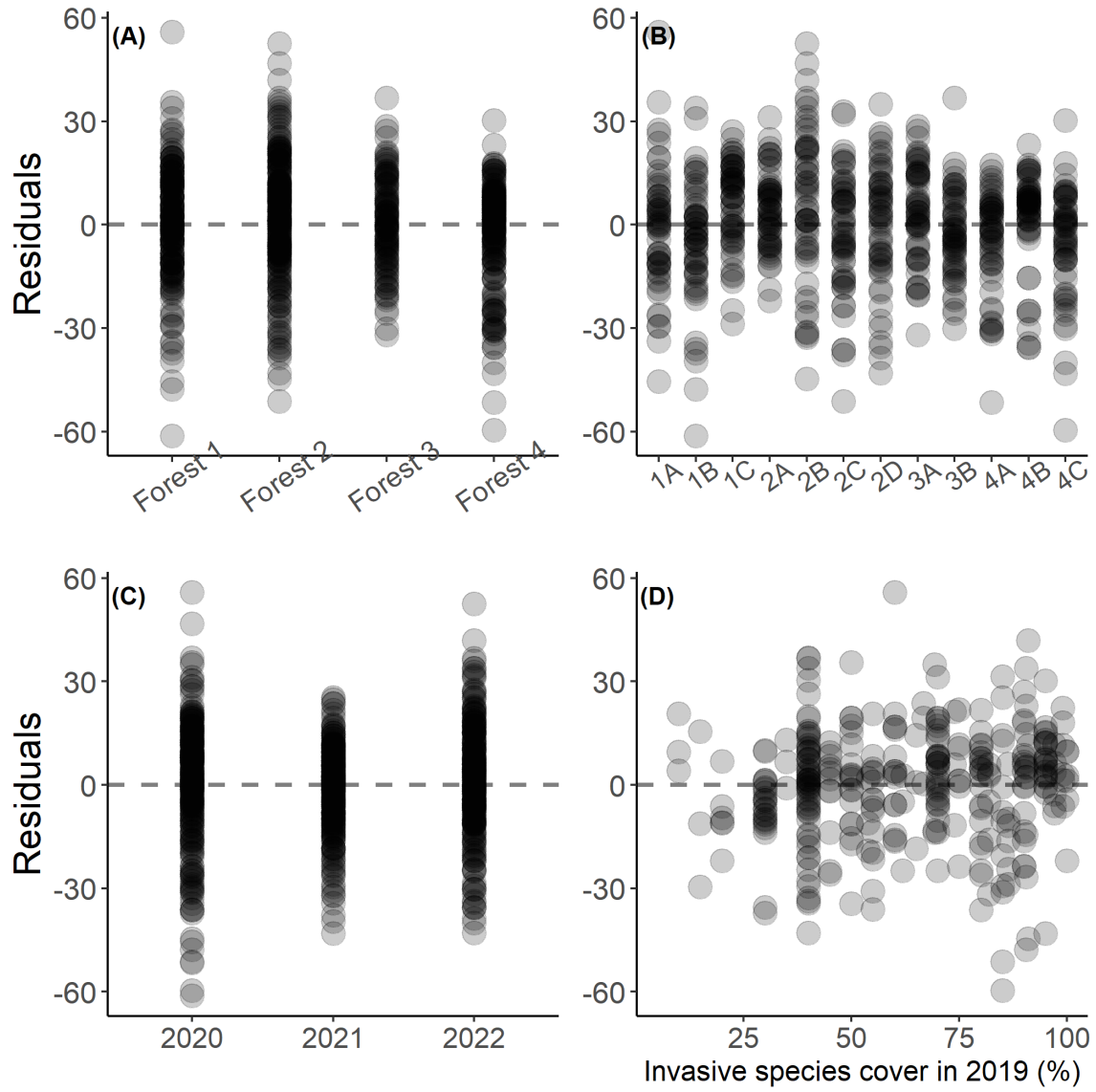
Figure S 3.4: Model residuals distributed per dominant invader (i.e., species with larger percent cover in subplot per year) and location (colors).

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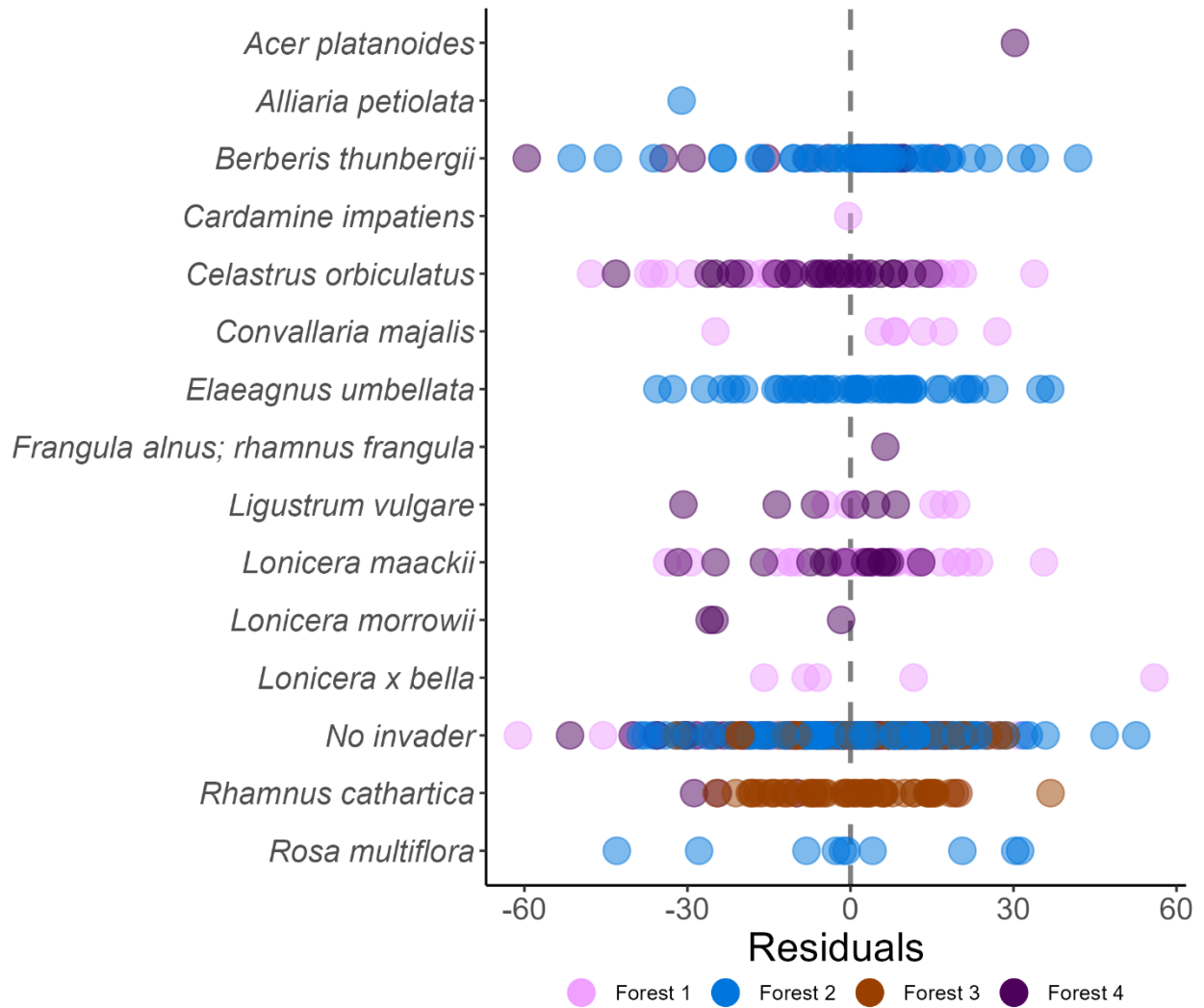
Figure S 3.5: Mean percent native cover of all across years, seeding treatments, and removal frequencies. Parameters which 95% confidence intervals (CI) that do not overlap with zero are statistically significant (solid symbols). Native richness per forest is, respectively, 94,79,78,57.
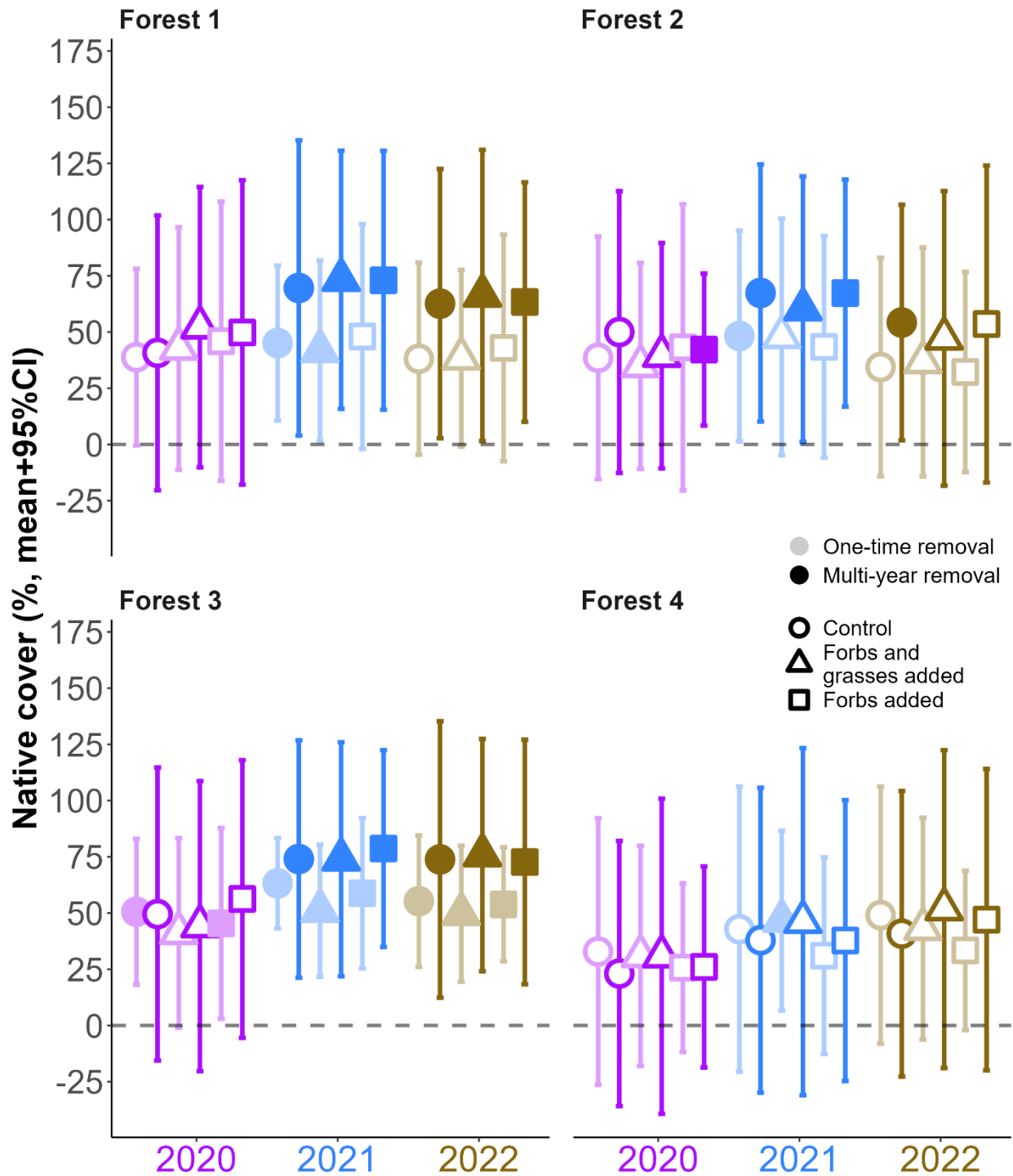
Figure S 3.6: Effect of added seeds treatments on native richness per frequency of invasive plant removal. Positive ES values mean that adding seeds aided native cover, negative ES values mean that adding seeds had a detrimental effect on native cover, while ES values of zero mean no effect.
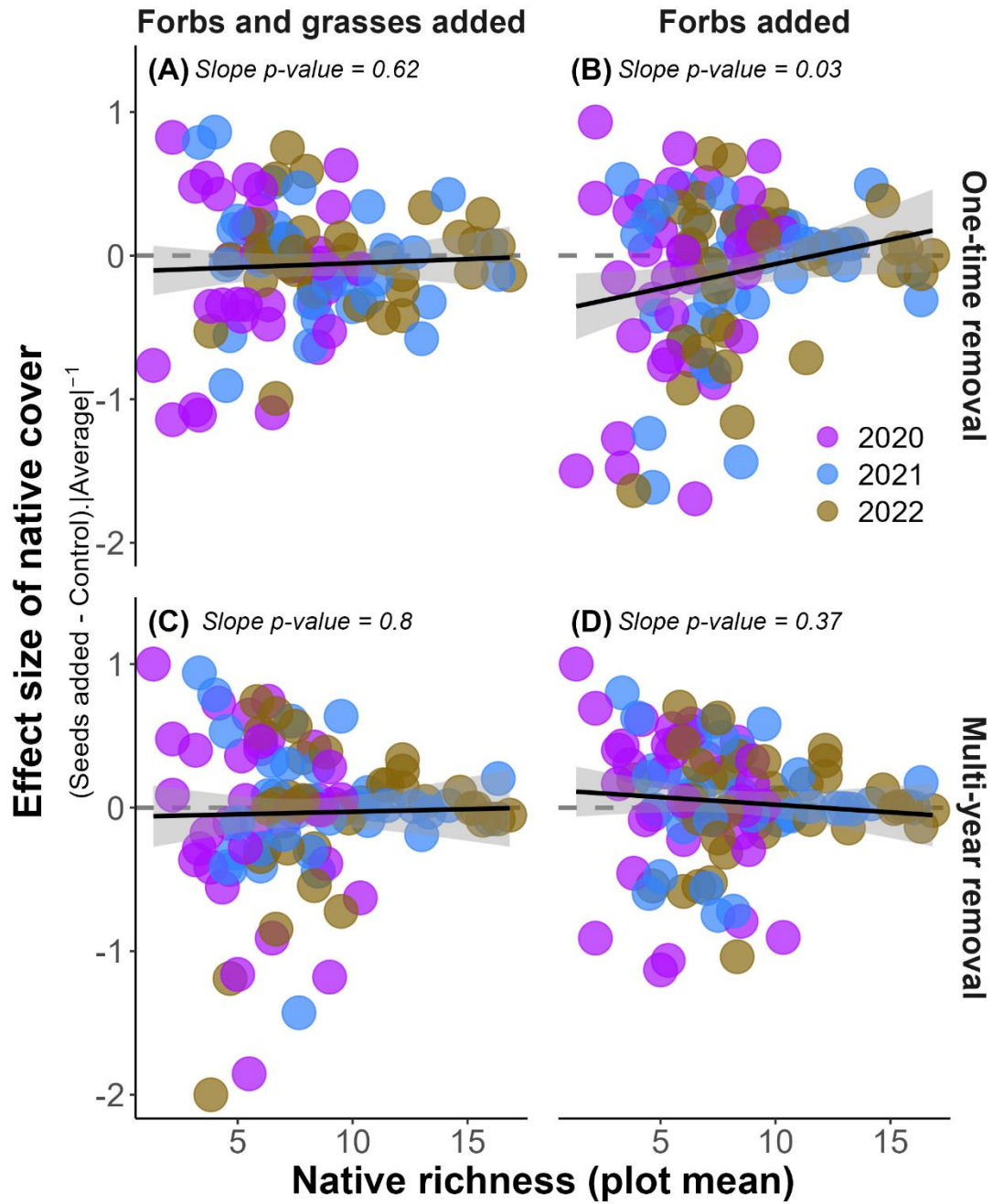
Code S 3.1: Model code.

```
model{

 for(i in 1:P){ #number of subplots
    for(t in 1:Y){ #number of years

      Cover[i,t]~dnorm(C[i,t],tau)#T(0,100) #likelihood, removed T(0,) constrained to be positive
      Cover.pred[i,t]~dnorm(C[i,t],tau)#T(0,100) #predicted values, removed T(0,) to compare
with observed

      residuals[i,t]<-Cover.pred[i,t]-Cover[i,t] #calculating residuals

     }

    C[i,1]<-
B[treatment[i],1]*Cover2019[i]+alpha[1]*RichN[i,2]+alpha[2]*SLA[i,2]+alpha[3]*light[i,2]+al
pha[4]*sm[i,2] #process model for 2020

    C[i,2]<-
B[treatment[i],2]*(w[1]*grassAG20[i]+w[2]*forbsAG20[i]+w[3]*woodyAG20[i])+alpha[1]*Ri
chN[i,2]+alpha[2]*SLA[i,2]+alpha[3]*light[i,2]+alpha[4]*sm[i,2] #process model for 2021

    C[i,3]<-
B[treatment[i],3]*(w[1]*grassAG21[i]+w[2]*forbsAG21[i]+w[3]*woodyAG21[i])+alpha[1]*Ri
chN[i,2]+alpha[2]*SLA[i,2]+alpha[3]*light[i,2]+alpha[4]*sm[i,2] #process model for 2022


  }

for(i in 1:4){
alpha[i]~dnorm(0,0.01) #tested with (0,0.0001) and the results are the same
}

for(i in 1:S){ #number of treatments
for(t in 1:Y){
   B[i,t]~dnorm(0,0.1)
}
}

w[1:3]~ddirich(W[])
for(i in 1:3){
W[i]<-1
}

tau~dgamma(0.0001,0.0001)
varC<-1/tau} #end of model"
```

3.9.1 References

USDA & NRCS (2022) The PLANTS Database National Plant Data Team, Greensboro, NC USA.

Chapter 4 Functional Changes in Understory Forest Community After Invasion Are Driven by Complementarity Rather Than Displacement

4.1 Abstract

Forests support a variety of functions essential for the provisioning of ecosystem services. However, invasive plants can disrupt forest functioning by altering community-level trait distributions. Invasive plants, which are frequently characterized by acquisitive traits, such as higher specific leaf area and N content, may either outcompete native species which have a different set of trait values (displacement), or add to the existing community (complementarity). Understanding which process takes place becomes critical informing management aimed at maintaining ecosystem functionality. Yet, little is known about the impact of invasion on the co-occurring native community trait distribution that can further affect ecosystem functionality these traits provide. To address this knowledge gap, we leveraged survey data on temperate forest understories along a gradient of invasion. We aggregated leaf trait data at the community level by calculating the community-weighted mean of leaf nitrogen, specific leaf area, and leaf dry matter content– traits strongly linked to invasion, sensitive to environmental changes, and affecting ecosystem functions. With this data, we aimed to answer two key questions: (Q1) how does the total community, native plus invasive, change in ecosystem functionality with invasion? (Q2) How does invasion impact native community trait distribution? Our findings show that increasing invasion had a significant positive effect on total community leaf nitrogen, but had no impact on native community trait distributions. This suggests that potential impacts on

ecosystem functions, such as increased primary productivity and nitrogen cycling, are primarily driven by trait complementarity and not displacement. We did not find any differences, in the total or native communities with respect to specific leaf area or leaf dry matter content. By disentangling trait displacement from trait complementarity of ecosystem functions, our study contributes to the growing body of literature aiming to understand how invasion affects forest understories. Additionally, our results provide valuable information to facilitate evidence-based decisions for the management of ecosystem functionality.

Keywords: alien species, ecosystem functioning, introduced species, invasion gradient, leaf economic spectrum, multinormal, non-native species, plant traits.

4.2 Introduction

Forests play a crucial role in providing a multitude of ecosystem services, including carbon storage, water supply, pollination, food production and climate regulation (Thompson *et al.* 2011; Decocq *et al.* 2016; Liang *et al.* 2016; Brockerhoff *et al.* 2017; Mori, Lertzman & Gustafsson 2017). These services are supported by ecosystem functions, e.g., net primary productivity, decomposition, and nutrient cycling, which arise from the interaction and arrangement of biotic and abiotic components and ecosystem processes (Brockerhoff *et al.* 2017). The primary biotic component of forest ecosystems is plant communities (Wallace 2007; Fu *et al.* 2013). Alterations in plant community composition, species relative abundance, and trait distributions as a result of plant invasions are expected to modify the functionality of these ecosystems (Chacón-Labella *et al.* 2023). The relevance of these alterations to native ecosystems can inform management approaches geared at maintaining function. On one hand, if invasive plants are displacing native species, removal of invasive species might not lead to a full functional recovery. On the other hand, if invasive plants are complementing, i.e., adding to the

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native community, their removal may return functionality to its original level. While research has extensively documented linkages between traits and ecosystem functions (EFs), e.g., Lavorel & Garnier 2002; Lavorel & Grigulis 2012; van der Plas *et al.* 2020; Hagan, Henn & Osterman 2023, there is little knowledge on how invasive impacts EFs through changes in the trait distributions of natives or of entire communities, natives plus invasives (Jo, Fridley & Frank 2015; Lee *et al.* 2017; Livingstone, Isaac & Cadotte 2020). In this study, we surveyed plant communities in temperate forest understories across a gradient of invasion, and linked these surveys with trait data from the TRY database (Kattge, Díaz & Lavorel 2011). We then investigated the effect of invasive species on both changing total community and native community trait distributions.

Ecosystem functions are shaped by the environment and plant communities (Brockerhoff *et al.* 2017; Chacón-Labella *et al.* 2023). They are directly influenced by the environment via variations in its biophysical characteristics, but also indirectly, via environmental sorting of plant species which influence composition of plant communities (Chacón-Labella *et al.* 2023). Invasive plants can disrupt some of these functions (Ehrenfeld 2003; Castro-Díez *et al.* 2014; Seabloom *et al.* 2015; Lee *et al.* 2017; Parra-Tabla & Arceo-Gómez 2021) mostly via alterations of competitive hierarchies within the full community, both native and invasive, and within the native community (Pysek *et al.* 2012). Therefore, changes in the functionality of ecosystems via invasion-driven alterations in trait distributions should be reflected in the makeup of both the native community and the total community: native plus invasive (Díaz & Cabido 2001; Lavorel & Garnier 2002).

Plant traits can be aggregated into ecological strategies (Weigelt *et al.* 2021). One of the most well-established strategies is related to the conservation gradient in leaf traits, the leaf

economic spectrum, LES (Wright *et al.* 2004). The LES describes a resource use trade-off from the acquisitive, 'fast' end, to conservative strategies or 'slow' end in terms of carbon processing (Wright *et al.* 2004; Weigelt *et al.* 2021). In our study, we selected traits that are part of the LES, i.e., leaf nitrogen (leaf N), specific leaf area (SLA) and leaf dry matter content (LDMC). These three traits are considered both response and effects traits, i.e., they respond to resource availability and affect ecosystem properties (Díaz & Cabido 2001; Lavorel & Garnier 2002). Both leaf N and SLA have positive links with key ecosystem functions, including aboveground productivity (Lavorel & Garnier 2002; Garnier *et al.* 2004; Violle *et al.* 2007; Reich 2012), leaf decomposition rates (Cornwell *et al.* 2008; Pietsch *et al.* 2014; Jo, Fridley & Frank 2016), N cycling (mainly, nitrification), soil N pools, and soil C pools (Ehrenfeld 2003; Orwin *et al.* 2010; Laughlin 2011; Lienin & Kleyer 2012; Castro-Díez *et al.* 2014; Lee *et al.* 2017). Conversely, increases in LDMC are negatively associated with aboveground productivity (Lavorel & Garnier 2002; Garnier *et al.* 2004), and nitrification rates (Laughlin 2011).

Given the trait aggregation at the end of the LES, it is crucial to recognize that traits are simultaneously shaped by not only environmental conditions but also ecological and evolutionary trade-offs leading to a lack of independence when investigating ecosystem functions from trait distributions (Chacón-Labella *et al.* 2023). This covariation among functional traits contributes to the expectation that multiple traits are associated with a given ecosystem function (Chacón-Labella *et al.* 2023). Among many examples, evidence suggests that increases in both SLA and leaf N content are both positively correlated with net primary productivity (Liu *et al.* 2021). Therefore, isolated analysis of one-to-one trait-EF relationships should be avoided and trait covariation should be accounted for as a pathway to improve the accuracy of predicted impacts from invasion on forest functionality.

Invasive plants usually possess traits that confer advantages in resource acquisition and use (Ordonez & Olff 2013; van Kleunen, Dawson & Maurel 2015; Montesinos 2021), allowing competitive advantages to gain dominance in the community (Bernard-Verdier & Hulme 2019). When these competitive advantages are combined with changes in trait distributions within the native community due to displacement, the potential for amplified effects on ecosystem functions arises (Vila *et al.* 2011; Vilà & Hulme 2017). This is because by dominating the forest understory, invasive species might locally extirpate native species displaying certain traits or favor native species with similar traits, both situations would alter the levels of ecosystem functionality which the native community only provide. However, if invasive species do not alter the trait distribution of the native community but rather add to or complement it, then the impact of invasion on functionality is limited to the dominance of invasive species, and the native community continues to provide similar functionality. These pathways accentuate the need to understand the interplay between increasing levels of invasion, trait distributions, and ecosystem function. This framework is represented in Figure 4.1, where we visually lay out our hypotheses on how invasion could alter trait distribution via these different pathways and, therefore, ecosystem functionality.

The extent to which invasive species alter community trait distribution, particularly, of the native species community and the potential implications of these changes in ecosystem functions have only recently been considered (Livingstone, Isaac & Cadotte 2020; Fernandez *et al.* 2021). Effects of invasion on native communities are usually quantified by comparing invaded and non-invaded communities. While this approach captures the changes in the community, it does not isolate the changes in the remaining native community (Thomsen *et al.* 2016). Some studies looking at those changes have found that invasion does not always impact

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native communities, e.g., Livingstone, Isaac & Cadotte 2020; Fernandez *et al.* 2021; Parra-Tabla & Arceo-Gómez 2021. As a result, recent literature recommends excluding invasive species from response metrics (Thomsen *et al.* 2016). In our study, we adopted this framework to assess whether the traits of the native community changed or not in response to invasion and what kind of change took place. In scenarios where invasion could result in increases in total community trait values (Figure 4.1a), such change might have (i) a positive association, as native species with traits similar to those of invaders would be favored, while dissimilar species would be outcompeted (i.e., displacement, B); (ii) no significant association, as native species traits would remain similar across the invasion gradient (i.e., complementarity, D); and (iii) a negative association, reflecting the selection of native species with trait values different from invaders, while similar species would be outcompeted (i.e., displacement, C). Conversely, invasion could also result in a decrease in total community trait values (Figure 4.1b), with such change similarly potentially leading to, (i) a negative association, where invasion favors native species also with low trait values (i.e, displacement, B); or (ii) no significant association, where native community trait distribution remains unaffected by invasion (i.e., complementarity, C). Lastly, increases in invasive species abundance might not impact total community trait values (Figure 4.1c). This outcome could be the result of (i) no alteration in the trait values of the native community because where this particular trait is strongly influenced by environmental filtering rather than invasion, regardless of species origin (i.e., no impact, B), or (ii) native species with specific trait values are extirpated from the community while invasive complement such function and ecosystem functionality remain similar across invasion gradient (i.e., displacement, C). Our aim was to quantify changes in functional trait at the community level that could result in potential changes in ecosystem function resulting from invasion. Specifically, we asked: (Q1) how does

the total, native and invasive, community change in trait functionality with invasion? (Q2) How does invasion impact native community trait distribution? By understanding the effects of invasion-driven changes in community functionality through alterations in trait distributions, we can improve our ability to predict the consequences of invasions on ecosystems and tailor management practices. Insights on answers to these questions can aid land managers in making evidence-driven decisions when managing ecosystems toward functionality.

4.3 Methods

To understand how plant communities in temperate forests may change their functionality during plant invasion we carried out an observational field study in summer 2021 and sampled plant communities in an area with different levels of invasion. We assessed species identity, native or invasive status, and their abundance. We then calculated the community weighted mean for three critical functional traits, leaf nitrogen, specific leaf area, and leaf dry matter content.

4.3.1 Study location

We conducted this study at the Edwin S. George Reserve (ESGR), a 525-ha ecological reserve in southeast Michigan (-84.022079 W, 42.457242 N). ESGR features a deciduous temperate forest primarily dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.), with common sub-canopy species being red maple (*Acer rubrum* L.), black cherry (*Prunus serotina* Ehrh.), and witch-hazel (*Hamamelis virginiana* L.) (Allen *et al.* 2020). The most prevalent invasive species in the study area are the shrubs autumn-olive (*Elaeagnus umbellata* Thunb.), and barberry (*Berberis thunbergii* DC.) and the vine multiflora rose (*Rosa multiflora* Murray). For a full list of invasive species based on our survey see Table S 4.1. Climate data based on

based on measurements taken from 1991 to 2020 (Arguez *et al.* 2010) for the region indicates

that the mean annual temperature is 8.7˚C, with a minimum mean temperature in January of -

4.7˚C and a maximum in July of 21.3˚C. The average annual rainfall is 822 mm.

4.3.2 Observational setup and plant data

In the summer of 2021, we selected 10 forest stands within ESGR with varying canopy

openness and soil water conditions (Figure S 4.1). Within each forest, we installed three transects

50 x 20 m positioned at least 50 m apart. We further divided each transect into five 20 m^2 plots,

yielding a total of 150 plots. We sampled five different forest strata in portions of the plot (visual

classification modified from Spicer, Mellor & Carson (2020): canopy (20 m^2, live trees with

diameter at breast height [DBH] > 30 cm), subcanopy 1 (10 m^2; live trees 10 cm $\leq$ DBH $\leq$ 30

cm), subcanopy 2 (5 m^2; live trees DBH < 10, and height > 2m), understory (5 m^2; shrubs and

trees 0.5 m < height < 2m) and forest floor (1 m^2; all growth forms height > 0.5 m). Plants were

identified to species and we recorded abundance data as: DBH for the canopy and subcanopy 1

and 2 strata, the maximum diameter and the diameter at a 90-degrees to maximum for the

understory stratum, and percent cover for the floor stratum (estimated visually with a precision

of 1%). We calculated percent cover per species within each stratum after DBH was converted

into basal area, and crown area was calculated as an ellipse based on two measurements, one

being the maximum diameter and other one the diameter at a 90-degrees to maximum. No

individual stratum exceeded 100% cover, but the cumulative species-level cover summed across

strata could surpass 100% cover. Refer to Figure S 4.2 for a diagram of the transect set up.

We based species name harmonization on Taxonomic Name Resolution Service (Boyle *et*

al. 2013) and assigned nativity (i.e., native vs. introduced) following (Reznicek *et al.* 2014).

Here, we consider all introduced species as invasive species given our knowledge of the studied

area. We obtained species level trait data on leaf N (mg/g), specific leaf area (SLA; mm^2/mg) and leaf dry matter content (LDMC; g/g, oven-dry mass of leaf/ water-saturated fresh mass of leaf) from TRY database (Kattge, Díaz & Lavorel 2011). We calculated the community weighted mean (CWM) within species coverage percentage following, e.g., Lavorel *et al.* 2008; Le Bagousse-Pinguet *et al.* 2017, for each trait and community type: (a) total community, encompassing both invasive and native species, and (b) native community, consisting of native species only. To maintain a representative sample of each plot-level community, we analyzed only plots with a minimum of 80% of cover with associated trait values across all three traits as suggested by Pakeman & Quested (2007). The Pielou's Evenness index was calculated at the plot level for both community types by dividing the Shannon index per log of richness. The Shannon index was obtained via the '*vegan*' package (Oksanen *et al.* 2022).

4.3.3 Environmental data

We collected all environmental data during the summer of 2021. To estimate light availability, we took canopy photos at three points within each plot in August. We used a fish-eye lens attached to a tripod-mounted smartphone positioned at a height of 1.2 m. Photos were analyzed following methods outlined by Bianchi *et al.* (2017). To estimate soil water availability, we measured soil volumetric water content (%) in May, June and August using the Fieldscout TDR300 Soil Moisture Meter at the same points we took canopy photos within each plot. In the model, we decided to use data from August only which represented the overall driest month among the three months. We obtained one measurement per plot for both light and soil water measurements by calculating the mean and associated standard deviation across the three points. We obtained soil nutrient availability estimates by deploying one ion-exchange resin capsule at a randomly selected transect within each forest. We purchased the capsules from UNIBEST which

was also responsible for their analysis. We performed all data wrangling using the family of packages "tidyverse" (Wickham *et al.* 2019) in R (R Core Team 2022).

4.3.4 Data analysis

To answer how invasion may affect plant community functionality via changes in trait distribution (Q1), for each plot we analyzed community weighted mean (*CWM*) of each trait for the total community (native and invasive; Figure 4.1 green). We used a multinormal (MNR) likelihood to analyze the three traits simultaneously. We used this approach to account for the established relationships across the three selected traits in the LES (Wright *et al.* 2004). Plot-level (i) community weighted mean for each trait (k) was estimated as a function of invasive percent cover, to assess the effect of invasion ($CoverInv$), of native richness ($NativeRich$) and Pielou's Evenness index for the total community ($EvennessT$) to account for any effects of diversity on trait distributions, and of light ($Light$) and soil water availability ($SoilWater$) as these resources may also drive the distribution of traits (Chacón-Labella *et al.* 2023). The likelihood:

$$CWM_{i,k} \sim Normal_k(muT_{i,k}, \Sigma T_{k,k})$$

Being the process model:

$$muT_{i,k} = A_{forest(i),k} + \alpha_1 CoverInv_{(i,k)} + \alpha_2 NativeRich_{(i,k)} + \alpha_3 EvennessT_{(i,k)}$$
$$+ \alpha_4 Light_{(i,k)} + \alpha_5 SoilWater_{(i,k)}$$

Parameter A represents a different intercept for each forest, estimated from an overall intercept value, hyperparameter AA. Parameter Σ represents a variance-covariance matrix of the three CWM. We estimated all parameters from non-information prior distributions,

$AA_*, \alpha_* \sim Normal(0,1000)$, and $\Sigma_{k,k} \sim Wishart(\begin{smallmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{smallmatrix}, k)$. We retrieved posterior

distributions and parameter values after convergence, using 100,000 iterations with a thinning

interval of 50. We calculated correlation values between each pair of CMW ($\rho_{x,y}$) from the

covariance and standard deviation in Σ, $\rho_{x,y} = \frac{Cov_{x,y}}{Stdev_x * Stdev_y}$.

To assess how invasion impacts native community trait distribution (Q2), we ran a

similar analysis as above by changing the response variable to the plot-level community

weighted mean of each trait for native species only (Figure 4.1 purple). Among the covariates,

we only modified the Pielou's Evenness index to reflect calculation of the native species only.

We generated model predictions of each CWM, total community and only natives, along a

gradient of invasion by setting all other model covariates to their mean values. To quantify

changes in community functionality due to invasion, total community and only natives, we

calculated the difference between the predicted community weighted mean for each trait under

its maximum invasion and at no invasion (Figure 4.1).

We ran the MNR models in JAGS (Hornik *et al.* 2003) through R using "rjags" (Plummer

2022). We retrieved posterior distributions and parameters values after convergence, using the

least 100,000 iterations with a thinning interval of 500. We assessed model fit by plotting the

observed response data as a function of the response data predicted by the model. We then fit a

simple linear regression and retrieved R^2 values. We checked model convergence by visually

inspecting plots of posterior distributions of each model parameter retrieved. Model code is

provided in the Supporting Information, Code S 2.

4.4 Results

We excluded 60 plots (or 40% of the total surveyed plots) from our analysis due to

missing trait values, resulting in a total sample size of 90 plots. These exclusions also

consequently lead to a reduction of the total number of forests from 10 to nine. The invasive

percent cover varied from 0 (13 plots) to 184 % (1 plot), with a mean of 56.1 %. The plot-level

richness of native species ranged from four (3 plots) to 21 species (1 plot), with a mean of 11

species. The mean value of Pielou's Evenness index for the total community was 0.65 and for the

natives only, 0.71. At the plot level, light availability ranged from 6.85 % to 54.84 % of full

sunlight across plots. And soil water, measured as volumetric water content, ranged from 2.7 %

to 20 %. All parameter values from the analyses are reported in Table S 4.2, and model fit in

Figure S 4.3. The general patterns of trait distributions (i.e., raw data) across invasion gradients

shows an increase in total community weighted mean (CWM) of leaf nitrogen concentration

(leaf N) with increased level of invasion (Figure 4.2, top panels). For CWM of specific leaf area

(SLA), data patterns showed a decrease in the variability of trait distribution but held similar

mean values (Figure 4.2, middle panels). The CWM of leaf dry matter content (LDMC) had

almost no visual change across levels of invasion (Figure 4.2, lower panels). Finally, the native

CWM of all traits was visually similar across levels of invasion and trait types (Figure 4.2,

purple curves).

Covariate effects on community weighted mean trait values

Increase in percent cover of invasive species was positively and significantly associated

with total community weighted mean distributions of both leaf N and SLA. Conversely, across

all traits, CWM of only natives remained unchanged during invasion (Figure 4.3). Increases in

native richness were associated with a decrease in leaf N community trait distributions

irrespective of invasive species being in the CWM estimates. Higher soil water was associated

with higher CWM of SLA values, regardless of community grouping (Figure 4.3). All other

covariates had no significant associations with CWMs.

(Q1) How does the community change in trait functionality with invasion?

Simulations showed an increase in the total community leaf N with increasing level of invasion (Figure 4.4, top panel green lines). Total community values of CWM leaf N at maximum invasion were significantly different from those at no invasion (Figure 4.5a). The total community SLA values tended to increase with higher levels of invasion (Figure 4.4, middle panel), but the association was not significant (Figure 4.5a). Total community LDMC values remained similar across the gradient of invasion.

(Q2) How does invasion impact native community trait distribution?

There was a gradual positive slope in the native community SLA values with higher levels of invasion (Figure 4.4, middle panel purple lines). However, the difference between predicted trait values at highest invasion and no invasion was not significant (Figure 4.5a). Native community leaf N and LDMC values were similar across invasive cover levels.

Correlation between traits weighted by species abundance

Community weighted mean leaf N and SLA trait values were positively and significantly associated in communities computed with and without invaders (Figure 4.5b). And both leaf N and SLA trait values were negatively associated with LDMC, although relationships were not significant (Figure 4.5b).

4.5 Discussion

Invasive plants can affect the functioning of ecosystems in a variety of ways (Charles & Dukes 2007; Vila *et al.* 2011; Vilà & Hulme 2017), by impacting the growth, abundance, diversity, and richness of native plants (Vila *et al.* 2011; Pysek *et al.* 2012), as well as by altering trait distributions of the co-occurring native plants (Loiola *et al.* 2018; Fried *et al.* 2019; Sodhi *et al.* 2019; Livingstone, Isaac & Cadotte 2020; Fernandez *et al.* 2021). The consequences of plant

invasion on EFs through changes in native community trait distributions have only recently begun to be explored (Livingstone, Isaac & Cadotte 2020; Fernandez *et al.* 2021). We investigated these changes by analyzing both total and native communities. Our results revealed that invasion significantly and positively changed total community leaf N and SLA, although differences in community-level trait values were only significant for leaf N. In contrast, native community functionality remains largely unchanged (i.e., no loss of function) across the invasion gradient for the traits we analyzed, indicating invasive species are complementing and not displacing native function. Overall, our results provide insights into the extent of alterations in ecosystem functions via community-level responses to invasion.

Traits from plant invaders often show substantial differences compared to their native counterparts (Van Kleunen, Weber & Fischer 2010; Ordonez & Olff 2013). Invasive plants tend to have higher trait values for both leaf N and SLA while maintaining low investment in leaf tissue resulting in low LDMC trait values (Leishman *et al.* 2007; Van Kleunen, Weber & Fischer 2010; Ordonez & Olff 2013; Henn, Yelenik & Damschen 2019). These trait differences are particularly relevant in explaining the success and dominance of invasive species in high-resource environments, such as post-disturbances or in canopy gaps (Funk 2013; Jauni, Gripenberg & Ramula 2015; Ibáñez *et al.* 2021). However, these differences are also present, albeit less frequently, in low-resource environments, such as forest understories (Funk & Vitousek 2007; Funk 2013). Consequently, when invasive species dominate forest understories, they likely promote shifts in the community-level mean trait values, thereby modifying the functionality associated with these traits (Cadotte *et al.* 2017; Livingstone, Isaac & Cadotte 2020; Fernandez *et al.* 2021). What is not clear in this process is whether invasive species are displacing or complementing the functionality of the native community.

4.5.1 (Q1) How does the community change in trait functionality with invasion?

Our results show that communities with high dominance of invasive plants were associated with higher levels of leaf N, and had a tendency towards higher levels of SLA. These findings suggest that as invasive species become abundant, community-level trait characteristics change and therefore community functionality also changes. Increases in leaf N and SLA at the community level have positive effects on aboveground biomass, N cycling rates, and soil N pools (Lavorel & Garnier 2002; Ehrenfeld 2003; Garnier *et al.* 2004; Violle *et al.* 2007; Orwin *et al.* 2010; Laughlin 2011; Lienin & Kleyer 2012; Reich 2012; Castro-Díez *et al.* 2014; Lee *et al.* 2017). In fact, we observed a positive association between elevated levels of soil ammonium, soil nitrate, and total soil N with increasing invasion abundance at the forest level (Table S 4.3 one ion-exchange resin capsules per forest during the summer of 2021).

The lack of a significant effect of invasion on LDMC contrasted with our expectations, suggesting that invasive species exhibit similar strategies with respect to this trait when compared to natives. It is likely that regardless of their acquisitive ability, invaders also need to have some level of shade tolerance to cope with low-light conditions (Funk & Vitousek 2007; Funk 2013). Investment in leaf construction, e.g., high LDMC, increases leaf lifespan and confers shade tolerance advantages in forested environments (Funk 2013; Pérez-Harguindeguy *et al.* 2016). Also, LDMC tends to positively correlate with physical resistance and protection against herbivory (Pérez-Harguindeguy *et al.* 2016), characteristics that also slow tissue breakdown by associated biota (Pichon *et al.* 2020) and are common in understory plants. Therefore, decomposition rates likely interact with LDMC, trait values which were unchanged across invasion levels.

4.5.2 (Q2) How does invasion impact native community trait distribution?

We attempted to capture invasive impact on the native community and changes in ecosystem's functionality by differentiating between displacement and complementarity of natives once invasion is in place. After excluding invasive species from our response metric, our results showed no changes in the CWM of native species for all three traits across the invasion gradient (Figure 4.4 and Figure 4.5a). This result indicates that the shifts observed in CWM trait distributions of the total community (discussed above) and consequent changes in ecosystem functionality are a sole consequence of invasive species complementing the native community. Our findings align with most other studies that explored a similar approach in other ecosystems. These studies also found no effects of invasion on the CWM of SLA (Fried *et al.* 2019; Livingstone, Isaac & Cadotte 2020; Fernandez *et al.* 2021) or LDMC (Fried *et al.* 2019) of the native community (but see Loiola *et al.* 2018).

4.5.3 Correlation between traits weighted by species abundance

Leaf traits can be arranged along the acquisitive-conservation gradient, representing a trade-off between leaf structures' life-span and resource acquisition and allocation (Wright *et al.* 2004). On one end, species with acquisitive leaves are characterized by low investment in tissue per area, high nitrogen content, and high specific leaf area (Wright *et al.* 2004; Diaz *et al.* 2016; Weigelt *et al.* 2021). These traits are associated with lower survival, shorter leaf lifespan, higher light demands, and higher maximum photosynthetic rates (Wright *et al.* 2004; Diaz *et al.* 2016). On the opposite end, plant species with conservative leaves exhibit tolerance to low resource environments by heavily investing in leaf tissue, resulting in higher leaf mass per area and leaf dry matter content, longer leaf lifespan, and chemical and physical protection from herbivory all at the expense of slow growth (Wright *et al.* 2004; Diaz *et al.* 2016). Therefore, leaf traits positioned within each end of the spectrum are expected show positive correlations, while traits

at opposite ends should have negative correlations (Wright *et al.* 2004; Diaz *et al.* 2016). We found significant and positive correlations between leaf nitrogen and SLA, while both traits tended to be negatively correlated to LDMC, although not significant (Figure 4.5b). These associations align with the expected directionalities, and utilizing multinormal distributions allowed us to simultaneously account for trait covariation while exploring the effects of environmental and biotic covariates in explaining community-level trait variation.

4.5.4 Covariate effects on community weighted mean trait values

Richness and evenness are important metrics for understanding both ecosystem functionality and the impact of invasion. Native richness is expected to have positive effects on functionality, particularly on productivity, such as in the context of biodiversity-ecosystem-function (BEF) framework where positive relationships have been extensively documented (Hector & Bagchi 2007; Isbell *et al.* 2011; Maestre *et al.* 2012; Tilman, Isbell & Cowles 2014; Jing *et al.* 2015; Liang *et al.* 2016). Therefore, it seems counter-intuitive that invaded areas which are usually associated with low native diversity or low richness, either because invaders outcompete natives or because they colonize areas already with low native richness, still are highly productive (Livingstone, Isaac & Cadotte 2020). The loss of functionality via displacement of natives can be then compensated by the high performance of invaders with high dispersal abilities (Rejmanek & Richardson 1996; van Kleunen, Dawson & Maurel 2015), high resource-use efficiency (Funk & Vitousek 2007; Heberling & Fridley 2013) and/or presenting novel strategies, e.g., N-fixing invasive species such as *Eleagnus umbellata* (Paschke, Dawson & David 1989; Perry *et al.* 2010). Further, when resources are under-explored by natives in less diverse sites, invasive species likely occupy empty niches, complementing the system's functionality (Elton 1958; Chase & Leibold 2003; Hierro, Maron & Callaway 2005).

Our findings reveal that richer native communities, irrespective of community grouping (i.e., total or natives only), showed lower leaf N (Figure 4.3a). For all other traits, we did not find any association with richness (Figure 4.3b and Figure 4.3c). These results suggest that changes in functionality via increases in leaf N due to invasion are dissociated from native richness and related to a complementary effect of invasives only (Figure 4.4). It also indicates that, in our study system, native communities tend to be selected to have more conservative traits along the conservation gradient, characterized by low leaf nitrogen content, a trait linked to protection against herbivory (Laliberté *et al.* 2012; Weigelt *et al.* 2021 but see, Zheng *et al.* 2015). The relationship between evenness and EFs are believed to be closely linked to environmental variability, particularly with respect to productivity (Hillebrand, Bennett & Cadotte 2008). This is because more even communities (i.e., less dominance by one or a few species) are expected to have higher productivity as those communities would hold a larger diversity of species with different strategies to adapt to environmental variability (Hillebrand, Bennett & Cadotte 2008). Our results revealed no significant association of evenness with any of the traits and community groupings, suggesting that changes in species dominance with increasing invasion was not a significant factor driving alterations in ecosystem functionality via changes in leaf N trait distributions. We speculate that the range of variability in environmental conditions (namely, light and soil water availability) in our study site were insufficient to capture significant relationships between evenness and CWM traits. Despite sampling plant communities across a range of environmental conditions within our study area, the overall climatic factors that shape these communities are the same (Arguez *et al.* 2010).

Environmental factors shape both plant community composition and structure, as well as the overall functioning of the ecosystems (Jing *et al.* 2015; Chacón-Labella *et al.* 2023). In

forested ecosystems, in particular, light availability and soil water content are among the main limiting resources for species survival and growth (Landuyt *et al.* 2019), thereby influencing community trait distributions (Chacón-Labella *et al.* 2023). Our results revealed that soil water had a significant and positive effect on community-level SLA for both community types, while no other significant effects of soil water or light availability were observed. These significant results align with the literature as SLA is associated with higher growth and photosynthesis rates, which heavily rely on water and nutrient supply (Xu & Zhou 2011; Flexas *et al.* 2012; McAdam & Brodribb 2015; Novick *et al.* 2016; Lambers & Oliveira 2019; Westerband *et al.* 2023). Surprisingly, soil water did not have an effect on leaf N despite its high correlation with SLA (Figure 4.5b) and their shared position on the "fast" end of the LES (Wright *et al.* 2004; Diaz *et al.* 2016).

4.6 Conclusions

Invasion can impact community-level trait distributions, and consequently, ecosystem functionality through either displacement or complementarity of native species. To distinguish between these two processes, the effects of invasives on total (i.e., invasives and natives) versus native community trait distributions need to be differentiated (Thomsen *et al.* 2016). By doing so, our results indicate that for our study system, invasive plants indeed lead to changes in ecosystem functionality by increasing the mean trait values of leaf N, while having no significant impact on the trait distributions of the native community. Therefore, alterations in ecosystem functionality within our study system, based on representative traits of the LES, are primarily driven by the increased abundance of invasive species complementing the functionality exhibited by the native community. These findings have important management implications: if invasive species were to be removed, the co-occurring native community could recover its original trait

distribution with little impact on ecosystem functionality. In contrast, if invasion had displaced

native species function, the removal of invasive species would likely fail to achieve a full

recovery of functionality. By quantifying invasion-driven changes in ecosystem function and

differentiating between complementarity versus displacement, our study provides essential

information to allow land managers to make informed decisions regarding such consequences on

ecosystem functionality.

4.7 References

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4.8 Figures
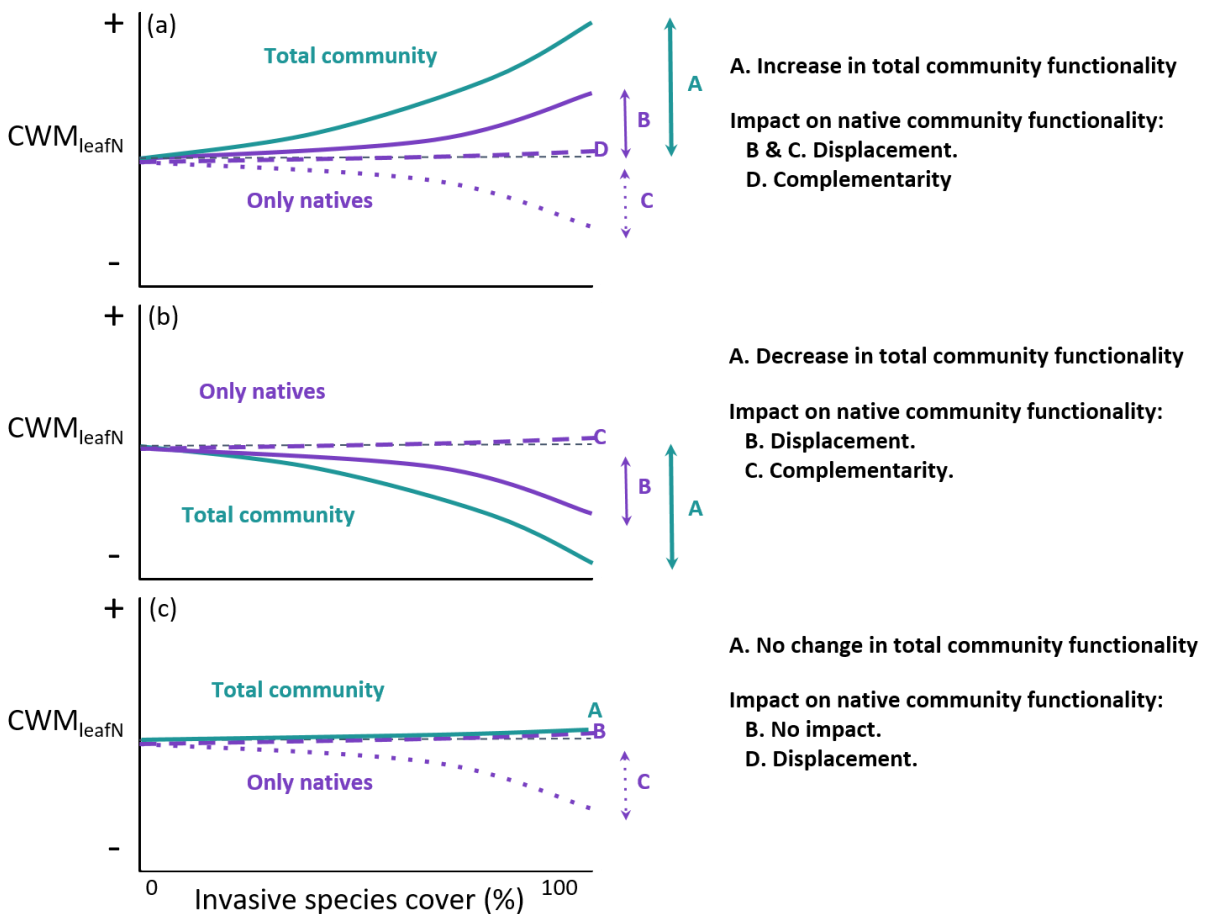
Figure 4.1*:* Conceptual figure of hypothesized ways in which invasion can affect total and native community functionality. CWM$_{leafN}$: community weighted mean of leaf nitrogen concentration. In scenarios where invasion could result in increases in total community trait values **(a)**, such change might lead to (i) a positive association, as native species with traits similar to those of invaders would be favored, while dissimilar species would be outcompeted (i.e., displacement, B); (ii) no significant association, as native species traits would remain similar across the invasion gradient (i.e., complementarity, D); and (iii) a negative association, reflecting the selection of native species with trait values different from invaders, while similar species would be outcompeted (i.e., displacement, C). Conversely, invasion could also result in a decrease in total community trait values **(b)**, which such change similarly leading to, (i) a negative association, where invasion favors native species also with low trait values (i.e, displacement, B); or (ii) no significant association, where native community trait distribution remains unaffected by invasion (i.e., complementarity, C). Lastly, increases in invasive species abundance might not impact total community trait values **(c)**. This outcome could be the result of (i) no alteration in the trait values of the native community where this particular trait regardless of species origin is strongly influenced by environmental filtering rather than invasion (i.e., no impact, B), or (ii) native species with specific trait values are extirpated from the community while invasive complement such function and ecosystem functionality remain similar across invasion gradient (i.e., displacement, C).
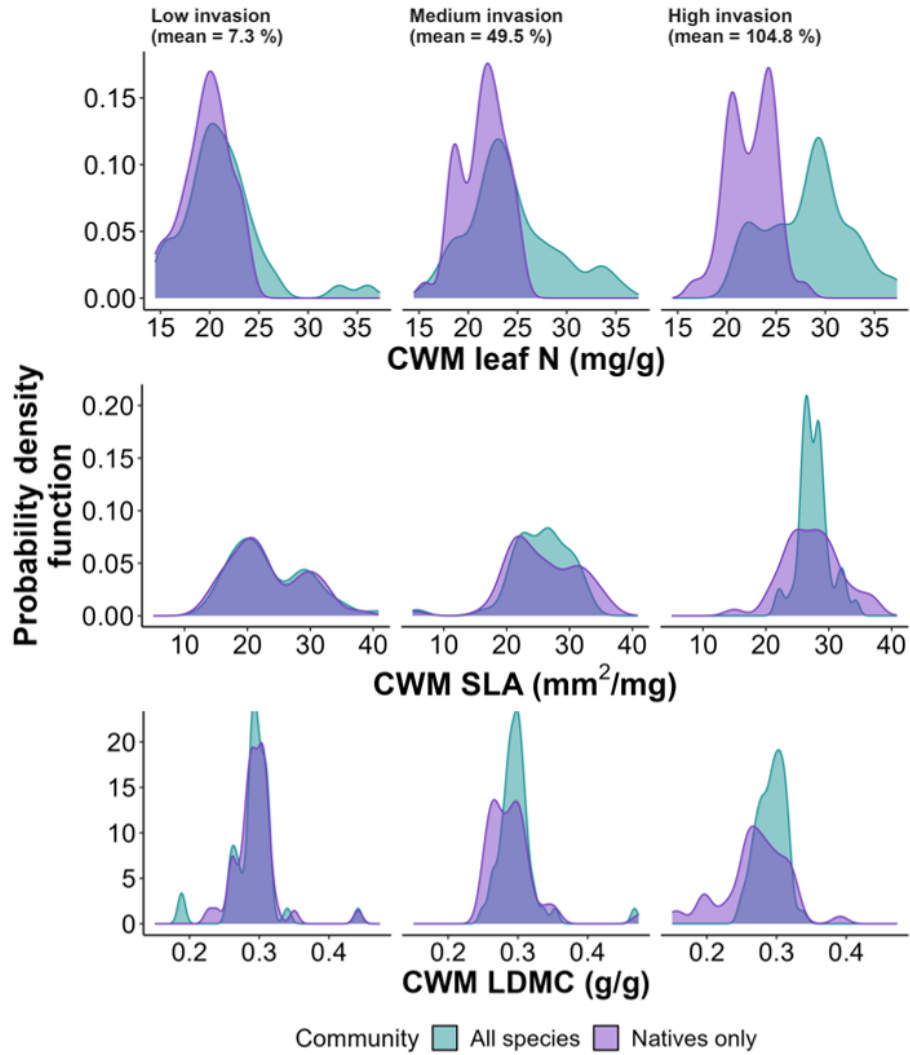
Figure 4.2: Trait distributions of plot-level community weighted mean (CWM) values per trait (leaf N: leaf nitrogen concentration; SLA: specific leaf area; LDMC: leaf dry matter content). Levels of invasion (from lowest to highest, left to right) were defined to contain an equal number of plots (n = 45).
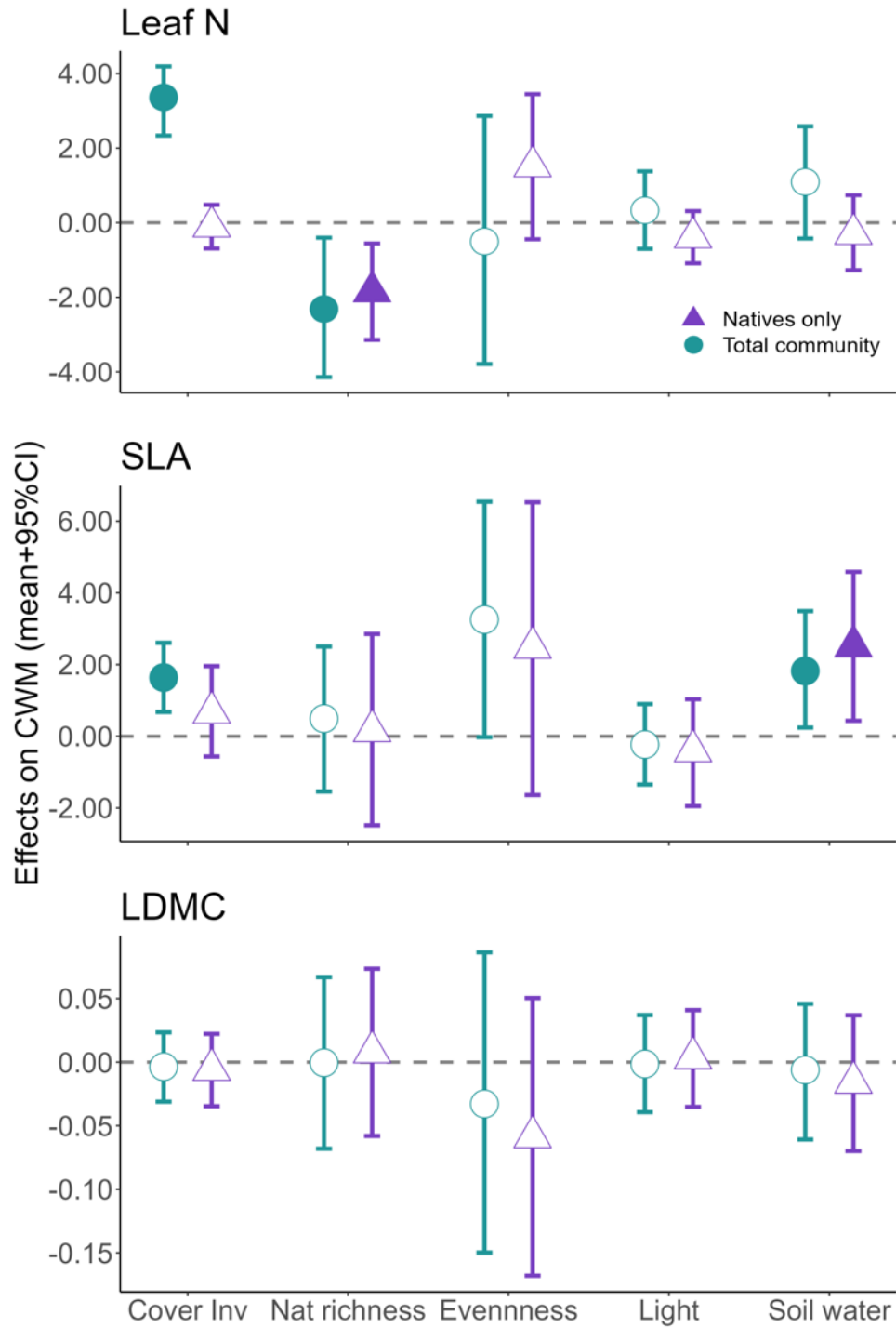
Figure 4.3: Posterior means and 95% CI of parameter values (standardized for comparisons) from covariates included in the multivariate multiple regression models. CWM: community weighted mean; Leaf N: leaf nitrogen concentration; SLA: specific leaf area; LDMC: leaf dry matter content; Cover Inv: invasive percent cover; Nat richness: native richness. Credible intervals [CI] that do not cross zero are statically significant (solid symbols).
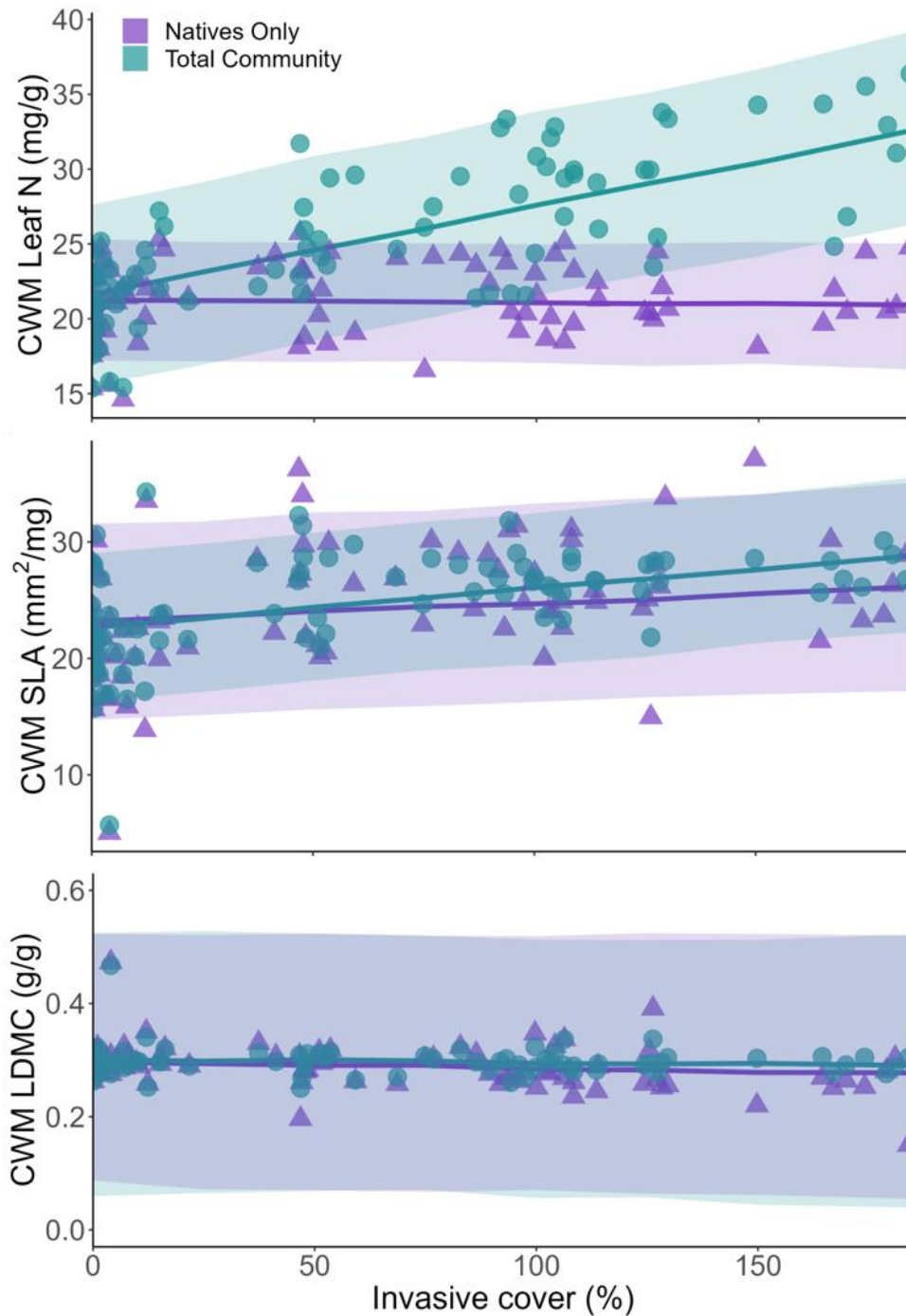
Figure 4.4: Model predictions of community weighted mean (CWM) per trait and community type (total community in purple and natives only in green) in the gradient of invasion. Predictions were performed with all covariates (besides invasive cover) at their mean value. Points are raw data for each plot. Leaf N: leaf nitrogen concentration; SLA: specific leaf area; LDMC: leaf dry matter content.

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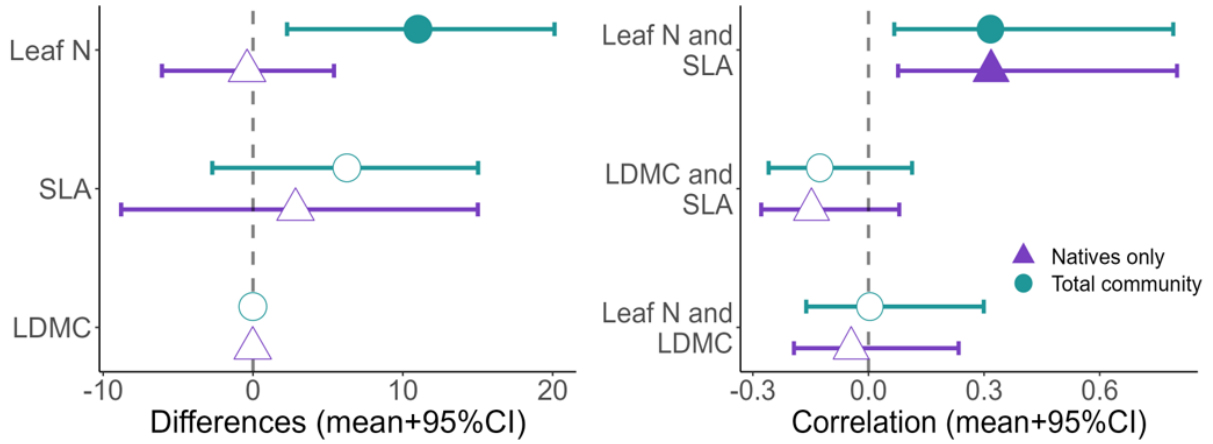
Figure 4.5: (a) Differences of predicted community weighted mean trait values between at maximum invasion and at no invasion. (b) Correlation values of each paired trait comparison derived from parameter Σ. Leaf N: leaf nitrogen concentration; SLA: specific leaf area; LDMC: leaf dry matter content. Credible intervals [CI] that do not cross zero are statically significant (solid symbols).

4.9 Supporting Information

Figure S 4.1: Map of the study location. Letters correspond to the different forests.
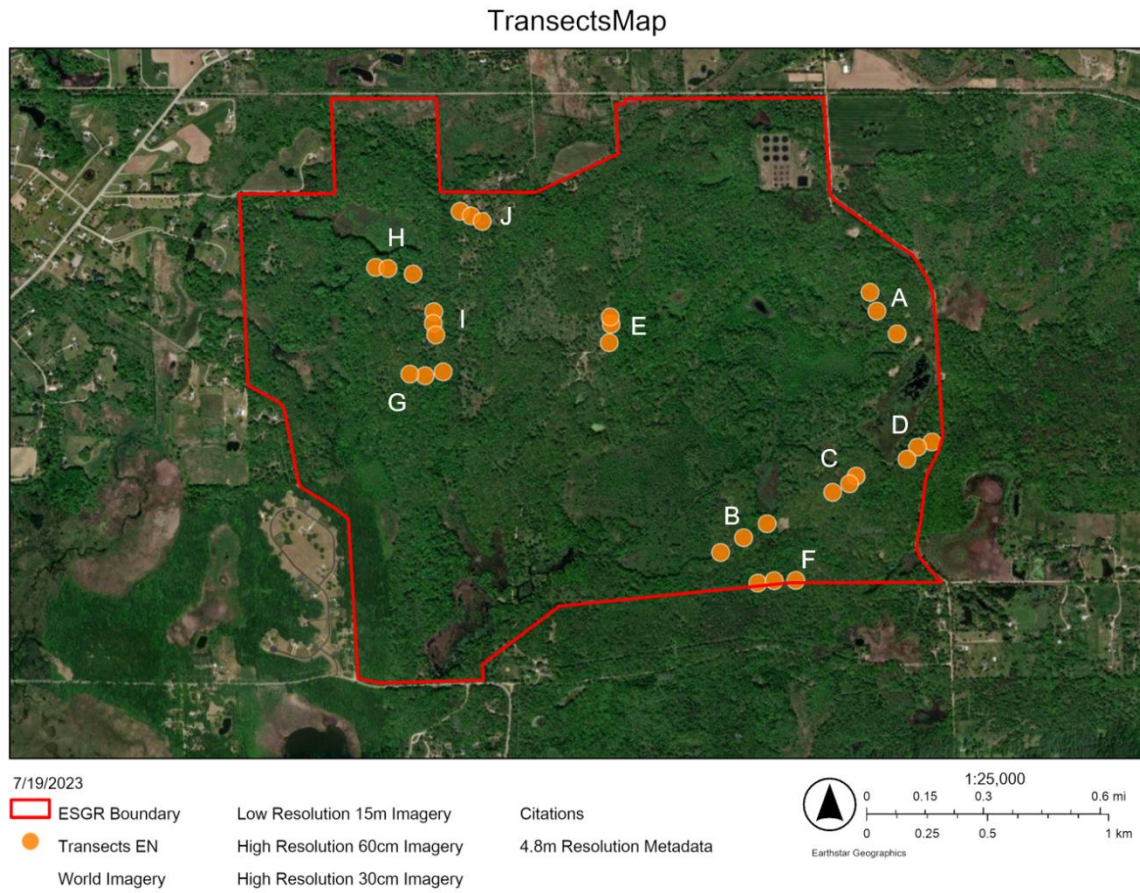
Figure S 4.2: Diagram of the transect set up. Not that the square sizes are not in scale.

Detailed subplots information:

Stratum: canopy
Live trees DBH >30 cm, height > 2m
Data on: DBH and height

Stratum: subcanopy 1
Live trees 10 cm ≤ DBH ≤ 30 cm, height > 2m
Data on: DBH and height

Stratum: subcanopy 2
Live trees DBH < 10, height > 2m
Data on: DBH and height

Stratum: understory
Shrubs + trees 0.5 m < height < 2m
Data on: max and min crown length, and height

Stratum: floor
All growth forms height > 0.5 m
Data on: % cover

Environmental data:
- Canopy photos: 1x in August
- Soil moisture: 3x (May, June, August)
- Plot 1 environmental data$_i$ = mean + SD of three points

Figure S 4.3: Model fit. Left panels are model using values for the total community (●) and right panels (▲), for natives only. Leaf N: leaf nitrogen concentration; SLA: specific leaf area; LDMC: leaf dry matter content.

Leaf N

$y = -0.527 + 1.021\ x$
$R^2 = 0.67$

$y = -2.563 + 1.121\ x$
$R^2 = 0.46$

SLA

$y = -1.210 + 1.050\ x$
$R^2 = 0.64$

$y = -2.569 + 1.107\ x$
$R^2 = 0.48$

LDMC

$y = -0.063 + 1.211\ x$
$R^2 = 0.21$

$y = -0.015 + 1.052\ x$
$R^2 = 0.33$
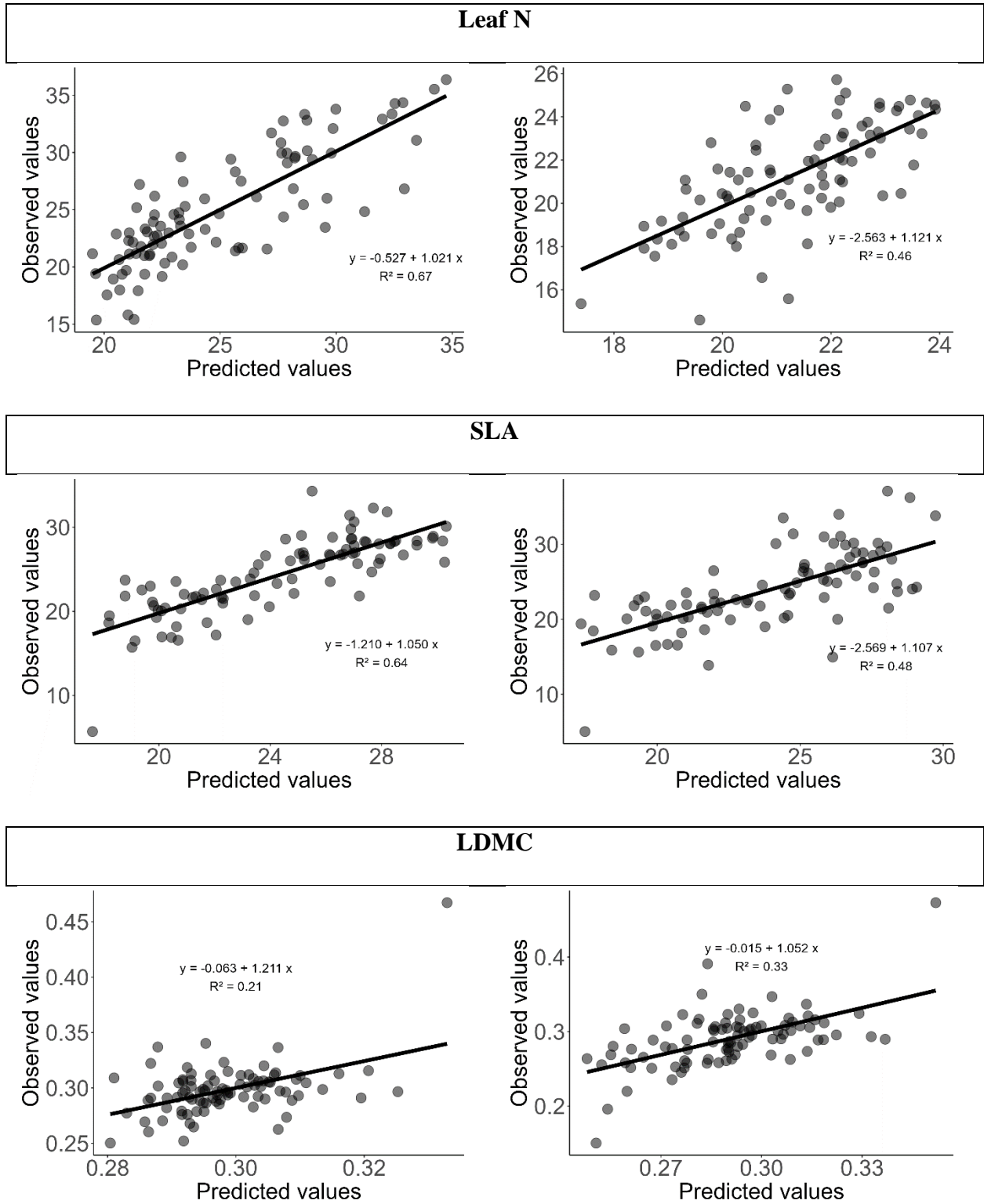
Code S 2: Model code.

```
data{


 #scenarios

 coverInvP<-c(0,25,50,75,100,125,150,185)


 for(i in 1:P){

   #estimating Light

   lightTau[i]<-1/pow(lightSD[i],2)

   light[i]~dnorm(lightM[i], lightTau[i])

   #estimating Soil Moisture

   soilwaterTau[i]<-1/pow(soilwaterSD[i],2)

   soilWater[i]~dnorm(soilwaterM[i], soilwaterTau[i])

  }

}

model{

 for(i in 1:P){


  cwmT[i,1:3]~dmnorm(muT[i,],RT[,]) #likelihood total community

  cwmT.pred[i,1:3]~dmnorm(muT[i,],RT[,]) #predicted

  cwmN[i,1:3]~dmnorm(muN[i,],RN[,]) #likelihood natives only

  cwmN.pred[i,1:3]~dmnorm(muN[i,],RN[,]) #predicted


  #residuals

  residualsT[i,1:3]<-cwmT.pred[i,1:3]-cwmT[i,1:3]

  residualsN[i,1:3]<-cwmN.pred[i,1:3]-cwmN[i,1:3]
```

```
#process models - total community

muT[i,1]<-

A[forest[i]]+alpha[1]*coverInv[i]+alpha[2]*richnessNat[i]+alpha[3]*evennessT[i]+alpha[4]*light[i]+alp

ha[5]*soilWater[i]

muT[i,2]<-

B[forest[i]]+beta[1]*coverInv[i]+beta[2]*richnessNat[i]+beta[3]*evennessT[i]+beta[4]*light[i]+beta[5]*s

oilWater[i]

muT[i,3]<-

C[forest[i]]+gamma[1]*coverInv[i]+gamma[2]*richnessNat[i]+gamma[3]*evennessT[i]+gamma[4]*light

[i]+gamma[5]*soilWater[i]


#process models - natives only

muN[i,1]<-

G[forest[i]]+zeta[1]*coverInv[i]+zeta[2]*richnessNat[i]+zeta[3]*evennessN[i]+zeta[4]*light[i]+zeta[5]*s

oilWater[i]

muN[i,2]<-

H[forest[i]]+eta[1]*coverInv[i]+eta[2]*richnessNat[i]+eta[3]*evennessN[i]+eta[4]*light[i]+eta[5]*soilW

ater[i]

muN[i,3]<-

I[forest[i]]+theta[1]*coverInv[i]+theta[2]*richnessNat[i]+theta[3]*evennessN[i]+theta[4]*light[i]+theta[5

]*soilWater[i]


}


#priors
```

```
##intercepts

for(i in 1:S){ #number of areas

  A[i]~dnorm(AA,tauA)

  B[i]~dnorm(BB,tauB)

  C[i]~dnorm(CC,tauC)

  G[i]~dnorm(GG,tauG)

  H[i]~dnorm(HH,tauH)

  I[i]~dnorm(II,tauI)

}


AA~dnorm(0,0.0001)

tauA~dgamma(0.0001,0.0001)

varA<-1/tauA


BB~dnorm(0,0.0001)

tauB~dgamma(0.0001,0.0001)

varB<-1/tauB


CC~dnorm(0,0.0001)

tauC~dgamma(0.0001,0.0001)

varC<-1/tauC


GG~dnorm(0,0.0001)

tauG~dgamma(0.0001,0.0001)

varG<-1/tauG
```

```
HH~dnorm(0,0.0001)

tauH~dgamma(0.0001,0.0001)

varH<-1/tauH


II~dnorm(0,0.0001)

tauI~dgamma(0.0001,0.0001)

varI<-1/tauI


##predictors

for(i in 1:5){

 alpha[i]~dnorm(0,0.001)

 beta[i]~dnorm(0,0.001)

 gamma[i]~dnorm(0,0.001)

 zeta[i]~dnorm(0,0.001)

 eta[i]~dnorm(0,0.001)

 theta[i]~dnorm(0,0.001)

}


##variance-covariance matrix

RT[1:3,1:3]~dwish(OmegaT[,],3)

RN[1:3,1:3]~dwish(OmegaN[,],3)


#scenarios

for(j in 1:8){

 # likelihoods

 cwmTP[j,1:3]~dmnorm(muTP[j,],RT[,]) #likelihood total community
```

```
    cwmNP[j,1:3]~dmnorm(muNP[j,],RN[,]) #likelihood natives only


    #covariates are mean values
    #process models - total community
    muTP[j,1]<-
AA+alpha[1]*coverInvP[j]+alpha[2]*11.04444+alpha[3]*0.6454031+alpha[4]*13.96526+alpha[5]*9.741
111
    muTP[j,2]<-
BB+beta[1]*coverInvP[j]+beta[2]*11.04444+beta[3]*0.6454031+beta[4]*13.96526+beta[5]*9.741111
    muTP[j,3]<-
CC+gamma[1]*coverInvP[j]+gamma[2]*11.04444+gamma[3]*0.6454031+gamma[4]*13.96526+gamma
[5]*9.741111


    #process models - natives only
    muNP[j,1]<-
GG+zeta[1]*coverInvP[j]+zeta[2]*11.04444+zeta[3]*0.7112588+zeta[4]*13.96526+zeta[5]*9.741111
    muNP[j,2]<-
HH+eta[1]*coverInvP[j]+eta[2]*11.04444+eta[3]*0.7112588+eta[4]*13.96526+eta[5]*9.741111
    muNP[j,3]<-
II+theta[1]*coverInvP[j]+theta[2]*11.04444+theta[3]*0.7112588+theta[4]*13.96526+theta[5]*9.741111
    }
 # #differences
 for(z in 1:3){
 diffT[z]<-cwmTP[8,z]-cwmTP[1,z]
 diffN[z]<-cwmNP[8,z]-cwmNP[1,z]}
}
```

Table S 4.1: List of invasive plant species found in our survey. Growth forms and duration follows USDA PLANTS (USDA and NRCS 2022).

Scientific name	Growth Form	Duration
Alliaria petiolata (M. Bieb.) Cavara & Grande	forb	biennial
Berberis thunbergii DC.	shrub	perennial
Celastrus orbiculatus Thunb.	vine	perennial
Cynanchum rossicum (Kleopow) Borhidi	vine	perennial
Elaeagnus umbellata Thunb.	shrub	perennial
Frangula alnus Mill.	shrub	perennial
Leucanthemum vulgare Lam.	forb	perennial
Lonicera tatarica L.	shrub	perennial
Rhamnus cathartica L.	tree	perennial
Robinia pseudoacacia L.	tree	perennial
Rosa multiflora Murray	shrub	perennial
Rumex crispus L.	forb	perennial
Taraxacum officinale F. H. Wigg.	forb	perennial
Torilis japonica (Houtt.) DC.	forb	annual
Veronica officinalis L.	forb	perennial

Table S 4.2: Model parameter values.

Parameter ID	Response variable	Description	Mean	SD	2.5 % quantile	97.5 % quantile
A₁	CWM leafN - total community	Intercept forest A	24.295	2.537	19.686	29.588
A₂	CWM leafN - total community	Intercept forest B	23.069	2.234	18.725	27.494
A₃	CWM leafN - total community	Intercept forest C	23.759	2.263	19.406	28.089
A₄	CWM leafN - total community	Intercept forest D	23.651	2.484	18.893	28.670
A₅	CWM leafN - total community	Intercept forest E	24.188	2.552	19.512	29.541
A₆	CWM leafN - total community	Intercept forest F	23.937	2.396	19.386	28.738
A₇	CWM leafN - total community	Intercept forest H	23.168	2.269	18.718	27.628
A₈	CWM leafN - total community	Intercept forest I	24.155	2.452	19.595	29.200
A₉	CWM leafN - total community	Intercept forest J	23.825	2.434	19.296	28.743
AA	CWM leafN - total community	Overall intercept	23.787	2.327	19.409	28.366
B₁	CWM SLA - total community	Intercept forest A	18.235	2.715	12.848	23.451
B₂	CWM SLA - total community	Intercept forest B	16.389	2.381	11.762	20.995
B₃	CWM SLA - total community	Intercept forest C	16.758	2.336	12.201	21.299
B₄	CWM SLA - total community	Intercept forest D	19.835	3.017	13.947	25.663
B₅	CWM SLA - total community	Intercept forest E	17.420	2.869	11.723	23.041
B₆	CWM SLA - total community	Intercept forest F	20.473	2.651	15.308	25.689
B₇	CWM SLA - total community	Intercept forest H	22.185	2.654	17.028	27.297
B₈	CWM SLA - total community	Intercept forest I	16.232	2.629	11.119	21.401
B₉	CWM SLA - total community	Intercept forest J	16.157	2.801	10.608	21.519
BB	CWM SLA - total community	Overall intercept	18.175	2.664	12.950	23.291
C₁	CWM LDMC - total community	Intercept forest A	0.332	0.083	0.172	0.502
C₂	CWM LDMC - total community	Intercept forest B	0.329	0.081	0.171	0.496
C₃	CWM LDMC - total community	Intercept forest C	0.330	0.081	0.175	0.497

Parameter ID	Response variable	Description	Mean	SD	2.5 % quantile	97.5 % quantile
C$_4$	CWM LDMC - total community	Intercept forest D	0.328	0.086	0.163	0.504
C$_5$	CWM LDMC - total community	Intercept forest E	0.332	0.084	0.168	0.503
C$_6$	CWM LDMC - total community	Intercept forest F	0.331	0.083	0.174	0.502
C$_7$	CWM LDMC - total community	Intercept forest H	0.330	0.082	0.172	0.500
C$_8$	CWM LDMC - total community	Intercept forest I	0.331	0.083	0.172	0.504
C$_9$	CWM LDMC - total community	Intercept forest J	0.336	0.085	0.173	0.515
CC	CWM LDMC - total community	Overall intercept	0.331	0.082	0.173	0.500
G$_1$	CWM leafN -natives only	Intercept forest A	22.196	1.694	18.911	25.551
G$_2$	CWM leafN -natives only	Intercept forest B	20.913	1.452	18.109	23.778
G$_3$	CWM leafN -natives only	Intercept forest C	22.162	1.423	19.420	24.992
G$_4$	CWM leafN -natives only	Intercept forest D	22.515	1.768	19.096	26.116
G$_5$	CWM leafN -natives only	Intercept forest E	21.460	1.674	18.192	24.807
G$_6$	CWM leafN -natives only	Intercept forest F	24.256	1.564	21.187	27.334
G$_7$	CWM leafN -natives only	Intercept forest H	21.021	1.536	18.023	24.083
G$_8$	CWM leafN -natives only	Intercept forest I	23.936	1.601	20.869	27.149
G$_9$	CWM leafN -natives only	Intercept forest J	24.073	1.611	20.928	27.323
GG	CWM leafN -natives only	Overall intercept	22.508	1.563	19.486	25.612
H$_1$	CWM SLA - natives only	Intercept forest A	20.032	3.461	13.133	26.783
H$_2$	CWM SLA - natives only	Intercept forest B	17.505	3.061	11.512	23.425
H$_3$	CWM SLA - natives only	Intercept forest C	17.939	2.989	12.027	23.736
H$_4$	CWM SLA - natives only	Intercept forest D	20.043	3.593	13.016	27.046
H$_5$	CWM SLA - natives only	Intercept forest E	19.064	3.401	12.417	25.657
H$_6$	CWM SLA - natives only	Intercept forest F	21.895	3.234	15.380	28.189
H$_7$	CWM SLA - natives only	Intercept forest H	21.730	3.304	15.301	28.146

Parameter ID	Response variable	Description	Mean	SD	2.5 % quantile	97.5 % quantile
H_8	CWM SLA - natives only	Intercept forest I	17.163	3.278	10.640	23.476
H_9	CWM SLA - natives only	Intercept forest J	17.610	3.279	11.252	23.867
HH	CWM SLA - natives only	Overall intercept	19.213	3.173	12.989	25.298
I_1	CWM LDMC - natives only	Intercept forest A	0.357	0.080	0.198	0.513
I_2	CWM LDMC - natives only	Intercept forest B	0.355	0.078	0.199	0.504
I_3	CWM LDMC - natives only	Intercept forest C	0.357	0.077	0.205	0.506
I_4	CWM LDMC - natives only	Intercept forest D	0.358	0.081	0.195	0.515
I_5	CWM LDMC - natives only	Intercept forest E	0.357	0.079	0.201	0.511
I_6	CWM LDMC - natives only	Intercept forest F	0.360	0.078	0.206	0.515
I_7	CWM LDMC - natives only	Intercept forest H	0.357	0.078	0.203	0.510
I_8	CWM LDMC - natives only	Intercept forest I	0.356	0.079	0.199	0.508
I_9	CWM LDMC - natives only	Intercept forest J	0.364	0.080	0.207	0.520
II	CWM LDMC - natives only	Overall intercept	0.358	0.078	0.203	0.507
$\Sigma N_{[1,1]}$	Natives only	Leaf N - Leaf N	0.313	0.050	0.225	0.417
$\Sigma N_{[2,1]}$	Natives only	SLA - Leaf N	-0.046	0.018	-0.082	-0.013
$\Sigma N_{[3,1]}$	Natives only	LDMC - Leaf N	0.233	0.556	-0.852	1.313
$\Sigma N_{[2,2]}$	Natives only	SLA - SLA	0.072	0.012	0.050	0.096
$\Sigma N_{[3,2]}$	Natives only	LDMC - SLA	0.358	0.263	-0.143	0.888
$\Sigma N_{[3,3]}$	Natives only	LDMC - LDMC	81.514	12.064	59.461	106.329
$\Sigma T_{[1,1]}$	Total community	Leaf N - Leaf N	0.125	0.020	0.089	0.168
$\Sigma T_{[2,1]}$	Total community	SLA - Leaf N	-0.038	0.015	-0.070	-0.009
$\Sigma T_{[3,1]}$	Total community	LDMC - Leaf N	-0.020	0.351	-0.710	0.671
$\Sigma T_{[2,2]}$	Total community	SLA - SLA	0.134	0.022	0.095	0.179
$\Sigma T_{[3,2]}$	Total community	LDMC - SLA	0.415	0.366	-0.295	1.137
$\Sigma T_{[3,3]}$	Total community	LDMC - LDMC	83.621	12.880	60.732	110.433
$diffN_{leafN}$	CWM leafN -natives only	Difference predicted slope	-0.252	2.899	-5.882	5.527
$diffN_{SLA}$	CWM SLA - natives only	Difference predicted slope	3.076	6.119	-9.018	14.981
$diffN_{LDMC}$	CWM LDMC - natives only	Difference predicted slope	-0.020	0.169	-0.355	0.312
$diffT_{leafN}$	CWM leafN - total community	Difference predicted slope	10.900	4.589	2.083	19.976

Parameter ID	Response variable	Description	Mean	SD	2.5 % quantile	97.5 % quantile
$diffT_{SLA}$	CWM SLA - total community	Difference predicted slope	5.791	4.506	-3.103	14.643
$diffT_{LDMC}$	CWM LDMC - total community	Difference predicted slope	-0.010	0.166	-0.336	0.312
α_1	CWM leafN - total community	Invasive cover	0.059	0.008	0.041	0.073
α_2	CWM leafN - total community	Native richness	-0.211	0.089	-0.382	-0.035
α_3	CWM leafN - total community	Evenness total community	-1.211	2.567	-6.253	3.804
α_4	CWM leafN - total community	Light	-0.028	0.046	-0.118	0.061
α_5	CWM leafN - total community	Soil water	0.145	0.086	-0.024	0.316
β_1	CWM SLA - total community	Invasive cover	0.031	0.009	0.014	0.048
β_2	CWM SLA - total community	Native richness	0.049	0.093	-0.130	0.228
β_3	CWM SLA - total community	Evenness total community	4.405	2.626	-0.623	9.644
β_4	CWM SLA - total community	Light	-0.066	0.046	-0.155	0.027
β_5	CWM SLA - total community	Soil water	0.230	0.093	0.049	0.412
γ_1	CWM LDMC - total community	Invasive cover	0.000	0.000	-0.001	0.000
γ_2	CWM LDMC - total community	Native richness	0.000	0.003	-0.007	0.006
γ_3	CWM LDMC - total community	Evenness total community	-0.045	0.094	-0.231	0.137
γ_4	CWM LDMC - total community	Light	0.001	0.002	-0.003	0.004
γ_5	CWM LDMC - total community	Soil water	-0.001	0.003	-0.007	0.006
ζ_1	CWM leafN -natives only	Invasive cover	-0.001	0.005	-0.012	0.010
ζ_2	CWM leafN -natives only	Native richness	-0.166	0.061	-0.283	-0.047
ζ_3	CWM leafN -natives only	Evenness total community	1.752	1.615	-1.515	4.895
ζ_4	CWM leafN -natives only	Light	-0.039	0.030	-0.098	0.022
ζ_5	CWM leafN -natives only	Soil water	-0.021	0.060	-0.140	0.094
$\eta1$	CWM SLA - natives only	Invasive cover	0.017	0.011	-0.005	0.038
$\eta2$	CWM SLA - natives only	Native richness	0.023	0.124	-0.215	0.266

Parameter ID	Response variable	Description	Mean	SD	2.5 % quantile	97.5 % quantile
$\eta 3$	CWM SLA - natives only	Evenness total community	3.310	3.351	-3.294	9.768
$\eta 4$	CWM SLA - natives only	Light	-0.097	0.064	-0.225	0.029
$\eta 5$	CWM SLA - natives only	Soil water	0.281	0.124	0.034	0.520
θ_1	CWM LDMC - natives only	Invasive cover	0.000	0.000	-0.001	0.000
θ_2	CWM LDMC - natives only	Native richness	0.001	0.003	-0.006	0.007
θ_3	CWM LDMC - natives only	Evenness total community	-0.087	0.090	-0.261	0.091
θ_4	CWM LDMC - natives only	Light	0.001	0.002	-0.003	0.004
θ_5	CWM LDMC - natives only	Soil water	-0.001	0.003	-0.008	0.005
$1/\sigma_A^2$	CWM leafN - total community	Overall intercept	640.64 5	2454.9 00	0.171	6831.499
$1/\sigma_B^2$	CWM SLA - total community	Overall intercept	0.222	0.980	0.042	0.603
$1/\sigma_C^2$	CWM LDMC - total community	Overall intercept	6306.8 93	6463.4 23	518.543	24253.369
$1/\sigma_G^2$	CWM leafN -natives only	Overall intercept	0.525	0.352	0.114	1.411
$1/\sigma_H^2$	CWM SLA - natives only	Overall intercept	31.847	456.64 1	0.042	7.842
$1/\sigma_I^2$	CWM LDMC - natives only	Overall intercept	6055.5 06	6387.3 04	516.375	23968.419

Table S 4.3: Soil nutrient values raked from less invaded to most invaded forest. Data was collected by deploying one ion-exchange resin capsule per forest.

Forest	Mean % Invasive cover	Total soil N (ppm)	Soil nitrate (ppm)	Soil ammonium (ppm)	Days resin capsules was deployed
B	2.44	10.09	2.31	7.78	61
C	4.40	10.03	2.73	7.3	61
H	15.03	10.21	4	6.21	55
J	41.22	8.4	3.62	4.78	55
I	47.86	7.4	2.6	4.8	55
E	59.48	17.73	2.9	14.83	61
F	65.38	13.1	3.71	9.39	61
A	120.19	24.63	15.8	8.83	61
D	128.83	22.47	12.26	10.21	61

Chapter 5 Conclusions

In this dissertation, I used a three-pronged approach, i.e., meta-analysis, long-term field experiment, and collection of observational data, to understand the mechanisms and processes by which native plant communities in forest understories are impacted by invasion. The knowledge gained through my research allowed me to outline specific management approaches that can help increase native resistance to plant invasion.

In **Chapter 2**, using a meta-analytical approach I explored the mechanisms (i.e., high propagule pressure, occupying empty niches, and low biotic resistance) by which shrub invasion in forest understories occurs and what their impacts on the native community are. In summary, I found that invader performance was not linked to any particular mechanism of invasion. This widespread success of shrub invaders, irrespective of mechanism, suggests that these species likely have a wide array of resource acquisition strategies and competitive abilities. Moreover, impacts of invasive shrubs on the native community performance were significant only under low biotic resistance, and marginally significant when invasion was driven by propagule pressure. Together, my results suggest that having a functionally diverse native community or restoring these characteristics is key for successful native recovery after invasive removal, enabling native species to compete effectively against the breadth of strategies invaders express. In light of these results, effective management strategies should also prioritize reducing the sources of invader propagules at the landscape level while simultaneously promoting native seed dispersal.

The global scope of the meta-analysis presented in **Chapter 2** showed the importance of a wide representation of resource-use strategies and competitive abilities among the native community. These results underscore the importance of carefully selecting native species when addition is required to promote successful restoration (Ostertag *et al.* 2015; Laughlin *et al.* 2017). An ancillary finding from this chapter was that disturbance was only simultaneously detrimental to the native community and beneficial to invasive shrub performance when driven by human activities– results supported by previous literature (Jauni, Gripenberg & Ramula 2015; Lembrechts *et al.* 2016; Ibáñez *et al.* 2021). This information is particularly important when evaluating whether removing invasive species will likely have a positive impact on understory native recovery or not. If the co-occurring native community does not have the capacity to recover or fulfill the system's functionality after invasive removal, this management practice might itself promote disturbance favoring re-invasion (Kuebbing, Nunez & Simberloff 2013; Pearson *et al.* 2016). Therefore, controlling or avoiding extra disturbance in invaded forest understories should be a central goal of management. Careful consideration of how the native community is expected to respond to management instead of solely focusing on the invader should be a priority.

Lastly, like many other meta-analyses on similar topics (e.g., Pysek *et al.* 2008; Sorte *et al.* 2013; Ibáñez *et al.* 2021), this study heavily represents the northern hemisphere, and, in our case, temperate forests in the U.S. in particular. While this geographical bias reflects a broader systemic issue of unequal resource distribution for research and publication, as researchers we should be mindful that the findings presented here are geographically biased (Pysek *et al.* 2008). By actively prioritizing and promoting research in the southern hemisphere, particularly in

developing countries, we can enhance the representativeness of scientific knowledge on plant

invasions in forest ecosystems.

In **Chapter 3**, I carried out a field experiment where I focused on temperate forest

understories in Southeast Michigan to test whether priority effects could be a successful

mechanism of forest recovery, and assessed which characteristics of the native community led to

faster recovery rates. I found, contrary to initial expectations, that priority effects were not the

main mechanism driving community assembly following invasive removal. Instead, I observed

that native communities composed of a higher number of species and species with higher

specific leaf area (SLA) were more successful in exploiting unused resources, such as light and

water, leading to higher recovery rates. Light availability had a significant and positive

association with native recovery rates. And native recovery rates were higher in the year with

lower atmospheric water demands. My results highlight the importance of assessing the

characteristics of the co-occurring native community prior to invasive removal, particularly with

respect to richness and leaf trait composition, to ensure the native species can effectively use the

incoming high-resource environment created after plant removal.

Mechanisms of community assembly are rarely investigated in field settings of forested

ecosystems. A recent systematic review highlighted that priority effects, in particular, have been

primarily studied in controlled settings and in temperate grasslands (Weidlich *et al.* 2021). The

study I performed in **Chapter 3** fill this knowledge gap, where in a natural setting I tested

priority effects after removing invasive species from temperate forest understories. My work was

also innovative in monitoring the newly assembling plant community for three subsequent years

after treatment implementation. Typically, priority effects, and post-management actions, are

only investigated for a short period of time, often less than a year (e.g., Kettenring & Adams

2011; Sarneel, Kardol & Nilsson 2016; Weidlich *et al.* 2020; Weidlich *et al.* 2021). By revisiting the plots multiple times every summer, I captured essential year-to-year variation, crucial for understanding the complexity of the recovery dynamics taking place. This extended monitoring period allowed for a more comprehensive assessment of how other factors, besides priority effects, influenced the community assembly process in recently managed forest understories.

Finally, in **Chapter 4**, I zoomed in spatially and collected observational data on plant community composition of invaded forest understories at the Edwin S. George Reserve, in southeast Michigan. Here, I tried to understand the interplay between increasing levels of invasion, trait distributions, and ecosystem functions. Specifically, I investigated how invasion changed total community (invasive and native co-occurring species) ecosystem functionality and what specific impact invasion had on native community functionality via alterations in trait distributions. The results revealed that, in my study system, invasion led to a significant increase in community-level leaf nitrogen while native trait values remained unchanged for all tree leaf traits we analyzed. This suggests that invasion changed the functionality of these forest understories, via complementarity with native community trait distributions rather than displacement. These findings have important implications for forest management, as invasive removal would likely restore function to trait levels similar to pre-invasion conditions.

The patterns I observed are consistent with existing literature, where invasive species tend to increase community trait values on the "fast" of the leaf economic spectrum (Leishman *et al.* 2007; Van Kleunen, Weber & Fischer 2010; Ordonez & Olff 2013; Henn, Yelenik & Damschen 2019), and the lack of impact on native community with respect to functionality (Livingstone, Isaac & Cadotte 2020; Fernandez *et al.* 2021). However, the results would likely be more refined and better representataive of changes in community level trait values and the

environmental conditions detected if I would have been able to collect local trait values. Collecting local trait values would capture local intraspecific trait variation and allow me to quantify potential shifts in trait expression, particularly at such local scale, given the environment and invasion (Siefert *et al.* 2015; Chacón-Labella *et al.* 2023).

Collectively, the results of my dissertation underscore that a thorough understanding of the native community responses to invasion and their post-removal responses is necessary to effectively restore forest understories. Although its importance has long been documented (Daehler 2003), the focus on the native community rather than on specific invasive species–approach I adopted here is a perspective that only has recently been actively pursued (e.g., Ostertag *et al.* 2015; McGeoch *et al.* 2016; Ibáñez *et al.* 2021) besides biotic resistance, a concept explored for many decades (Elton, 1958). The results of my dissertation offer valuable insights into targeted management practices which should improve native community resistance to invasion. Furthermore, my findings contribute to a better understanding of the potential outcomes of current restoration efforts. Therefore, land managers and conservation practitioners can benefit from evidence to aid their decisions of when and how to manage invaded forests by focusing on maximizing native recovery and on restoring ecosystem functionality. More targeted management will also allow for more effective allocation of limited funds and resources. My work was built around these goals and it provides specific management recommendations while being transparent about context dependencies, which are inherent in biological invasions. Without precise restoration actions (Castro *et al.* 2021), invasive species could profoundly impact forest structure and composition threatening the long-term persistence of forests, their functions and the services they provide.

5.1 References

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