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Effect of Phylogenetic and Functional Diversity on Invasion Resistance in Restored Tallgrass Prairies

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SCIENCE ABSTRACT

The question of how native species diversity affects a community's ability to resist invasive species has inspired decades of research. One of the oldest invasion biology hypotheses is that more species rich ecosystems are less invaded. While there has been strong support for this hypothesis, there is also strong evidence of a contradictory trend wherein more species rich communities are more prone to invasion. This question has been explored thoroughly at different spatial scales, different ecosystems, time periods, and from both experimental and observational perspectives. However, this question has been predominantly explored with species richness—a measure of taxonomic diversity. In my dissertation, I set out to explore this question with two diversity metrics hypothesized to better represent niche-based processes: phylogenetic and functional diversity. As the relationship between diversity and invasion has been shown to vary depending on how it is studied, I explored how phylogenetic and functional diversity affected invasion through multiple lenses.

In my first chapter, I used a dataset that tracked grassland sites across Illinois over a fifteen-year period. With this chapter I was able to demonstrate that more phylogenetically diverse sites were more invaded when I viewed that data from a static perspective, but that more phylogenetically diverse sites resisted invaders over time.

My second and third chapter both take place within experimentally restored prairie plots with varied phylogenetic and functional diversity. Within this experiment were two smaller experiments, the same communities were established from seed and from plugs. The seed plots were managed more similarly to a restoration, while the plug plots were more intensively managed to control for the effects of the diversity. I conducted two invasion experiments in each

of the plots mirroring their management differences, an observational invasion in the seed plots (Chapter 2) and an experimental invasion in the plug plots (Chapter 3).

Chapter 2 followed invasion in the seed plots over three years, with invaders allowed to establish from the background, and characterized how the native plant community developed alongside the invaders. In these plots, I saw that more phylogenetically diverse communities had a higher abundance of invasive species. However, I also saw that the presence of a dominant clade at my site, the Asteraceae or sunflower family, coincided with both lowered invasion and lowered phylogenetic diversity. This suggests that early in a restoration, dominant native species may suppress both invaders and subordinate native species.

For Chapter 3, I experimentally introduced three invader species into the more intensively maintained plug plots. The invaders were tracked over two years. For one of the invaders, I saw evidence that more phylogenetically diverse communities resisted invaders. In this chapter, by examining native functional traits individually, I was also able to demonstrate that there are multiple ecological strategies by which native species suppress invaders.

Across all three chapters, I found evidence linking phylogenetic diversity to invasion, supporting the idea that a community's evolutionary history meaningfully reflects ecological dynamics. I found a negative relationship between phylogenetic diversity and invasion over longer time scales: in the first chapter, this relationship was only apparent looking over time, and in the experimental prairie plots I only saw evidence of resistance in the more established communities started from plugs.

PRACTITIONER ABSTRACT

Tallgrass prairies are one of the most endangered ecosystems in the world. Their drastic decline has sparked efforts to restore prairies. However, many restoration projects struggle to obtain sufficient resources to control invasive species or deal with the negative consequences of control on native species. I am investigating if changing plant species composition can bolster resistance to invasive species, in theory improving restorations while advancing basic ecological research. A central debate in ecology is how differences in ecological strategies among species drive plant community dynamics. In theory, maximizing ecological strategies among species minimizes available resources for invaders to exploit. Most studies count species as a way of estimating how many different ecological strategies are present in a community, but this ignores ecological differences. My research uses two metrics hypothesized to better reflect different ecological strategies among species: functional and phylogenetic diversity. These metrics quantify ecological roles by measuring plant traits and evolutionary history, assuming relatedness reflects ecological similarity. My dissertation asks if increased functional and phylogenetic diversity decreases invasion. My first chapter works with a long-term observational dataset of 150 grassland sites in Illinois, providing large-scale characterization of diversity-invasion dynamics. My next two chapters take place in 410 experimentally restored prairie plots at the Morton Arboretum. The plots have varied phylogenetic and functional diversity with different management styles and methods of invasion. Comparing results from these studies speaks to the applicability of traditional ecology experiments to the less-controlled conditions of restorations, and sheds light on the nature of the diversity-invasion relationship.

Looking across grasslands in Illinois, I found that more phylogenetically diverse communities were more invaded. However, when I examined this relationship over time, I found the opposite, more phylogenetically diverse communities were less invaded. Likely this reflects the fact that site conditions and history as well as the native community both influence invasion.

In the experimentally restored prairie plots, I again found contradiction. My second chapter examined background invasion in communities started from seed. I found that more phylogenetically diverse plots underwent higher invasion, although this may have been driven by a dominant family exerting disproportionate effects. I found that plots with higher abundance of Asteraceae, a dominant tallgrass prairie family, had both lower abundance of invaders and lower phylogenetic diversity. This suggests a trade-off wherein dominant native species may prove effective in suppressing invaders in a young restoration, but it may come at the cost of preventing the establishment of native species which are sensitive to competition.

I experimentally introduced three species of invader into plug plots for my third chapter and my results differed from the second. In these more carefully maintained and established plots, I found evidence from one of the invaders that more phylogenetically diverse plots did better resist invasion. I also found evidence that both “fast” and “slow” plant strategies conferred resistance against invaders, refuting the idea that selecting fast-growing natives is necessarily the best way to suppress invasive species.

Despite the seemingly conflicting results in my dissertation, there are some clear trends for managers. It seems that the effect of phylogenetic diversity on invaders is apparent over longer time scales and in more established communities. In the short term, phylogenetic diversity of a seed mix may not have a meaningful impact on invasion resistance. My second chapter suggests that a more phylogenetically diverse seed mixes is unlikely to suppress invaders in the first few years of restoration. However, from the first and third chapters, I see some evidence that more established communities with higher phylogenetic diversity are less likely to be invaded. Management efforts that focus on maximizing phylogenetic diversity over the course of a restoration may be more likely to build a community more resilient against invasion.

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DEDICATION

To my mother, Kathy Ernst, the strongest person I know, and my father, Bob Ernst, who taught me to never stop asking questions. Thank you both for introducing me to the wonders of nature and the joys of science.

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CHAPTER ONE

The invasion paradox dissolves when using phylogenetic and temporal perspectives

Abstract

Elton’s prediction that higher biodiversity leads to denser niche-packing and thus higher community resistance to invasion has long been studied, with species richness as the predominant measure of diversity. However, few studies have explored how phylogenetic and functional diversity, which should more faithfully represent niche space, influence community invasibility, especially across longer time frames and more locations. I expected more phylogenetically and functionally diverse communities to exhibit higher invasion resistance.

I used a 15-year, 150-site grassland dataset to assess relationships between invasive plant abundance and phylogenetic, functional, and taxonomic diversity of recipient native plant communities. I analyzed the dataset both pooled across all surveys and longitudinally, leveraging time-series data to compare observed patterns in invasion with those predicted by two community assembly processes: biotic resistance and competitive exclusion.

With the pooled dataset, I found support for the longstanding observation that communities with more native species have lower abundance of invasive species, and a more novel finding that more phylogenetically diverse communities had higher abundance of invasive species. I found no influence of aggregate (multivariate) functional diversity on invasion, but assemblages with taller plants, lower variability in plant height, and lower seed mass were less invaded. Viewed longitudinally, the phylogenetic diversity relationship was reversed: the most phylogenetically diverse communities were most resistant to invasion. This apparent discrepancy can be explained by invasion dynamics being influenced by both site attributes and biotic resistance.

My results provide insight into the nuances of the diversity-invasibility relationship: invasion dynamics differed for different dimensions of diversity and depending on whether the relationship was evaluated longitudinally. My findings highlight the limitations of using single time-point "snapshots" of community composition to infer invasion mechanisms.

Keywords: biotic resistance hypothesis, community assembly, community phylogenetics, competitive exclusion, functional traits, invasion ecology, invasion paradox

Introduction

Invasive species threaten biodiversity, ecosystem health, and restoration efforts (Simberloff et al., 2013; Vilà et al., 2011). Due to the severity of these threats, and the opportunities that invasions pose for addressing fundamental ecological questions, a rich subfield of ecology has developed around invasive species. Invasion biology owes much of its legacy to Charles Elton's pioneering work *The Ecology of Invasions by Animals and Plants* (Elton, 1958). One of the most influential ideas Elton proposed is that invasive species will be less likely to establish in communities with more native species. This prediction—that diversity confers invasion resistance—has important management implications: if true, promoting native plant diversity, already a priority for conservation and restoration, will have ancillary benefits of reducing invasive plant dominance.

The relationship between plant community diversity and invasibility has been described as paradoxical: while some studies have shown that more diverse communities have fewer invaders

(Beaury, Finn, Corbin, Barr, & Bradley, 2020; Kennedy et al., 2002; Naeem et al., 2000), others have shown the exact opposite relationship, with more species-rich communities being more invaded (K. F. Davies et al., 2005; Peng, Kinlock, Gurevitch, & Peng, 2019; Smith & Côté, 2019; Stohlgren, Barnett, & Kartesz, 2003). Studies have drawn heavily on Elton's original idea to explain negative diversity-invasibility results (Richardson & Pysek, 2008). Under the biotic resistance hypothesis, the number of native species correlates with the amount of niche space occupied, such that maximizing native richness minimizes niche space available for invasive species (Elton, 1958).

In scenarios that do not support the biotic resistance hypothesis, environmental factors are commonly invoked to explain invasion patterns (Fridley et al., 2007; Levine & D'Antonio, 1999). Explanations for this discrepancy have been attributed to different processes operating between: 1) large and small spatial scales (K. F. Davies et al., 2005; Tomasetto, Duncan, & Hulme, 2019), 2) experimental and observational studies (Fridley et al., 2007; Levine & D'Antonio, 1999), and 3) abundance-based and presence/absence-based measures of invasion (Cleland et al., 2004; Smith & Côté, 2019). Generally, biotic resistance is better supported at smaller spatial scales, in experimental settings, and in explaining invader abundance rather than richness. While recent advances have helped disentangle this invasion paradox, relatively few studies have moved beyond species richness as the key measure of native diversity (but see work related to Darwin's naturalization conundrum; e.g., Ma et al., 2016; Marx, Giblin, Dunwiddie, & Tank, 2016; Pinto-Ledezma et al., 2020). Overreliance on richness is a potential limitation of diversity-invasibility studies evaluating biotic resistance, as the number of native species present in a community may be a poor proxy for available niche space.

Specifically, while species richness is a critical component of diversity, it captures neither the ecological differences between species nor the evolutionary dynamics—selection and drift—that shape those differences (Cadotte, Albert, & Walker, 2013). Using metrics of diversity that potentially better reflect niche differences and/or their origins may better test the biotic resistance hypothesis. In this paper, I test two such metrics: functional and phylogenetic diversity of the native community. Functional diversity, as a measure of trait distribution, is thought to capture some aspects of the niche directly and can reflect the breadth of strategies used by the organisms that make up a community (Diaz & Cabido, 2001; McGill, Enquist, Weiher, & Westoby, 2006). However, the utility of functional diversity as a proxy for the niche hinges on selecting ecologically relevant traits, a notoriously difficult task (Funk et al., 2017; Lefcheck, Bastazini, & Griffin, 2015). By integrating over the evolutionary history of a species and the lineage from which it arises, phylogenetic diversity is hypothesized to capture further aspects of niche differentiation (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Webb, Ackerly, McPeek, & Donoghue, 2002). Phylogenetic diversity has been used as a proxy for functional trait diversity or as a way to capture the evolutionary history of traits that cannot be easily measured or are not currently recognized as influential for ecosystem processes (Larkin et al., 2015a; Pearse & Hipp, 2009; Tucker, Davies, Cadotte, & Pearse, 2018). However, phylogenetic diversity will only reflect ecological differences between species at phylogenetic scales at which ecologically important traits are conserved or exhibit phylogenetic signal (Cavender-Bares, Ackerly, Baum, & Bazzaz, 2004; Mayfield & Levine, 2010; Tucker et al., 2018). Given the potential and limits of each of these components of diversity, it is important to consider multiple facets and evaluate the degree to which they provide similar versus distinct insights into community assembly generally, and invasion dynamics more specifically.

A shared limitation of both phylogenetic diversity and multivariate functional diversity measures is that summarizing multiple niche axes as a single number can mask important ecological dynamics, particularly opposing trends in niche axes (Roscher et al., 2012; Trisos, Petchey, & Tobias, 2014). By breaking multivariate functional diversity into component traits, ecological trade-offs may become apparent (Pellissier et al., 2018; Spasojevic & Suding, 2012). Thus analyses of individual functional traits can elucidate the community assembly processes shaping invasion dynamics and allow identification of particularly influential traits (Butterfield & Suding, 2013; Carboni et al., 2016; Funk et al., 2017). Paired with phylogenetic diversity and functional diversity, single trait indices can help provide mechanistic insights into invasion.

Observational tests of the diversity-invasibility hypothesis are frequently limited by the availability of data at multiple time points. For example, some recent large-scale observational studies have found that communities with more native species had fewer non-native species, and concluded that biotic resistance drives this relationship (Beaury et al., 2020; Iannone et al., 2016). However, these studies lacked time-series data enabling changes in the relationship between native and non-native species richness to be evaluated over time, making it difficult to distinguish between two possible drivers: 1) increased native species exhibiting higher resistance to invasive species (biotic resistance), or 2) invasive species outcompeting native species, resulting in fewer native species (competitive exclusion). A challenge in synthesizing the diversity-invasibility relationship is that comparing observational and experimental findings is complicated by the relative paucity of observational studies that include temporal trends (Gallien & Carboni, 2017).

I sought to evaluate whether niche space occupied by native communities would be represented more faithfully by metrics that incorporate species differences. To test how plant invasions are influenced by phylogenetic, functional, and taxonomic diversity, I used a dataset encompassing 150 grassland sites located across a 10 million hectare area. The dataset includes comprehensive vegetation surveys with repeated surveys spanning a decade for most sites. These repeated surveys enabled us to track changes in diversity patterns over time and compare them to the patterns expected under different community assembly processes. With these data I investigated whether: 1) more diverse communities were less invaded, 2) native communities exhibited biotic resistance, and 3) invasive species competitively excluded native species.

Materials and Methods

Dataset

My dataset encompasses 150 grassland sites scattered across 10 million hectares in the state of Illinois, USA. The sites were surveyed under the Illinois Natural History Survey's Critical Trends Assessment Program (CTAP) between 1997 and 2016. Sites were randomly selected from grassland habitats throughout the state and encompass a range of grassland habitat types (Carroll et al., 2002). At each site, 20 0.25-m^2 plots were placed at 2-m intervals along a 41-m transect. Plots were placed 1-m away from the transect on alternating sides. GPS coordinates and permanent metal markers were used to resample the same locations each year. Ground cover was estimated for each species rooted into each plot using a modified Daubenmire method. In some cases, plants could only be identified to genus. For more detailed methods, see Carroll et al. (2002). When possible, sites were re-surveyed every 5 years. Seventy three percent of sites were surveyed at least twice, 59% were surveyed at least three times, and 28% were surveyed four times. Any sites noted as having been managed with herbicide or weeding were excluded from my analysis for that year.

To prepare the dataset for analysis, I standardized species names using the Taxonomic Name Resolution Service (Boyle et al., 2013) and manually assigned species origin (native or non-native) based on Taft et al. (1997) and invasive status following the Midwest Invasive Plant Network (MIPN 2019).

Characterization of Phylogenetic Diversity

To construct a phylogeny for all 704 species observed in the vegetation surveys, I followed the methods described in Barak et al., (2017). Briefly, I used a published mega-phylogeny of 32,223 plants (Zanne et al., 2014). Using the weldTaxa and makeMat functions from the Morton R Project (https://github.com/andrew-hipp/morton), I grafted in species that were present in the survey data, but were absent from the tree (190 identified to species, 70 identified to genus) and pruned species that were part of the original tree but absent in the survey data.

For each plot within each site and year, I calculated abundance-weighted mean nearest taxon distance (MNTD) and mean pairwise distance (MPD) to characterize phylogenetic diversity of the native community. MNTD is calculated as the mean phylogenetic distance between each species and its closest co-occurring relative and MPD is calculated as the mean phylogenetic distance between all pairs of co-occurring species (Webb, 2000). MNTD and MPD were selected because they quantify phylogenetic divergence, are hypothesized to capture niche differentiation, and are commonly used in community phylogenetic analysis, facilitating comparison among studies (Tucker et al., 2017). As MPD is calculated by averaging relatedness between all co-occurring species, it spans the full depth of the community phylogeny, reflecting deeper divergences and older evolutionary relationships. In contrast, MNTD is calculated between closest relatives, reflecting more recent evolutionary relationships. Both MNTD and MPD require the presence of multiple co-occurring species; plots were excluded from analysis if they had fewer than three native species.

Differences in species richness can affect both MPD and MNTD (Webb, 2000). To remove the effect of species richness, I calculated standardized effect sizes of both MPD and MNTD ([observed value – expected value]/standard deviation of the expected value). Expected values were calculated under an 'independentswap' null model with 999 permutations using the *picante* package in R (Kembel et al., 2010). This null model randomizes species co-occurrences while maintaining species richness and species occurrence frequency and has been shown to detect niche-based assembly more reliably than other commonly used null models (Kembel, 2009). Standardized effect sizes of MNTD (SES MNTD) and MPD (SES MPD) > 0 indicate that co-occurring species are more distantly related than expected by chance, while values < 0 indicate closer relatedness than expected by chance. In other words, higher positive values of SES MNTD and SES MPD indicate higher phylogenetic diversity.

Characterization of Functional Diversity

To characterize the functional composition of the plots over time at each site, I sourced trait data from the TRY database (Kattge et al., 2020) and used the bien package (Maitner et al., 2018) to access the BIEN database (Enquist, Condit, Peet, Schildhauer, & Thiers, 2016). Eleven candidate traits were selected based on their availability and prevalence in functional ecology literature (Table S1.1). All available trait data for the 704 species found in vegetation surveys were downloaded from TRY and BIEN. Next, I developed a two-step procedure for trait selection. First, following Pakeman 2014, I narrowed the candidate traits to those that were available for > 80% of the total abundance across all species at the site level. Second, I filtered candidate traits to minimize trait correlation while providing coverage across key axes of functional trait strategies—resource acquisition, competitive ability, and reproductive strategy (Lefcheck et al., 2015). Multiple traits that met the coverage thresholds were related to the leaf economic spectrum, which are often highly correlated and potentially functionally redundant (Laughlin, 2014b). From these leaf economic spectrum traits, I selected specific leaf area (SLA), as it had the highest coverage and is well supported as a proxy for resource acquisition (Violle et al., 2009; Wright et al., 2004). Second, I selected vegetative height, which is associated with competitive ability (Fréville, Mcconway, Dodd, & Silvertown, 2007; Leach & Givnish, 1996). The third trait selected was seed mass, which is linked to reproductive strategy (Grime & Jeffrey, 1965; Turnbull, Rees, & Crawley, 1999). To characterize the functional composition of the resident native community in each plot, I calculated both multivariate functional diversity and single functional trait indices. For multivariate functional diversity, I used functional dispersion (FDis) because it reflects functional divergence—arguably the most important aspect of functional diversity under the biotic resistance hypothesis (Laliberte & Legendre, 2010a). FDis is the weighted mean distance in multidimensional trait space of individual species to the abundance-weighted centroid of all species.

Single Functional Trait Metrics

I also calculated three indices to capture variation within individual traits in the native community: 1) weighted mean absolute deviation (MAD), the sum of the relative-abundance weighted difference between each species and the average trait value for the assemblage—a single trait analogue to FDis (Laliberte & Legendre, 2010a); 2) range, the difference between the maximum mean trait value and the minimum mean trait value in a community; and 3) community-weighted means (CWM), the abundance-weighted mean trait value for a community (Violle et al., 2007). I calculated these indices using standardized mean trait values (each trait was scaled to mean = 0, standard deviation = 1) to facilitate comparison between traits and for comparability with multivariate functional diversity.

Statistical Analysis

My overall approach was to analyze how invasive species cover responded to characteristics of native communities. As my analyses occurred at the plot level, I did not analyze invasive species richness—most plots had few invasive species making their richness essentially a binary response. I implemented models to address the following questions: 1) How does native community diversity correlate with invasive species abundance when viewed without a temporal perspective? (*pooled model*) 2) Do native communities exhibit biotic resistance to invasion? (*longitudinal biotic resistance model*) 3) Do invasive species competitively exclude (displace) native species following invasion? (*longitudinal competitive exclusion model*). For each of these models, I tested the following 11 measures of native community diversity as fixed predictors: SES MNTD, SES MPD, FDis, species richness, CWM seed mass, CWM height, seed mass range, height range, MAD SLA, MAD seed mass, and MAD height. I additionally considered CWM and range for SLA; however, they were eliminated because the three SLA metrics were highly correlated (Pearson’s correlation coefficient > 0.7). I tested for correlation among all of the fixed predictors considered using the corrplot package and no other pairs of predictors had correlations above my cutoff of 0.7 (Figure S1.1). For model selection, I implemented both forward and backward selection based on log-likelihood ratio tests following Zuur, Ieno, Walker, Saveliev, & Smith, 2009. Analyses were carried out in R version 3.6.1 (R Core Team, 2019).

Pooled Model: Does native diversity correlate with invader abundance?

For the first model, I analyzed how invasive species cover related to diversity of native communities in all plots for all years, regardless of when the data were collected (invasive species abundance ~ native diversity). The level of invasion was calculated as the summed cover of all invasive species in each plot. I estimated GLMMs with a negative binomial distribution to account for overdispersion. Fixed predictors considered were the 11 diversity metrics noted above plus year. To control for the spatially nested structure of the data and repeated sampling of the same plots, both site and plot within site were included as random effects.

Longitudinal Biotic Resistance Model: Are more diverse communities less likely to be invaded?

To disentangle interactions between the native and invasive communities, I examined invasion over time following Muthukrishnan et al. (2018) (invasive abundance at subsequent visit ~ initial native diversity prior to invasion). To test if native diversity confers resistance to invasion, I compared the native diversity metrics at each plot’s initial survey to the invader abundance at the subsequent survey. For this model, I excluded all plots with invasive species present at the first survey to remove effects of established invaders, e.g., an “invasional meltdown” (Simberloff & Von Holle, 1999) wherein the presence of one invasive species facilitates further invasion. I also excluded plots that were only sampled once and had no subsequent measure of invasive species abundance. As there were relatively few plots that fit these criteria and had more than two visits, I compared the diversity at the first visit to the abundance of invasive species at the second visit. I used linear mixed effect models for this analysis, the fixed predictors considered were the same suite of diversity metrics as above and site was the sole random effect. As the model did not include more than one subsequent visit per plot, it was not necessary to include plot as a random effect.

Longitudinal Competitive Exclusion Models: Do invasive species outcompete native species?

I investigated whether invasive species competitively excluded native species, and how the characteristics of the native community shifted following invasion (change in diversity ~ invasive species abundance). I used linear regressions to model the change of each diversity metric over time in those plots that had at least two surveys. I estimated separate linear regressions for each diversity metric where the response was the diversity metric and the explanatory variable was year (diversity metric ~ year). The rates of change reflect the average annual change in diversity and were calculated using the model coefficients. The rate of change in each diversity metric was then compared with invasive species cover. I compared plots that were uninvaded throughout all surveys to those that were invaded.

Results

Pooled Model

The pooled model was a “snapshot” that estimated the relationship between native diversity and invasive cover at all plots across all sites and all years. It included 1,606 unique plots from 125 sites with 1–4 surveys each, of which 737 plots from 69 sites included repeated visits; pooled across surveys, it encompassed 2,826 plot-years. The average numbers of native and invasive species per plot per visit were 5.9 ± 3.0 (S.D.) and 1.9 ± 1.4, respectively. My final model included native phylogenetic diversity (SES MNTD), species richness, CWM height, CWM seed mass, and plant height range as predictors of invasive species abundance (Figure 1.1).

I observed a negative diversity-invasibility relationship when native diversity was measured as species richness (χ^2 =32.415, $p < 0.001$), indicating that plots with more native species were less likely to be invaded. However, I found a positive relationship between native phylogenetic diversity and invasive species abundance ($\chi^2 = 7.194$, $p < 0.001$). On average, the least-invaded plots had native plant species that were more closely related to each other. I found a negative relationship between native CWM height and invader abundance ($\chi^2 = 4.334$, $p = 0.037$) and positive relationships between both native height range ($\chi^2 = 8.141$, $p = 0.004$) and native CWM seed mass ($\chi^2 = 5.897$, $p = 0.015$) and abundance of invasive species, i.e., less-invaded plots had native plants that had lighter seeds, were taller, and had lower variability in height.

Longitudinal Biotic Resistance Model

My analyses supported native phylogenetic diversity (SES MPD) conferring biotic resistance against invaders ($\chi^2 = 4.66$, $p = 0.031$) (Figure 1.2). That is, plots with higher native SES MPD had lower invasive species abundance at the next survey. The biotic resistance model only included plots that were uninvaded in the first survey, comprising 329 plots from 52 sites. There was no relationship between native diversity and invasive species abundance at a subsequent survey for other native diversity metrics.

Longitudinal Competitive Exclusion Models

I did not observe any significant relationships between invasive species abundance and change in native diversity over time. For several attributes of the native community, the change over time ranged widely in the plots that were never invaded (Figure 1.3). The species richness model included 820 plots from 75 sites. As the other native community attributes are calculated based on co-occurring species and required presence of 3+ native species at both time points, there were fewer locations included: 737 plots from 69 sites.

Discussion

My results show that, while phylogenetic and functional diversity of native species are linked to invasive species abundance, the dynamics may be more complicated than theory suggests. Based on the fine spatial resolution of my dataset (0.25-m^2 plots) and my use of an invasion metric accounting for abundance, I anticipated a negative diversity-invasibility relationship. I tested for effects of both phylogenetic and functional diversity, hypothesizing that they would have similar relationships with invasibility, and potentially stronger effects than species richness given their greater potential to reflect species' niches. My results are only partially consistent with this hypothesis. I found that communities with higher phylogenetic diversity (SES MPD) had lower abundances of invasive species at subsequent surveys. This is a phylogenetic analogue to the long-standing observation that, at fine spatial resolution, communities with more native species are less susceptible to dominance by invasive species (Kennedy et al., 2002; Naeem et al., 2000). However, when pooled across surveys, rather than a time series, communities with higher phylogenetic diversity (SES MNTD) had higher levels of invasion, suggesting that sites that support high diversity also support high invasion. This pattern has often been reported in observational studies, which, like my pooled model, typically lack temporally explicit data

(Marcantonio, Rocchini, & Ottaviani, 2014; Stohlgren et al., 2003). I further found that two traits (native community plant height and seed weight) predicted abundance of invasive species such that communities with taller plants and lighter seeds had lower cover of invasive species. However, I found no evidence connecting multivariate functional diversity or SLA to invasive species abundance.

Phylogenetic pattern of biotic resistance

In my biotic resistance model, the relationship between phylogenetic diversity and invasion aligned with my expectations: plots with higher initial phylogenetic diversity had lower abundances of invasive species in subsequent surveys. To my knowledge, few studies have demonstrated that native phylogenetic diversity confers invasion resistance as measured by decreased abundance of invasive species over time (Galland et al., 2019; Qin et al., 2020). And my study is the first to demonstrate this trend outside of experimental communities through a large-scale observational study. Although previous studies have found that more phylogenetically diverse communities are less invaded, they either did not account for change over time or only measured invasion as presence/absence (Gerhold et al., 2011; Iannone et al., 2016; Loiola et al., 2018; Lososová et al., 2015; Whitfeld, Lodge, Roth, & Reich, 2014; Yessoufou, Bezeng, Gaoue, Bengu, & Van Der Bank, 2019). As native species richness did not confer invasion resistance in my study, this supports the idea that phylogenetic diversity may be a more faithful representation of species' niches than species richness.

There have also been few studies testing whether phylogenetic diversity affects the likelihood (rather than relative abundances) of invasions over time. Those that have been performed have varied in their findings. An experimental study demonstrated that phylogenetic diversity conferred biotic resistance within wetland microcosms and was a better predictor of invasion resistance than species richness (Qin et al., 2020). Another experimental study found that phylogenetic diversity decreased colonization by unplanted species (Galland et al., 2019). One study found a negative relationship between phylogenetic diversity and invasive species reproduction, but no effect on survival or biomass (Feng, Fouqueray, & van Kleunen, 2019). Other studies have shown a positive effect of phylogenetic diversity on experimental invaders (El-Barougy et al., 2020), and that invasive species drove such a relationship by decreasing native phylogenetic diversity (Bennett, Stotz, & Cahill, 2014). Even within my dataset, I found that the relationship between phylogenetic diversity and invasion changed direction when the data was pooled and change over time was not explicitly considered.

Biotic interactions key to invasion, but no clear community assembly process

While I found partial evidence that biotic resistance mitigates invasion in these grassland communities, I found several lines of evidence that could be consistent with biotic resistance or competitive exclusion and were not able to disentangle the two. In my pooled model, plots with the most native species had the lowest invasive species abundance. In the context of Elton's invasibility hypothesis, some recent observational studies concluded that more species-rich communities confer biotic resistance based on a snapshot of invasion (Beaury et al., 2020; Iannone et al., 2016). Other non-longitudinal observational studies have concluded that the negative relationship between species richness and invasion is due to invasive species driving decline in native species via competitive exclusion (Hejda, Pyšek, & Jarošík, 2009; Michelan, Thomaz, Mormul, & Carvalho, 2010). The differences in these studies' conclusions are difficult to resolve, as observational studies that do not examine changes over time cannot differentiate causation from correlation, or the relative roles of biotic resistance by native species vs. competitive exclusion by invasive species (Warren, King, Tarsa, Haas, & Henderson, 2017). In my study, the effect of native species diversity was demonstrated only by measuring its effect on changes over time in abundance of invasive species. Thus, my results highlight the importance of longitudinal data and the limits of using snapshots to infer invasion dynamics.

Communities with taller native species underwent less invasion, which could be consistent with either competitive exclusion or biotic resistance. Height is generally thought to confer a competitive advantage because it directly correlates with a species' ability to intercept light (Keddy & Shipley, 1989). As height was not retained in the biotic resistance or competitive exclusion model, I cannot say whether taller native communities conferred invasion resistance or if invasive species drove the outcome by displacing shorter native species. Previous work supports the idea that taller invasive species are more successful and have a greater negative impact on native communities (Divíšek et al., 2018; Hejda & de Bello, 2013).

No evidence for competitive exclusion

I found no direct evidence that competitive exclusion by invasive species decreased native diversity. Competitive exclusion can be a slow-acting process, so the time frame I studied (up to 15 years) may not have been sufficient to observe this phenomenon (Yackulic, 2017). There was also high variability in diversity metrics in the uninvaded sites, which challenged detection of differences within the invaded sites. Furthermore, I had reduced statistical power due to removing sites that did not meet my analytical criteria. In other systems, competitive exclusion has been shown to shape the invasion process (Jucker, Carboni, & Acosta, 2013; Muthukrishnan et al., 2018). Based on my analyses, it appeared that biotic resistance played a stronger role than competitive exclusion. However, I did not find significant effects of species richness on biotic resistance despite finding a negative relationship between species richness and invasion in the pooled model. Given that biotic resistance and competitive exclusion are the primary community assembly processes thought to drive negative diversity-invasion relationships and I did not find evidence consistent with either process, it is likely that my models did not identify signals of all major community assembly processes.

Linking individual traits to invader abundance

Some of my findings could be consistent with biotic and/or environmental processes, which I were unable to distinguish due to limitations of my data. For example, in the pooled model, I found that plots with larger height variability among native species had higher abundance of invasive species. If small differences in height range were due to native communities with consistently taller species, this could reflect a competitive advantage of tall-statured species impeding invader success (Fréville et al., 2007; Leach & Givnish, 1996). However, this is unlikely as there was little correlation between variation in plant height and mean plant height ($r = 0.13$). These results could also be explained by disturbance, which drives trait divergence and can promote invasive species (Grime, 2006; Hierro, Villarreal, Eren, Graham, & Callaway, 2006; Jauni, Gripenberg, & Ramula, 2015).

Native communities with heavier seeds underwent greater invasion. Seed mass alone is not particularly informative of competitive ability and is usually linked with reproductive output (Leishman & Murray, 2001; Moles, 2018) through a trade-off between seed size and number of seeds produced for a given amount of energy—though this does not necessarily reflect differences in lifetime fitness (Moles, Falster, Leishman, & Westoby, 2004; Moles & Westoby, 2006). Large seeds are more likely to survive, especially in stressful conditions including high competition and low light, but reproduction of large-seeded species may be limited by seed numbers (Catford et al., 2019; Grime & Jeffrey, 1965; Turnbull et al., 1999). In contrast, smaller-seeded species are generally more prolific, have increased dispersal, remain viable in the seed bank longer, and grow out of their vulnerable juvenile stage faster (Moles & Westoby, 2006; Rejmánek & Richardson, 1996). Additionally, multiple studies have shown that native communities with heavier seeds are more heavily invaded. While the exact mechanism remains unclear, this pattern has been attributed to hierarchical differences in competitive ability driven by seed size, increased ability to withstand invasion pressure at the seedling stage, and increased microsite availability for smaller-seeded invasive species (Carboni et al., 2016; Catford et al., 2019; Fried, Carboni, Mahaut, & Violle, 2019).

The rich get richer?

When I viewed the data pooled across surveys, more phylogenetically diverse assemblages were more invaded. This trend held when I implemented the pooled model and restricted the plots included to those used in the longitudinal biotic resistance model. Positive relationships between diversity and invasibility are usually found when the spatial resolution of a study is large (Cleland et al., 2004; Levine & D’Antonio, 1999). This is generally attributed to greater environmental heterogeneity or other factors that covary with spatial scale and increase diversity in general, i.e., across native and invasive species alike (K. F. Davies et al., 2005; Fridley et al., 2007). While it remains somewhat unclear what drove positive diversity-invasibility relationships at neighborhood scales in my study, it is likely that aspects of the sites or their management selected for both high phylogenetic diversity and high invasion abundance. For instance, moderate grazing has been shown to increase native diversity by suppressing dominant species (Hallett, Stein, & Suding, 2017), but can also increase opportunities for establishment and seed dispersal by invasive species (Jauni et al., 2015).

The unexpected positive relationship between phylogenetic diversity and invasion in the pooled model casts doubt on the underlying assumptions of my hypotheses, specifically that more closely related species are more ecologically similar and biotic interactions are the primary drivers of community assembly at small scales. Indeed, there are reasons to expect inconsistency in these patterns (Mayfield & Levine, 2010). For example, these results could be explained by trait diversity being concentrated within a small number of families. Most of the dominant species in North American grasslands represent three families (Asteraceae, Fabaceae, and Poaceae; (Towne, 2002)), and previous work has shown that communities assembled from few lineages are more likely to have overdispersed traits (Prinzing et al., 2008). It is also possible that assemblages composed of distantly related species have lower niche overlap/packing and thus more empty or underutilized niche space for invaders to exploit. A recent experimental study found that colonization of more functionally diverse communities was greater and came to a similar conclusion: that higher functional diversity may increase unsaturated niche space (Galland et al., 2019). Likewise, biotic resistance is not always the primary factor determining invasive species establishment, even at the local scale (El-Barougy et al., 2020; Gallien & Carboni, 2017). Other factors, such as disturbance (e.g., human habitat modification; Tomasetto, Duncan, & Hulme, 2013), changes in resource availability, and environmental stress, can facilitate invasion and alter diversity-invasibility relationships (Clark & Johnston, 2011; M. A. Davis & Pelsor, 2001; Fridley et al., 2007).

While other observational studies have found higher native diversity in invaded communities, they are similarly limited in their ability to narrow the processes driving this pattern (Loiola et al., 2018; Marcantonio et al., 2014). Previous observational studies have typically treated invasion as binary (presence/absence) rather than comparing differences in invader abundance. Such differences in invasion metrics have been shown to change the direction of the diversity-invasibility relationship (Cleland et al., 2004; Smith & Côté, 2019).

The contrasting effects of phylogenetic diversity on invasion in my pooled and biotic resistance models were unexpected. A possible explanation is that phylogenetic diversity could have different effects at different stages of invasion, consistent with the ecological strategies that make for a successful invasive species being fluid across invasion stages (Gallien & Carboni, 2017; C. Ma et al., 2016). It could be that the functional traits of the recipient community that were key to resisting early-stage invasions were more phylogenetically conserved than traits that confer resistance at later invasion stages. Most plots in my sites had already been invaded and invasive species may facilitate one another via invasional meltdown (Simberloff & Von Holle, 1999). The effects of invasional meltdown were controlled for in the biotic resistance model by only including plots with no initial invasion, but this was not the case for the pooled model. Additionally, the lack of invasion in the previously uninvaded plots that I restricted my analysis to may indicate something unique about them. That is, they may not constitute a representative sample.

Differences in phylogenetic diversity metrics may also explain the opposing effects I found in my pooled and biotic resistance models. The phylogenetic diversity metric selected in the biotic resistance model reflects deeper relationships within the tree (MPD), whereas the metric selected in the pooled model (MNTD) reflects more recent divergences. These differences in phylogenetic depth makes them sensitive to different processes (Mazel et al., 2016). Studies on relatedness between invader and recipient communities have found that invaders tend to occur in communities when they have at least one close relative (measured via shallow metrics like MNTD), but are more distantly related to the community as a whole (measured via deep metrics like MPD) (Marx et al., 2016; Qian & Sandel, 2017). It could be that deeper divergences better reflect aspects of niche differentiation important to invasive species establishment.

The absence of a relationship between multivariate functional diversity and invasion

I expected native assemblages with higher multivariate functional diversity (FDis) to be less invadable, but it is not entirely surprising that this was not the case. Functional diversity is only meaningful if the traits included are linked to ecological processes relevant to invasion (Funk et al., 2017; Lefcheck et al., 2015). The traits included in this study may not adequately capture key niche axes involved in the invasion process; notably, I had no belowground traits, which are important in competition (Broadbent, Stevens, Peltzer, Ostle, & Orwin, 2018; Foxx & Fort, 2019). I was also unable to obtain functional traits for all species in the dataset. While I attempted to minimize the effects of missing trait data, the lack of complete trait coverage could have biased my estimates of functional trait diversity (Májeková et al., 2016; Pakeman, 2014).

Previous observational studies have found that uninvaded native communities have higher functional diversity than invaded communities, which was interpreted as evidence of invasive species decreasing functional diversity through competitive displacement (Hejda & de Bello, 2013; Jucker et al., 2013; Loiola et al., 2018). Of the few invasion studies to manipulate functional diversity experimentally, two found that invader performance decreased in more functionally diverse native communities, providing support for the biotic resistance hypothesis (Byun, de Blois, & Brisson, 2020; Feng et al., 2019). However, another experiment found that colonizers were more successful in higher functional diversity plots and attributed this to more available niche space in functionally diverse assemblages (Galland et al., 2019).

Conclusion

This study demonstrates that our understanding of invasion dynamics is highly sensitive to treatment of time and selection of diversity metrics. Without the inclusion of phylogenetic diversity, my findings would primarily confirm the well-documented phenomenon that, at a given point in time, more species-rich communities are less invaded. The patterns I observed with phylogenetic diversity illustrate that temporal context is critical to elucidating invasion dynamics. If only snapshots in time were considered, the positive correlation between native diversity and abundance of invasive species would suggest that site attributes select for both diversity and abundance. In contrast, based on time-series data it appears that high diversity enables native communities to resist invasion. Both may be true. Thus the “invasion paradox” dissolves into a discrepancy in perspectives. And it suggests that managing grasslands for invasion resistance will require an attention to both site conditions and native community diversity. This conclusion, which will align with the field observations of many land managers and community ecologists, is drawn from my synthesis of pooled and longitudinal studies. Diversity-invasibility relationships are likely too complex to study from one standpoint alone.

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CHAPTER TWO

Neither phylogenetic nor functional diversity increase invasion resistance in an experimental grassland restoration

Abstract

Phylogenetic and functional diversity have been theorized to increase resistance to invasion. Experimentally testing whether communities higher in these components of diversity are indeed less invadable is an important step toward designing native plant restorations for reduced invasion—a key restoration objective.

To investigate how phylogenetic and functional diversity affect invasion resistance in a restoration setting, I established experimentally restored prairie plots. The experiment crossed three levels of phylogenetic diversity with two levels of functional diversity while species richness was held constant. Invaders were allowed to colonize plots from the nearby environment, which included species from neighboring experimental plots and those from an old field dominated by weeds of Eurasian origin. I tested if invader biomass was predicted by plots' phylogenetic diversity, functional diversity, and phylogenetic and hierarchical trait distances between invaders and planted species.

I categorized invaders as those that established from neighboring experimental plots (site-specific invaders), native species that were not part of the experimental species pool (native invaders), and non-native species (non-native invaders). I found that different types of invaders were not equivalent. In general, both non-native and native invaders became more abundant in more phylogenetically diverse plots, counter to expectations. However, higher abundance of planted Asteraceae, a dominant family of the tallgrass prairie, led to lower invader biomass for both native and non-native invaders. I also found that non-native invaders that were taller than planted species and native invaders with lower specific leaf area than planted species became most abundant. Site-specific invaders were not influenced by any of the plot-level diversity metrics measured.

My results suggest that, in early restorations, establishment of dominant native species may confer more invasion resistance than phylogenetic and functional diversity. Additionally, examination of trait differences between likely invaders and candidate species for restoration could be used to design more invasion-resistant assemblages. Finally, I unexpectedly found that greater phylogenetic diversity could *lower* resistance to invasion, possibly due to greater availability of unsaturated niche space for colonization.

Keywords: Biotic resistance, community assembly, community phylogenetics, diversity-invasibility, invasion ecology, invasion paradox, prairie, trait hierarchy

Introduction

Invasive species management is among the most resource-intensive aspects of ecological restoration (Li & Gornish, 2020; Rowe, 2010). Most methods of invasive species control are costly in time and money, and many have non-target effects that damage native species (D'Antonio & Meyerson, 2002). This has led to increasing interest in leveraging community ecology and invasion theory to design restored assemblages to resist invasive species (Funk, Cleland, Suding, & Zavaleta, 2008; Laughlin, 2014a). Bolstering invasion resistance by modifying the native community could allow reallocation of limited restoration resources from invasion control to increasing native species diversity, which aligns with multiple restoration objectives (Brudvig, 2011; Temperton et al., 2019). Testing characteristics of native assemblages that confer invasion resistance offers a way to build on fundamental questions in community assembly theory while guiding restoration practices towards an appealing alternative to resource-intensive control measures.

Most research on how species diversity affects invasion has been centered on species richness (Tomasetto et al., 2019). Biotic resistance theory suggests that more species-rich communities will occupy more niche space, resulting in fewer opportunities for invaders to colonize (D’Antonio & Thomsen, 2004; Elton, 1958). However, studies of diversity-invasibility relationships have found that higher species richness tends to be associated with either communities that are most resistant to invasion or those most susceptible to invasion, depending on context. These contrasting results have been attributed to differences in spatial and temporal scale (Clark & Johnston, 2011; Levine & D’Antonio, 1999), invasion metric (Cleland et al., 2004), and whether observational or experimental approaches are used (Fridley et al., 2007; Tomasetto et al., 2019). When diversity confers invasion resistance, it is usually attributed to fuller occupancy of niche space, whereas positive correlations between diversity and invasion are often attributed to covarying factors that increase both native and invasive diversity.

However, previous diversity-invasibility studies may also be limited by over-reliance on species richness to characterize resident community diversity, as species counts are an imprecise proxy for niche occupancy. Incorporating dimensions of diversity that better reflect niche space may deepen understanding of diversity-invasibility relationships, enabling native diversity to be leveraged more effectively in restoration. Both phylogenetic and functional diversity are hypothesized to correspond with niche space (Cavender-Bares et al., 2009; C. Webb, 2000). Phylogenetic diversity encompasses the shared evolutionary history of a species assemblage while functional diversity describes the distribution of traits within an assemblage. Both of these components of diversity are expected to better reflect niche space filled by an assemblage than simple species counts, and recent work has found that phylogenetic and functional diversity are improved (and positive) predictors of invasion resistance (Byun et al., 2020; Qin et al., 2020). However, other studies found higher phylogenetic and functional diversity associated with greater susceptibility to invasion, even in small-scale experimental contexts (El-Barougy et al., 2020; Galland et al., 2019) where evidence of biotic resistance might be expected to be more pronounced (Fridley et al., 2007). Thus phylogenetic and functional diversity join species richness in having contradicting relationships with invasion.

Phylogenetic diversity is frequently used as a proxy for functional diversity (Cavender-Bares et al., 2009; C. Webb, 2000) because of the limited availability of trait data and challenge of selecting ecologically relevant traits (Cadotte et al., 2013). Phylogenetic diversity may capture unmeasured traits while functional diversity may incorporate traits under strong selection, convergent across clades, or otherwise not phylogenetically conserved (Cavender-Bares et al., 2009). Because both diversity metrics can provide distinct insights into ecological processes (Cadotte, Carboni, Si, & Tatsumi, 2019), more investigation into their relative ability to predict invasion is warranted.

The success of an invader depends on both niche differences and competitive ability differences (Kunstler et al., 2012; Mayfield & Levine, 2010; Shea & Chesson, 2002a). Species with traits that confer a competitive advantage are more likely to overcome biotic resistance (Conti et al., 2018). Considering only niche differences, I would expect successful invaders to be dissimilar to the native community, such that competitive interactions are weaker, but similar enough to coexist in the same environment (known as Darwin's Naturalization Conundrum; see Feng, Fouqueray, & van Kleunen, 2019; Marx, Giblin, Dunwiddie, & Tank, 2016; Thuiller et al., 2010). However, for traits linked to competition, hierarchies may exist such that a species' relative position on a trait gradient is directly related to its competitive ability (e.g. taller plants intercept more light) (Goldberg & Landa, 1991; Kunstler et al., 2012; Mayfield & Levine, 2010). An invader's fate would then be expected to depend on a combination of the resident community's diversity, its ecological similarity to the native community, and its relative position in the community's competitive trait hierarchies.

A common problem in restoration ecology and invasion biology is the applicability of research to practice (Cabin, Clewell, Ingram, McDonald, & Temperton, 2010; Funk et al., 2020). Many management recommendations are made based on studies conducted in settings dissimilar to the natural areas where management occurs. For example, most grassland restoration projects are started from seed due to scalability and lower cost, while many ecology experiments transplant plugs into sites to bypass germination and establishment bottlenecks (Palma & Laurance, 2015). Management of field ecology experiments is also frequently more intensive than most restoration projects (Hulme, 2014). Definitions of invasive species may also differ between experiments and management settings (Funk et al., 2020; Shaw, Wilson, & Richardson, 2010). As the context of a study may influence the direction of the diversity-invasibility relationship, a study's applicability hinges on its setting and scope. To understand how phylogenetic and functional diversity influence invasion dynamics in a restoration setting, invasion should be studied in relevant contexts, which few studies have done to-date (though see Barber et al., 2017; Williams, Barak, Kramer, Hipp, & Larkin, 2018). The field experiment was designed to resolve four common disparities between ecological experimentation and restoration practice, attempting to reflect restoration conditions more accurately by establishing plants from seed, using high-richness assemblages representing restoration targets, managing the site in ways that mirror common constraints in restoration, and evaluating multiple categories of "invaders"—from unseeded native species to aggressive non-native species frequently targeted for control in restorations.

The experimentally restored plots consist of tallgrass prairie communities of 15 species established from seed, with varied functional and phylogenetic diversity. I measured invasion by tracking all unplanted species that established in plots over a three-year period. I investigated how phylogenetic and functional diversity of a plot affected (1) total invasive species biomass, (2) biomass of individual invasive species, and (3) the trajectory of invasion. I further investigated phylogenetic distance and hierarchical trait differences between each invasive species and its recipient native community to assess how differences between invaders and recipient communities affected invasion.

Materials and Methods

Study site and experimental design

The experiment was conducted at The Morton Arboretum (Lisle, IL, USA). The full design is described in Hipp et al. (2018) and Karimi et al. (*In revision*). Briefly, the experiment was designed with three levels of phylogenetic diversity and two levels of functional diversity in a fully factorial design. To isolate the effects of phylogenetic and functional diversity without confounding by richness, each 2-m × 2-m plot was sown with 15 species. In total, the experiment includes 127 species selected because they are used regionally in tallgrass prairie restorations and were commercially available. Diversity treatments were established by simulating 2×10^6 15-species communities and calculating their phylogenetic and functional diversity. This was used to determine the range of phylogenetic and functional diversity and identify suitable bins for low-, medium-, and high-diversity treatments. For each of the 6 diversity treatments (3 levels of phylogenetic diversity × 2 levels of functional diversity), 6 communities were drawn at random for a total of 36 unique communities, each replicated twice in the experiment. The experiment consisted of diversity treatments in mixture plots established from seed and from plugs and monoculture plots established from plugs. Only the seed plots are discussed here. The experiment was fully blocked with six blocks and two super blocks; each community occurs once in each super block and two communities from each of the six diversity treatments occur in each block.

Site management

The plots were established from seed sown in fall 2016. Plots were sown at a rate of 129 seeds species^{-1} m^{-2}. Prior to planting, the site was dominated by mostly non-native ruderal species, particularly *Bromus inermis* (smooth brome), *Dipsacus laciniatus* (cutleaf teasel), and *Pastinaca sativa* (wild parsnip) and the aggressive native species *Solidago altissima* (tall goldenrod) (Schramm, 1976; Weber, 2000). The site was plowed, disked, planted with a cover crop, and underwent two rounds of herbicide application in fall 2015 and spring 2016. The plots were burned in early spring 2018 and 2019. Prescribed burns were the primary method of weed control; however, to facilitate establishment of seeded species, the most aggressive weeds were removed from the experiment (Table S2.1). Plots were weeded either once or twice per summer; biomass data were always collected immediately prior to weeding efforts. The site preparation and management techniques used are consistent with those commonly used in restorations (Harmon-Threatt & Chin, 2016; Rowe, 2010).

Data Collection

In each 4-m^2 plot, I collected biomass from a 1-m × 1-m subplot. I further subdivided each subplot into four 0.25-m × 1-m strips. For each biomass collection, I selected one of the four strips at random and collected from the same strip in all plots to control for edge effects. I clipped all plants rooted within the strip at ground level. The plants were then sorted to species or lowest feasible group, placed in an herbarium drier for 72 hours, and weighed. Most non-native grasses were grouped because they lacked species-level identifying characteristics when biomass was collected.

Biomass was collected five times from 2017-2019: June and September of 2017 and 2018, and September only in 2019. Due to low establishment of native species in the first growing season (2017), only presence-absence was recorded—biomass was not collected for native species that year.

Categorizing invaders

Any species not planted into a plot was considered an invader and its biomass recorded. I binned invaders into three categories corresponding to their geographic origins and concern from a management perspective. The first set of species, *site-specific invaders*, are any of the 127 experimentally planted species collected in a plot they were not sown into; in a restoration context this set of species would not likely be targeted for weed management. The second set of species, *native invaders*, are native species not among the 127 experimentally introduced species. While volunteer native species are not typically a management concern, some that colonized are considered ecologically invasive and targeted for removal by regional restoration practitioners. The final set of species are *non-native invaders*, which are a higher management priority and, resources permitting, frequently targeted for control. All statistical analyses were completed for each group separately.

Functional traits

Functional traits for the 127 species established in the experiment were gathered from published sources (Amatangelo, Johnson, Rogers, & Waller, 2014; Sonnier, Johnson, Amatangelo, Rogers, & Waller, 2014) and supplemented with additional trait data gathered for the experiment (TRY dataset ID 671; Kattge et al., 2020). This trait dataset, further described in Hipp et al., (2018) encompassed 29 traits: 12 continuous leaf traits, 7 categorical traits, 8 binary root traits, seed mass, and genome size (Table S2.2). Additional trait data were gathered from the experiment in summer 2020. When possible, I measured height from 5-10 individuals and SLA from five leaves from five individuals following Pérez-Harguindeguy et al., (2013). Seed mass data were obtained from the Chicago Botanic Garden’s seed bank (“Science Collections Database,” 2020). With these additions, 17.7% of the trait matrix was unfilled. Missing values were imputed using multivariate imputation by chained equations (MICE) using the *mice* package v.3.8.0 in R (van Buuren & Groothuis-Oudshoorn, 2011). For all trait analyses, I used both raw trait data and the complete matrix with imputed data. The results were similar regardless of the matrix used; results based on the complete trait matrix are presented.

A separate trait dataset was generated for any species observed in the plots that was not among the 127 experimentally established species. Data were gathered from the TRY database (Kattge et al., 2020), BIEN database (Enquist et al., 2016) using the *BIEN* R package v.1.2.4 (Maitner et al., 2018), and seed bank database ("Science Collections Database," 2020). Trait data for these species were gathered to calculate hierarchical trait distances with the native community for three traits: height, SLA, and seed mass.

Diversity metrics

The experiment was designed using Faith's phylogenetic diversity (PD) and functional dispersion (FDis) to measure phylogenetic and functional diversity, respectively. Faith's PD is calculated by summing phylogenetic branch lengths of co-occurring species and correlates with richness. This did not pose a problem for the original design as richness was held constant. However, for the current analysis I did not use Faith's PD because: (1) not all sown species established, leading to richness differences among plots; and (2) Mean Nearest Taxon Distance (MNTD), a measure of divergence between species, may better elucidate diversity-invasibility relationships (Tucker et al., 2017). MNTD is the average distance between each species and its most closely related co-occurring species and was calculated using the *picante* package v. 1.8.2 in R (Kembel et al., 2010), with standardized effect sizes (SES) to control the influence of richness on MNTD. Positive SES MNTD values indicate that a community is more phylogenetically diverse than expected, while negative values indicate lower diversity than expected. For functional diversity, I used the same metric as the original design, FDis, which is hypothesized to capture niche differentiation. FDis is the abundance-weighted average distance of each species to the community's centroid in multivariate trait space. FDis was calculated using the *FD* package v. 1.0-12 (Laliberte & Legendre, 2010b; Laliberte, Legendre, & Shipley, 2014).

Calculating differences between native and invasive species

I calculated phylogenetic and trait differences between each invasive species and the planted community in which it occurred. For phylogenetic distances, I used the cophenetic function in *picante* package v. 1.8.2 to generate a matrix of relatedness (Kembel et al., 2010). I then generated two distance measures: (1) mean pairwise phylogenetic distance to the invader (MPD.i), the average distance between an invasive species and every co-occurring native species, and (2) mean nearest taxon distance to the invader (MNTD.i), the distance between an invader and its most closely related native species.

Additionally, I examined hierarchical trait differences between each invasive species and its recipient community (Kunstler et al., 2012). These measures reflect differences between trait values of a given invader and its co-occurring planted species. Hierarchical, unlike absolute, trait differences can be positive or negative, allowing an explicit test of whether the invader having higher versus lower values of a given trait mediates its interactions with native species. Hierarchical trait differences were calculated for seed mass, specific leaf area (SLA), and plant height, which correspond with three key functional trait axes: reproduction, resource acquisition, and height, respectively (Fréville et al., 2007; Leach & Givnish, 1996; Westoby & Wright, 2006; Wright et al., 2004). The traits used for hierarchical trait differences had few missing species: seed mass data were missing for one unsown species, height data for one sown species, and SLA data for six sown and seven unsown species. Biomass that could only be identified to genus, and non-native grass biomass, was excluded from analyses incorporating hierarchical trait differences.

Statistical analyses

I implemented models addressing how planted community diversity affects: (1) total biomass for each invader category (summed invader biomass), (2) individual biomass of invaders in each category (individual invader biomass), and (3) the temporal trajectory of total biomass for each category (invasion trajectory). For each of these models, the following were included as fixed predictors: SES MNTD, FDis, and sampling year and month. Block was included as a random effect. To facilitate comparison of effect sizes, all continuous predictors were scaled to a mean of 0 and standard deviation of 1. For model selection, I implemented both forward and backward selection based on log-likelihood ratio tests. To avoid over-fitting models, I also assessed fit using k-fold cross validation and root mean square error implemented with the *caret* package v. 6.0-86 (Kuhn, 2020). To visualize all planted community characteristics considered, I implemented global models and created partial effect plots for all predictors using the *ggeffects* (Lüdecke, 2018) and *ggplot2* packages (Wickham, 2016) (Figures S2.1-S2.3). All analyses were implemented in R v. 4.0.3 (R Core Team, 2020).

As many sown species did not establish, observed diversity levels differed from sown diversity. However, measuring native community diversity from biomass collected concurrently with invader biomass presents challenges, as invaders both influence and respond to the native community. To untangle these effects, native diversity levels were calculated from the previous year’s biomass collection, better characterizing attributes of the established native community that shaped invasion dynamics.

Summed invader biomass

I used linear mixed models to assess how planted diversity influenced biomass attained for each category of invader in aggregate (total invader biomass ~ native diversity at prior visit). To meet assumptions of normality, biomass data were *ln*(x + 1) transformed. I included plot as a random effect to account for non-independence of data collected from repeated sampling of the same plots. These models incorporate biomass data from 2018 and 2019, summed by invader category, as the response. Biomass data from 2017 were included as a fixed effect to account for spatial heterogeneity in initial invasion pressure across the site.

Solidago altissima (tall goldenrod) comprised roughly 90% of native invader biomass and 50% of total unplanted biomass. I replicated analyses with *S. altissima* as the focal invader and all native invader biomass summed. The results were similar, so only *S. altissima* is discussed due to its more significant management implications.

There are a small number of dominant families in the tallgrass prairie (Weaver & Fitzpatrick, 1934) and these families have been shown to have varying effects on the phylogenetic diversity of remnant prairie communities that are targets for restoration (Larkin et al., 2015a). I examined the relationship between the three most dominant families (Poaceae, Asteraceae, and Fabaceae) and invasion. I compared the biomass from each of these families in the planted community against total invader biomass to account for potentially disproportionate impacts of these families on plant community development.

Individual invader biomass

I used linear mixed models to assess how invasion changed over time for individual species in each plot (individual species biomass ~ planted diversity at prior visit + phy dist + hier dist). I estimated models for each of the three invader categories. In addition to the fixed predictors tested for all models, this model included two phylogenetic distance metrics (MNTD.i and MPD.i) and hierarchical trait difference for height, seed mass, and SLA. Plot and species identity were included as random effects.

*Invasion trajectory*

I used linear models to assess relationships between planted diversity and the temporal trajectory of invaders in each plot (change in total invader biomass over time ~ planted diversity). I performed linear regressions to model change in biomass over time in each plot (invader biomass ~ year). The model coefficients from these regressions, representing the trajectory of invader biomass in each plot, were then used as a response variable. To control for intra-annual variation, this analysis was split into two models: change over time from June to June in two years (2017–2018) and successive Septembers in three years (2017–2019). For the native invader category, I repeated analyses with all native invaders and with only *S. altissima*. As with summed invader biomass, I found similar results for both approaches; for clarity, I report only the *S. altissima* model.

Results

Invasion overview

Across all plots over three years, I observed 59 site-specific invaders, 31 native invaders, and 52 non-native invaders (Table 2.1). Non-native invaders were more abundant across the site in June than September for both 2017 and 2018. Non-native invader abundance decreased across the site relative to native and site-specific invaders (Table 2.2). The average number of sown native species per plot was 6.4 ± 2.1 (S.D.). The average number of invaders per plot was 5.6 ± 2.6 invaders across all categories, 1.5 ± 0.9 site-specific invaders, 2.3 ± 1.3 native invaders, and 2.7 ± 1.7 non-native invaders.

Summed biomass models

For site-level invaders, the final model only included year and initial invasive biomass—there were no observed effects of planted diversity (Table 2.3). The final model for *S. altissima* biomass indicated that its biomass increased with year ($\chi^2 = 66.36$, $p < 0.001$), and was greater in plots with higher phylogenetic diversity (SES MNTD, $\chi^2 = 3.84$, $p = 0.05$) or initial biomass ($\chi^2 = 9.12$, $p = 0.003$) and lower in plots with higher planted Asteraceae biomass ($\chi^2 = 14.41$, $p < 0.001$), i.e., plots with high phylogenetic diversity, low abundance of planted Asteraceae, and high initial abundance of *S. altissima* tended to have higher *S. altissima* biomass (Figure 2.2). For non-native invaders, biomass was lower in plots with higher biomass of planted Asteraceae ($\chi^2 = 20.10$, $p < 0.001$). Across all invaders, biomass increased over time ($\chi^2 = 73.28$, $p < 0.001$), and was greater in plots with higher phylogenetic diversity ($\chi^2 = 9.32$, $p = 0.002$) or initial invader biomass ($\chi^2 = 8.81$, $p = 0.002$).

Individual biomass models

For site-level invaders, there was no relationship between invasion and any of the planted community characteristics. The final model for native invaders indicated they had higher biomass in plots with higher phylogenetic diversity ($\chi^2 = 6.49$, $p = 0.01$) (Figure 2.2). Individual native invaders were also more abundant in plots where they had lower SLA than the recipient native communities ($\chi^2 = 2.79$, $p = 0.09$). In the non-native invader model, the sole fixed predictor included was hierarchical height difference, such that individual invaders had higher biomass in plots where they were taller than the planted species ($\chi^2 = 6.26$, $p = 0.01$). Including all invaders, biomass of invaders increased with year ($\chi^2 = 16.04$, $p < 0.001$) and month ($\chi^2 = 9.83$, $p = 0.002$) and was greater when the planted community had higher phylogenetic diversity ($\chi^2 = 5.07$, $p = 0.02$) or the invader had lower SLA than the planted community ($\chi^2 = 4.61$, $p = 0.03$).

Invasion trajectory models

I failed to reject the null model for any of the June trajectory models: no aspect of the planted community affected the invader trajectory between growing seasons. For the September trajectory models, there was no relationship between planted diversity and change in invader biomass over time for site-specific invaders. The trajectory of *S. altissima* biomass was positively correlated with abundance-weighted SES MNTD, i.e., *S. altissima* increased more over time in plots with higher phylogenetic diversity ($\chi^2 =14.9$, $p < .001$) (Figure 2.3). Non-native invader biomass also increased over time in plots with higher SES MNTD ($\chi^2 =5.99$, $p = 0.01$). The same pattern was found across all invaders: plots with higher phylogenetic diversity had greater increases in invader biomass over time ($\chi^2 =19.10$, $p < 0.001$).

Discussion

I found that phylogenetic and functional diversity did not increase resistance to invasion in an experimental restoration setting. Instead, phylogenetic diversity appeared to increase susceptibility to invasion, contrary to my expectations. There were clade-level effects on invasion resistance: abundance of Asteraceae, a dominant tallgrass prairie family, was associated with lower biomass of invaders. Site-specific invaders were not influenced by the native community, while native and non-native invader biomass increased with increasing planted phylogenetic diversity and decreased with increasing planted Asteraceae biomass. Trait differences between invaders and resident communities were important as well: non-native invaders taller than planted species and native invaders with lower SLA than planted species were more successful. The temporal scale considered was also important. I only found evidence that non-native invader biomass increased with phylogenetic diversity when data were analyzed longitudinally through the trajectory models.

Phylogenetic diversity and invasion

Phylogenetic diversity was positively correlated with invader biomass in the subsequent growing season for native invaders. In addition, I observed an increase in biomass over all three years for non-native invaders in more phylogenetically diverse plots. While positive diversity-invasion relationships are common at larger spatial scales and in observational studies, they often give way to negative relationships at the plot level, in experimental settings, or when an abundance-based metric is used to quantify invasion (Fridley et al., 2007; Smith & Côté, 2019). A common explanation for positive diversity-invasibility relationships—extrinsic factors that covary with native and non-native diversity—is less likely to apply in an experimental setting. Despite this, at least two other experimental studies have found that either higher phylogenetic or functional diversity was associated with increased invasion (El-Barougy et al., 2020; Galland et al., 2019). Both studies suggested that increases in these forms of diversity, which presumably diversified the range of niches occupied, may have increased availability of unsaturated niche space for invaders to exploit. In contrast, other studies have found that more phylogenetically diverse communities were less invaded—although several were observational and not all established phylogenetic diversity as the driver of the relationship (Feng et al., 2019; Gerhold et al., 2011; Iannone et al., 2016; Loiola et al., 2018; Lososová et al., 2016; Qin et al., 2020; Whitfeld et al., 2014; Yessoufou et al., 2019). There have been greenhouse and mesocosm experiments indicating that phylogenetic diversity conferred invasion resistance (Feng et al., 2019; Qin et al., 2020); however, to my knowledge, a negative relationship between phylogenetic diversity and invasion has not been demonstrated in any field experiments to date.

Functional diversity

I did not observe an effect of functional diversity on invader biomass, which may be a result of the traits selected. The utility of functional diversity for predicting ecological interactions is determined by how well measured traits reflect ecological processes, which can be difficult to determine (Mlambo, 2014). As traits can be linked to specific biological processes, they are frequently used to describe mechanisms of niche differentiation (Kraft, Godoy, & Levine, 2015). However, multidimensional trait space is not equivalent to niche space—although it can be a reasonable proxy—and the relationship between trait space and niche space can be altered by environmental conditions (D’Andrea & Ostling, 2016). I also did not account for trait variation within species, and intraspecific variation can change how functional diversity is quantified and which ecological patterns can be detected (Albert et al., 2012). These caveats notwithstanding, my work supports previous findings that phylogenetic diversity may more efficiently predict ecological interactions and ecosystem functions than traits or environmental niches (Cadotte, Cavender-Bares, Tilman, & Oakley, 2009; Pearse & Hipp, 2009; Xu et al., 2019).

Hierarchical trait differences

I found that non-native invaders had higher biomass in plots where they were taller than planted native species. Height has been identified as one of the traits underlying successful invaders (Van Kleunen, Weber, & Fischer, 2010). Taller species have been shown to have a competitive advantage due to greater light interception and overtopping/shading of shorter-statured species (Fréville et al., 2007; Leach & Givnish, 1996). This suggests displacement through competition for light is one of the processes shaping invasion in this experiment, which is not always true in grasslands. Shorter non-native species with high lateral spread and good dispersal ability were more successful invaders in European grasslands (Carboni et al., 2016). Another study found invaders performed better when they had a distinct height, whether taller or shorter, than native species (Catford et al., 2019).

I found that native invaders with lower SLA than planted natives were more abundant. This was an unexpected result, as higher SLA is often associated with invasion success (Carboni et al., 2016; Van Kleunen et al., 2010; but see Leishman, Thomson, & Cooke, 2010). Higher SLA can lead to higher relative growth rates, increased carbon capture, and shorter leaf lifespans (Westoby & Wright, 2006; Wright et al., 2004). These traits are typically more important in highly disturbed habitats, and suggests a slower growth rate and more conservative traits are favored at this experimental site, and possibly prairie restorations more generally. Previous grassland studies have shown that invaders with lower SLA have better competitive responses (Catford et al., 2019; Conti et al., 2018; Goldberg & Landa, 1991). These findings and ours are noteworthy, as the link between invasion success and high SLA has led to recommendations to plant native species with higher SLA to confer invasion resistance (Drenovsky & James, 2010). My work suggests that such recommendations may need to be tempered.

Differences across invader categories

My results differed between invader categories. I found no effect of planted diversity on site-specific invaders. For native invaders, biomass increased with increasing phylogenetic diversity of the experimentally established community in all three sets of models. However, I only saw this trend in the trajectory models for non-native invaders, such that more phylogenetically diverse plots had greater increases in non-native biomass over time. In contrast, more planted Asteraceae biomass was correlated with lower biomass of both native and non-native invaders. I also found that competitive hierarchies seemed to promote invasion, but the traits differed between invader categories. Specifically, for non-native invaders, being taller than experimentally established assemblages promoted invasion; for native invaders, having lower SLA than planted species was advantageous.

There is considerable debate about what constitutes an invasive species, particularly with regard to origin (Buckley & Catford, 2016; M. Davis et al., 2011; Simberloff, Souza, Nũnez, Barrios-Garcia, & Bunn, 2012). These differences in definition can change expectations of how invaders behave (Catford et al., 2016). Invasion biology as a discipline tends to focus on non-native species, with the concept of “native invaders” being contentious (Simberloff et al., 2012). Research suggests, however, that land managers care more about species’ impacts than origin (Kapitza, Zimmermann, Martín-López, & Wehrden, 2019). In my study, the most abundant invader, *S. altissima*, is native and prioritized for control by regional land managers (Schramm, 1976). As an applied discipline, invasion biology should focus on land manager priorities if the goal is preventing and reducing negative impacts of undesirable species. My study underscores that how invasion is defined matters, and that an emphasis solely on non-native species may not adequately address land managers' needs.

The Asteraceae effect

Dominant tallgrass prairie species are drawn disproportionately from a relatively small number of families, particularly the Asteraceae, Poaceae, and Fabaceae. The Asteraceae are by far the most diverse family in this experiment, comprising 41 species of the 127-species pool, and many of them are exceptionally robust competitors. Occurrence of species in the Asterales order has previously been linked to decreased phylogenetic diversity in prairie remnants (Larkin et al., 2015a). In the original experimental design, randomly generated low phylogenetic diversity communities tended to be dominated by Asteraceae. Consequently, to avoid an experiment in which dominance by Asteraceae confounded the effects of low phylogenetic diversity, communities were constrained so that only 3 of the 15 species could be Asteraceae (Hipp et al., 2018). However, where members of the Asteraceae became dominant in low phylogenetic diversity plots, despite being represented by few species, it remains difficult to disentangle effects of Asteraceae from those of low phylogenetic diversity. For example, low phylogenetic diversity treatments had, on average, 18.4% greater biomass of planted Asteraceae than high-diversity treatments. Furthermore, many aggressive invaders in my study are themselves Asteraceae, raising the possibility that limiting similarity caused the planted Asteraceae to offer greater competitive resistance to additional Asteraceae. However, I did not find evidence of a relationship between phylogenetic distance and invader biomass. Regardless, it may be that dominance by Asteraceae drove decreases in phylogenetic diversity and invader biomass in parallel. For the *S. altissima* summed model, the only one that included both phylogenetic diversity and planted Asteraceae, I compared the relative support for these two predictors and found that the best-supported model was reduced to only planted Asteraceae biomass. Young prairie restorations in particular are known to be dominated by Asteraceae (Schramm, 1990). Having locally dominant prairie species established may be a greater source of invasion resistance than phylogenetic and functional diversity, especially early in the development of a restoration. This relationship might change over time as prairie vegetation undergoes succession.

Solidago altissima *as a focal invader*

I highlighted the native *S. altissima* (an Asteraceae) in my analyses because it was the most dominant invader in my study, comprising nearly two-thirds of total invader biomass. *Solidago altissima* warranted special attention in my analyses because of its prevalence in the experiment and because it poses challenges for regional restoration managers. In addition to being considered invasive on multiple continents (Weber, 2000), *S. altissima* is regarded as a problematic species in tallgrass prairie restorations that can require aggressive management (Schramm, 1976; Weber, 2001) and be difficult to control manually (Meyer & Schmid, 1999; Weber, 2000). I found that *S. altissima* biomass was lower in plots where the native community had lower SLA and higher planted Asteraceae biomass. This is consistent with plots with sown Asteraceae conferring biotic resistance to invasion. However, it could also be due to an energetic zero-sum dynamic (Ernest, Brown, Thibault, White, & Goheen, 2008) wherein a plot can only produce a given amount of biomass so that, as *S. altissima* becomes more dominant, there is lower unclaimed productivity for other planted Asteraceae to account for. Nonetheless, the finding that increased Asteraceae biomass may confer resistance to invasion has applications to species selection for prairie restoration.

Conclusion

My results suggest that, despite the theoretical basis and practical appeal of phylogenetically and functionally diversifying restored assemblages to increase invasion resistance, establishing dominant native species may be the best defense against invasion in a young restoration. I also demonstrated that trait hierarchies may be helpful in predicting invasion. Traits of invaders of concern could be compared to those of native species that are candidates for use in restoration to design more invasion-resistant seed mixes. These recommendations may be at odds with other restoration goals and should be weighed against other priorities. These results may also change over longer time scales: phylogenetic and functional diversity may exert more influence with time as niche-based dynamics shape succession. Observational studies over longer time scales have found that invasion decreases in more phylogenetically diverse communities; however, ours and prior field experiments have shown the opposite relationship. My study underscores that phylogenetic diversity and trait hierarchies shape the invasion process, but do not provide a simple heuristic for restoring invasion-resistant assemblages.

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CHAPTER THREE

Phylogenetic diversity and variety in life history strategies promote invasion resistance in an experimentally restored tallgrass prairie

Abstract

Phylogenetic and functional diversity are theorized to increase invasion resistance, but there have been few experimental field tests of this question—and none that have experimentally introduced invaders. I explored this hypothesis in experimentally restored prairie plots with three levels of phylogenetic diversity and two levels of functional diversity. Our experiment also had monocultures planted of all native species occurring in the plots. I used these plots to assess how phylogenetic distance and functional traits of the native species affected invader performance. I also compared how phylogenetic distance and functional traits of the communities in diversity plots compared with phylogenetic and functional diversity in resulting invader establishment. I introduced three species as invaders—an ecologically aggressive native species, a non-aggressive non-native species, and an ecologically aggressive non-native species. I tracked the invaders individually over two growing seasons. Invaders did not behave as expected, forcing us to split analyses across species and across life stages within species. I found evidence that phylogenetic diversity conferred biotic resistance against the aggressive non-native invader. I also found evidence that tall species better suppressed invaders. Surprisingly, I found evidence that leaf traits associated with more conservative and more resource acquisitive life history strategies were both linked to worse invader performance. I saw a similar trend with seed mass. In the monoculture plots, I found evidence that species with lighter seeds had lower invader fitness. However, in the diversity plots, I found that communities with heavier seeds had higher

invader mortality. I also found evidence in both the diversity and monoculture plots that invaders were more successful with more closely related native species. The trends I found with the linear mixed models were generally echoed by the Aster models, models that allow joint analysis of lifetime fitness across multiple demographic stages.

Introduction

The question of how native species characteristics shape invasion, originally raised in invasion biology's foundational work (Elton, 1958), remains an active area of inquiry in the field. Decades of invasion research have heavily investigated biotic resistance—the idea that more diverse native communities are less likely to be invaded (Beaury et al., 2020; Catford, Jansson, & Nilsson, 2009; Richardson & Pysek, 2008; Smith & Côté, 2019). Theory suggests that niche differences drive biotic resistance, however biotic resistance has primarily been quantified with species richness—an imprecise proxy for niche. Within community ecology, there has been increasing interest in exploring axes of biodiversity with stronger conceptual links to niche, particularly phylogenetic and functional diversity (Cadotte et al., 2009; Cavender-Bares et al., 2009; T. J. Davies, 2021; Gallien & Carboni, 2016). However, few field experiments have explicitly manipulated phylogenetic or functional diversity (Byun et al., 2020; Galland et al., 2019), and none to my knowledge have experimentally introduced invaders. Increasing our understanding of what makes a native community more resistant to invasion simultaneously answers fundamental questions about how species coexist and potentially generates novel strategies for land managers to promote more resilient ecosystems.

A central tenet of the biotic resistance hypothesis is that invasion dynamics depend upon the niche overlap between the native community and the invasive species. Elton conceived the notion of empty niches that existed in species-poor communities and increased their susceptibility to invasion, but the idea can be traced further back to Darwin's work in 1859. He noted that more closely related species were generally more ecologically similar and had similar resource requirements. This led to two opposing conclusions: (1) invasive species are more likely to find a suitable habitat in communities with a closely related resident species, but that (2) ecological similarities would lead to intense competition that would decrease the invasive species' success. Empirical studies have found support for both of these conclusions forming Darwin's Naturalization Conundrum (Diez, Sullivan, Hulme, Edwards, & Duncan, 2008; Marx et al., 2016; Pinto-Ledezma et al., 2020). The consistent finding that phylogenetic distance predicts invasive species establishment underscores that phylogenetic distance generally reflects ecological similarities (though see Cavender-Bares et al. 2004, Mayfield and Levine 2010), and can be used as a line of evidence in understanding invasion dynamics.

Species coexistence should be governed by a combination of niche-based processes, like biotic resistance, as well as competitive differences (Mayfield & Levine, 2010; Shea & Chesson, 2002b). If an invasive species possesses strong competitive abilities, it may overwhelm biotic resistance exhibited by the native community. Competitive traits may have hierarchies wherein the trait has a clear directionality linked to competitive ability (Keddy & Shipley, 1989; Kunstler et al., 2012). Previous research suggests that hierarchical differences in traits has the potential to alter biotic resistance to invasion (Conti et al., 2018).

I investigated how phylogenetic and functional diversity affected invasion resistance within an experimental prairie restoration. My experimental team established communities with varied phylogenetic and functional diversity, but with species richness held constant (15 species).

planted three species of invaders into these plots and tracked them for two years. In addition to the diversity treatments, I also established monocultures of each native species that were also experimentally invaded. The monoculture plots enabled us to compare the relative role played by niche differences, measured by phylogenetic distance, and competitive differences, measured by hierarchical trait differences in pairwise interactions. With these data, I explored how these relationships scaled in the 15-species diversity treatments. I also investigated the relative importance of biotic resistance, ecological similarity and competitive differences in the diversity plots.

Methods

Experimental Design

Our experiment was established at The Morton Arboretum in Lisle, Illinois, USA. The full experimental design is described in detail in Hipp et al., (2018) and Karimi et al. (In revision). My research team experimentally restored 15 species communities in 2-m×2-m plots with three levels of phylogenetic diversity and two levels of functional diversity (Figure 3.1). For each diversity level, there were six different 15 species compositions selected. Each community was replicated twice in the experiment for a total of 72 diversity plots (= three levels of phylogenetic diversity × two levels of functional diversity × six communities × two replicates). A total of 127 commercially available prairie species used in restoration were included in these diversity plots. Each of the species that occurred in the diversity treatments were also established as monoculture plots with two replicates in the experiment. Soil A-horizon depth was measured prior to planting and was used to delineate two superblocks each containing three blocks.

The plots included in this study were all established from plugs in fall 2016. The experiment also included 72 diversity plots established from seed, which were not included in this study. Each 2-m×2-m plug plot was planted with 60 plugs. In the diversity treatments, the spatial arrangement of the species was randomized but constrained so that each 1-m×1-m quarter plot contained the full 15 species community. My invasion experiment took place in the northwest quarter of each plot such that my experimental invaders had the potential to interact with the full community. The plots were weeded such that all plants were removed except the native species and invaders that were intentionally planted into each plot.

I selected 3 species of invaders and planted 3 individuals from each species into each diversity and monoculture plots in spring 2019. Seed for each species was collected from areas surrounding the experimental site in summer 2018. Seedlings were grown in cone-tainers in a greenhouse and then hardened off in a hoop house for two weeks. Each of the species selected were biennials and the intent was to collect aboveground biomass of all invaders in summer 2020, although this was complicated by unforeseen circumstances detailed below.

Invader Species

For my experiment, I selected three species across an “invader continuum”. The definition of invasive species varies from non-native to ecologically harmful to simply an undesirable species. For my experiment, I chose *Oenothera biennis* L.—a native species that can be aggressive enough in prairie restorations to warrant control (Havercamp & Whitney, 1983), *Daucus carota* L.—a non-native species that can be undesirable but is usually not ecologically aggressive in local restorations, and *Rumex crispus* L.—a non-native species that can become aggressive in grassland settings and is one of the most widespread invasive species globally (Cavers & Harper, 1964; Zaller, 2004).

Data Measurement and Accounting for Differential Invader Responses

All three invaders are considered biennials and were expected to form a basal rosette in their first year and then bolt and bloom in their second year. However, I encountered unexpected challenges in each species (Table 1). A majority of *Oenothera biennis* bloomed in the first field season and due to time constraints, I was only able to record number of seed capsules produced by each individual as a measure of lifetime fitness. *Oenothera biennis* plants that survived and bloomed in the second field season had aboveground biomass measured as originally planned. Additionally, many *Rumex crispus* individuals did not bolt in their second growing season so biomass was collected for the basal rosettes and biomass analyses were separated by growth form. Finally, *Daucus carota* individuals underwent heavy herbivory by voles at the site causing drastically fewer species to survive. Only 6 individuals out of 216 planted into the diversity plots survived, so I was ultimately unable to measure the effect of diversity on *Daucus carota* survival or productivity.

Native species attributes

For my invasion experiment, I measured community diversity using the same metrics used to create the diversity treatments. Phylogenetic diversity was measured as Faith's PD—the summed branch lengths of all species in the community. Faith's PD measures phylogenetic richness, or the amount of evolutionary history represented in an assemblage (Tucker et al., 2017). PD was calculated using the *picante* package (Kembel et al., 2010). Functional diversity was measured via functional dispersion (FDis), calculated using the FD package (Laliberte et al., 2014). FDis is the average distance of species to the community's centroid in PCoA space (Laliberte & Legendre, 2010b).

I also measured phylogenetic distance between native species and invaders. Phylogenetic distances were calculated using the cophenetic function in the *picante* package (Kembel et al., 2010). For diversity treatments, I calculated phylogenetic distance of the community to each invader two ways: Mean Nearest Taxon Distance, or the distance between the invader and the most closely related native species, and Mean Pairwise Distance, which is the average of the distances between each native species and the invader (C. O. Webb et al., 2002).

I also calculated mean trait values of the native species for five traits: specific leaf area (SLA), vegetative height, seed mass, leaf carbon content (LCC), and leaf nitrogen content (LNC).

Functional trait measurement

Functional diversity was measured using 12 continuous traits, 6 categorical traits, 8 binary root traits, seed mass, a habit moisture trait, and genome size. I used the functional trait matrix described in Hipp et al., (2018) as a starting point. That dataset was compiled from published sources (Amatangelo et al., 2014; Sonnier et al., 2014) and supplemented with data gathered for this experiment from nearby prairies (TRY dataset ID 671; Kattge et al., 2020). This original species × traits matrix lacked data for 10.9% of the cells. Unmeasured trait data was imputed using multivariate imputation based on chain equations (MICE) using the mice package v. 3.8.0 (van Buuren & Groothuis-Oudshoorn, 2011).

For this experiment, I aimed to fill in missing data for SLA, vegetative height, seed mass, LCC, and LNC. I attempted to gather data for all native species that were missing trait data for this suite of traits, although some species had too few surviving individuals to enable trait collection. I also collected data on these traits for all 3 invader species. SLA, vegetative height, LCC and LNC were all collected from the experiment following protocol outlined in Pérez-Harguindeguy et al., (2013). For leaf traits, I sampled 5 leaves from 5 individuals when possible. Height data were collected from at least 10 individuals. LCC and LNC were calculated via combustion with an Elemental Combustion System 4010 (Costech Analytical Technologies, Valencia, CA, USA). Seed mass data were gathered from the Chicago Botanic Garden seed bank database ("Science Collections Database," 2020).

I implemented models using both the raw trait matrix, with missing values, and the imputed trait matrix. The results were similar for functional diversity, however the hierarchical trait differences, however I saw notable differences between the imputed and raw values that would alter my conclusions. I present results using only the raw trait data.

Linear Mixed Models

I implemented mixed effect models to test how native species attributes affected invaders' fates. I first tested each native species attribute individually. For predictors that had a significant relationship with the response, I then implemented both forward and backward selection using likelihood ratio tests. For diversity treatments I considered the following as predictors: PD, FDis, MPD.i, MNTD.i, SLA.hier, height.hier, seed mass.hier, LCC.hier, and LNC.hier. For monoculture plots I considered phylogenetic distance, and the same six hierarchical trait differences considered in the diversity plots. I included block as a random effect.

Due to the differential responses by each invader, the set of mixed models differed between species. For all species, survival and aboveground biomass in the second growing season were used as responses. Due to differences in growth form, *Rumex crispus*, was split into basal biomass and bolted biomass—only 9 individuals flowered in the diversity treatments, so I did not include bolted biomass in my set of diversity models for *Rumex crispus*. *Oenothera biennis* had an additional response considered, the number of capsules produced by flowering individuals in the first growing season. *Daucus carota* had only 6 plants that survived in the diversity plots, so I did not analyze the effect of diversity on *Daucus carota* survival or biomass.

Aster Models

As a way to integrate across the different demographic stages of the three invaders, I also implemented Aster models (Geyer, Wagenius, & Shaw, 2007). Aster models enable joint analysis of survival, reproduction, and fitness over a time-series. Aster models can combine life history components with different probability distributions and take into account the interdependence of different life history stages. I implemented Aster models using the *aster* package in R v.1.0-3 (Geyer, 2019).

The Aster model approach allowed us to test the effect of native species characteristics on each invader's fitness overall, rather than having a set of linear models for each life stage. However, it was developed with fitness and reproduction in mind which presented some challenges with my dataset. It is not possible to use biomass of both basal and bolted individuals of *Rumex crispus* within the Aster models, as such I used only the bolted biomass. Since so few *Rumex crispus* individuals bolted, this meant I were unable to implement the Aster models for *Rumex crispus* in the diversity treatments. I estimated 4 total Aster models: *Oenothera biennis* in the diversity plots, *Oenothera biennis* in the monoculture plots, *Daucus carota* in the monoculture plots, and *Rumex crispus* in the monoculture plots (Figure 3.2).

Results

Linear Mixed Models

<u>Oenothera biennis – *Diversity Plots*</u>

In diversity plots, individuals of *Oenothera biennis* were less likely to survive in heavier seeded native communities (χ^2=4.4, p =0.03) (Figure 3.3). None of the native community attributes measured affected the number of capsules produced. *Oenothera biennis* biomass was generally less in plots with taller native communities (χ^2=5.6, p =0.02).

<u>Oenothera biennis –*Monoculture Plots*</u>

In monoculture plots, the likelihood of *Oenothera biennis* survival decreased when it occurred with taller native species (χ^2=6.4, p =0.01). The number of capsules was lower when *Oenothera biennis* was planted into monoculture plots with species that were taller (χ^2=20.9, $p < 0.001$), had lighter seeds (χ^2=8.8, p =0.003), or less leaf carbon (χ^2=5.4, p =0.02). Biomass of *Oenothera biennis* tended to decrease when it occurred with native species with lower LNC (χ^2=5.8, p =0.02).

<u>Rumex crispus – *Diversity Plots*</u>

Survival of *Rumex crispus* was lower when the native community had heavier seeds (χ^2=6.0, p =0.01) and when the native community was composed of species that were on average more distantly related to *R. crispus* (χ^2=6.8, p =0.01) (Figure 3.4). Basal *Rumex crispus* individuals were smaller on average in more phylogenetically diverse communities (χ^2=5.2, p =0.02) and communities that were composed of species that had lower SLA (χ^2=5.8, p =0.02).

Rumex crispus –*Monoculture Plots*

Rumex crispus survival decreased when the native monoculture was more distantly related (χ^2=7.0, p =0.01), taller (χ^2=12.9, p <0.001), or had lower leaf nitrogen (χ^2=10.4, p =0.001). There was no effect of any measured native species attributes on basal individuals of *Rumex crispus* in the monoculture plots. Bolted biomass decreased with taller species (χ^2=4.0, p =0.04) or those with lower leaf carbon content (χ^2=7.3, p =0.01).

Daucus carota – *Monoculture Plots*

Likelihood of *Daucus carota* survival decreased when the native species had lower leaf carbon (χ^2=15.7, p < 0.001) or was more distantly related (χ^2=3.9, p =0.05) (Figure 3.5). Biomass of *D. carota* was less in native monocultures with lighter seeds (χ^2=8.3, p =0.003).

Aster Models

Oenothera biennis *(Diversity and Monoculture Plots)*

I found no evidence that any measured native community attributes significantly affected *O. biennis* in the diversity plots. In the monoculture plots, *O. biennis* fitness was lower when occurring with tall native species (χ2=6.9, p = .01) (Figure 3.6).

Rumex crispus *(Monoculture Plots)*

I only implemented Aster models for *Rumex crispus* in the monoculture plots. I found that *Rumex crispus* fitness was decreased in plots where the native species was taller (χ^2=6.8, p

=0.01), had lighter seeds (χ^2=6.5, p = 0.01), had lower carbon content (χ^2=13.3, p < .001), or lower nitrogen content (χ^2=4.3, p = 0.04).

Daucus carota *(Monoculture Plots)*

I found that native species with lower leaf nitrogen content decreased *Daucus carota* fitness (χ^2=4.9, p = 0.03).

Discussion

Despite the differential and unexpected responses of my three invader species, I found some generalizable trends in native species traits and invader performance across my three study species. Across species and invader response variables, I found evidence that invaders generally performed poorly when native species were taller than the invader or had lower leaf carbon or nitrogen content. I found evidence that seed mass may affect the invasion process differently at different stages: communities with heavier seeds than the invaders had higher invader mortality, however monocultures with lighter seeds had lower invader biomass. Additionally, communities with lower SLA values than *Rumex crispus* had reduced biomass, however SLA was not linked to invader performance in the other two species. I found evidence of the pre-adaptation hypothesis—survival of two invaders decreased among distant relatives. For one species, I saw that this trend scale to the diversity treatments, communities that were more distantly related to the invader on average had lower likelihood of survival. Finally, I found evidence of biotic resistance: more phylogenetically diverse communities decreased biomass of one invader species.

Phylogenetic diversity increases biotic resistance to non-native species

I found evidence that increased phylogenetic diversity conferred biotic resistance against *Rumex crispus*. Plots with higher phylogenetic diversity had reduced biomass of basal *R. cripsus*. Higher phylogenetic diversity was also correlated with reduced survival of *R. crispus*, although it was not included in the final model. This is a particularly notable finding as *R. crispus* was my aggressive non-native invader and the most likely of my study species to be targeted by invasion control methods. Additionally, this is the first field experiment I am aware of demonstrating phylogenetic diversity conferring increased biotic resistance (Galland et al., 2019). Negative relationships between phylogenetic diversity and invasion have been observed in lab and mesocosm experiments (Feng et al., 2019; Qin et al., 2020) as well as observational studies (Iannone et al., 2016; Yessoufou et al., 2019).

Invaders coexist better with more closely related species

Likelihood of invader survival generally increased when the invader was more closely related to the native species. I saw evidence of this for both *Rumex crispus* and *Daucus carota* in the monoculture plots, and for *R. crispus* in the diversity plots. In the Darwin's Naturalization Conundrum literature, more closely related invaders are generally thought to succeed because they share adaptations with close relatives that pre-adapt them to succeed in the same environment (Cadotte, Campbell, Li, Sodhi, & Mandrak, 2018; Diez et al., 2008). An important caveat to consider is that the three species studied were from families that were not well represented in my experiment. Among my established native species, I had three species that belonged to the same family as *D. carota* (Apiaceae), one species from the same family (and genus) as *Oenothera biennis* (Onagracae), and no species from the same family as *R. crispus* (Polygonaceae). If this experiment were designed explicitly to test Darwin's Naturalization

Conundrum, it would have been prudent to select invaders that varied in their phylogenetic and trait similarity to the native species and to ideally select species that had native congeners. Another relevant consideration is that the tallgrass prairie is characterized by dominance by a small number of families. None of the invaders are from these dominant families. The Asteraceae can have pronounced effects on community structure and dominate prairies in early successional stages (Hipp et al., 2018; Larkin et al., 2015b; Schramm, 1990). Many of the Poaceae species had very low survival of invaders beneath their thatch in the second year. It could be that phylogenetic distance to the invaders is entangled with phylogenetic identity of these dominant prairie families.

Height looms large in competitive landscape

Multiple lines of evidence suggest that tall native species better suppressed my invaders. From my linear mixed models, I saw that communities composed of taller species had lower *O. biennis* biomass. In the monoculture plots, I found that when planted into a tall monocultures, *O. biennis* had lower survival, capsule production, and overall fitness and *R. crispus* had lower survival, biomass, and overall fitness. Height is a trait with a well-established trait hierarchy (Fried et al., 2019; Keddy & Shipley, 1989; Kunstler et al., 2012). As taller species shade out shorter species, the difference in height between neighboring species determines how much light each receives. Planting taller native species may be an effective strategy to suppress invasive species.

Tortoise and the hare: more conservative leaf traits may win out against invaders

I found that invaders performed poorly when native species had leaf traits on the resource conservation end of conservation-acquisition spectrum. In the monoculture plots, native species with lower leaf nitrogen than the invaders had lower likelihood of survival and lower fitness for both *D. carota* and *R. crispus,* and *O. biennis* individuals had lower biomass. Leaf nitrogen is strongly linked to net CO_2 assimilation rate (Schulze, Kelliher, Korner, Lloyd, & Leuning, 1994), likely because most organic leaf nitrogen is used for photosynthetic machinery (Evans & Seemann, 1989). *R. crispus* had lower biomass in communities with lower SLA values. SLA is also linked to leaf nitrogen and photosynthetic rate. SLA reflects the amount of light a leaf can intercept per unit of mass. Leaves with higher SLA tend to have higher photosynthetic capacity, which is in turn linked to leaf nitrogen (Wright et al., 2004). High SLA and high nitrogen are linked to leaves that are cheaper to construct and have a shorter leaf lifespan. Finally, I also found that native monocultures with lower leaf carbon had smaller basal *R. crispus* individuals, reduced fitness in both *D. carota* and *R. crispus*, and lower *O. biennis* capsule production.

A common invasion strategy is to prioritize resource acquisition, putting carbon gains towards fast growth that maximizes photosynthetic rate rather than “investing” resources in longer lasting leaves or herbivory (Montesinos, 2021; Penuelas et al., 2010; Van Kleunen et al., 2010). One approach to suppressing invasive species is to plant similarly “fast” native plants that can outcompete invaders (Laughlin, 2014a; Yannelli, Karrer, Hall, Kollmann, & Heger, 2018). However, my research suggests that more conservative leaf traits confer a competitive advantage. This is supported by other recent studies of native-invader differences in grassland ecosystems (Catford et al., 2019; Ernst et al. In revision).

Less investment in leaf carbon pays off

I found that monocultures with a lower leaf carbon content decreased the capsule production in *O. biennis* and both flowering biomass and fitness of *R. crispus*. Leaf carbon content is not a part of the leaf economic spectrum and has a less clear relationship to resource usage than leaf nitrogen, however, it has also been shown to correlate with photosynthetic rate (Liao et al., 2021; S. Ma, Baldocchi, Mambelli, & Dawson, 2011). This would suggest that lower leaf carbon is associated with a "slower" trait syndrome. However, leaf carbon content is also frequently used as a proxy for structural investment in the leaf (Poorter, 1994; Poorter et al., 2006). In my study, this would suggest that species that invest less in their leaves and have a lower leaf lifespan are more competitive against invaders. This contradicts the trends I found in SLA and leaf nitrogen and suggests an alternate strategy wherein "faster" species may also exert competitive pressure against invaders.

Dissecting the role of seed mass

Communities with heavy seeded species had lower invader establishment as measured by survival of *R. crispus* and *O. biennis*. However, monocultures with lighter seeds had smaller *D. carota*, lower capsule production by *O. biennis*, and reduced fitness overall in *D. carota* and *R. cripsus*. While seed mass is linked to competitive differences in early life stages (J. P. Grime & Jeffrey, 1965; Turnbull et al., 1999), the significance of differences in seed mass in my experiment are likely more reflective of differences in life history strategy associated with seed mass. My experiment bypassed the germination and emergence bottlenecks—the native species in this experiment had been planted as plugs three years prior to the invader introduction, and the invaders themselves were introduced as seedlings. A "fast" to "slow" spectrum has been proposed for seed mass, as species with heavy seeds tend to be larger, live longer, and have lower reproductive output (Moles, 2018; Moles & Westoby, 2006). The communities of slower—that is heavier seeded and overall larger species—may be more likely to shade out and competitively exclude invaders altogether. Faster species at the other end of the spectrum are more likely to be annuals or otherwise reproduce quickly, so they may exist at a higher density, they may also grow faster during the season. The faster species may be less likely to competitively exclude invasive species, especially in monocultures—but may exert more competitive pressure during establishment.

Conclusion

My study demonstrates that there are multiple pathways to resisting invasive species. I found evidence that both “fast” and “slow” strategies suppressed invaders. Rather than focusing on introducing fast-growing, competitive native species that can “beat invaders at their own game”, my study suggests that planting a suite of ecological strategies is more likely to increase invasion resistance overall. This is further supported by my finding that more phylogenetically diverse plots better resisted the aggressive non-native invader in my study. There have been few experimental tests of how phylogenetic diversity affects invasion resistance and my study suggests that managing for a more phylogenetically diverse community may reduce the survival and growth of unwanted species in addition to increasing other key ecosystem functions.

Acknowledgements

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TABLES AND FIGURES

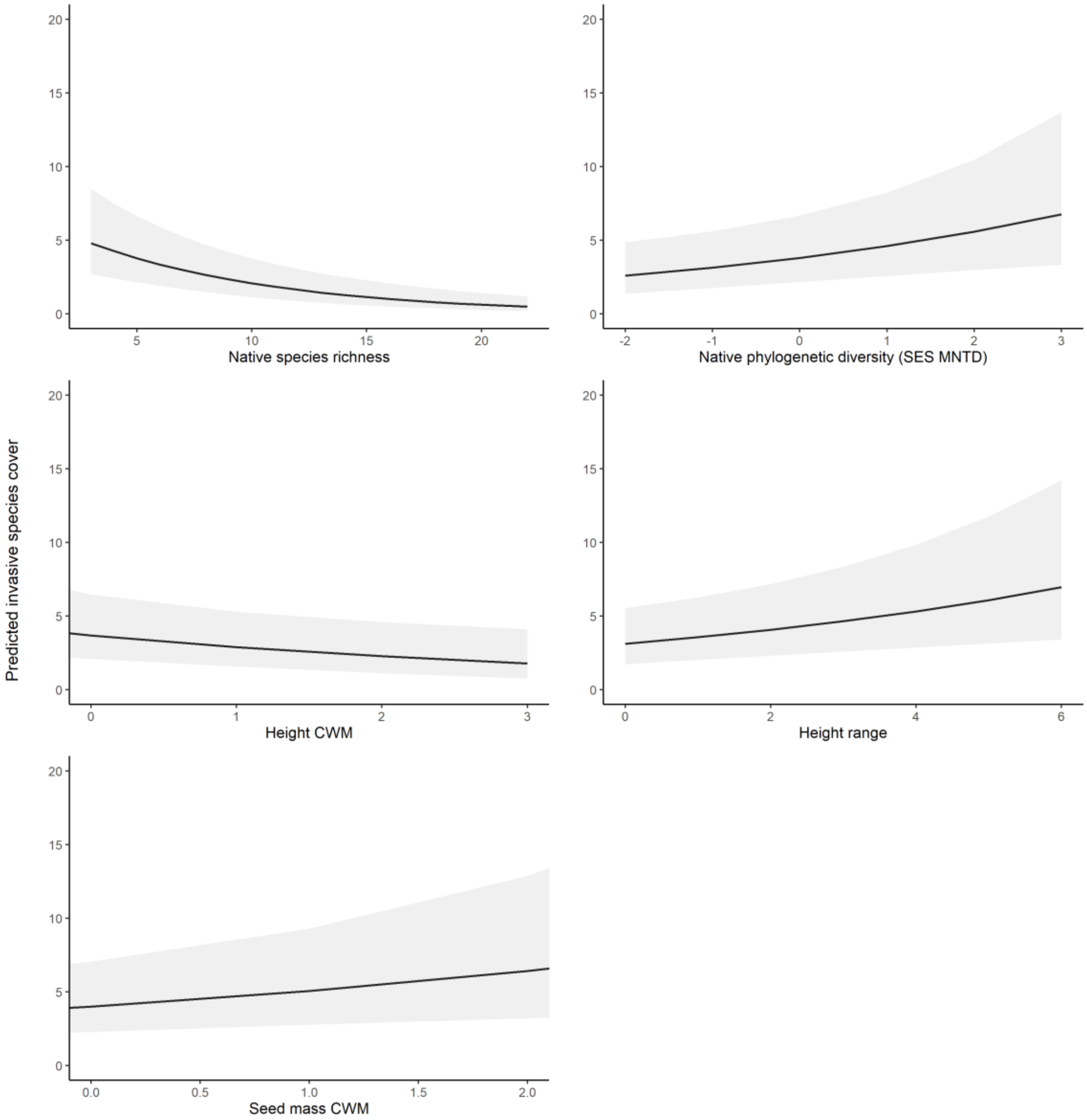

Figure 1.1: Partial effects of all diversity predictors included in the final pooled model of invasive species abundance (percent cover). Each plot represents the predicted partial effect of the predictor when all other predictors are held constant. The lines and ribbons indicate the mean and % confidence intervals predicted by the GLMM, respectively.

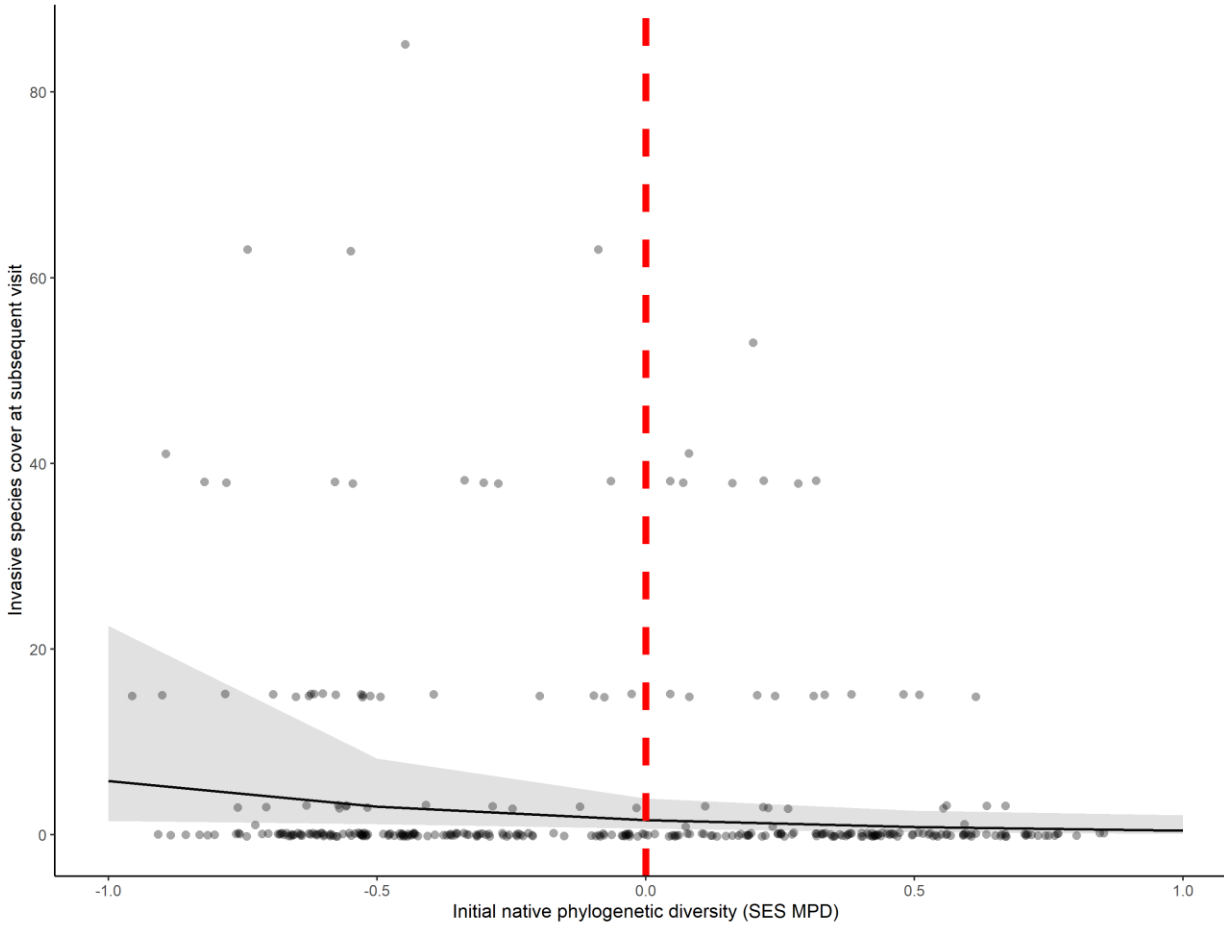

Figure 1.2: Relationship between initial native phylogenetic diversity and invasive species cover at subsequent visit. Values to the left of the red dashed line indicate native communities with lower MPD than expected by chance (phylogenetically clustered), while values to the right indicate native communities with higher than expected MPD (phylogenetically overdispersed). The black line and grey ribbon indicate the mean and 95% confidence intervals predicted by the GLMM, respectively.

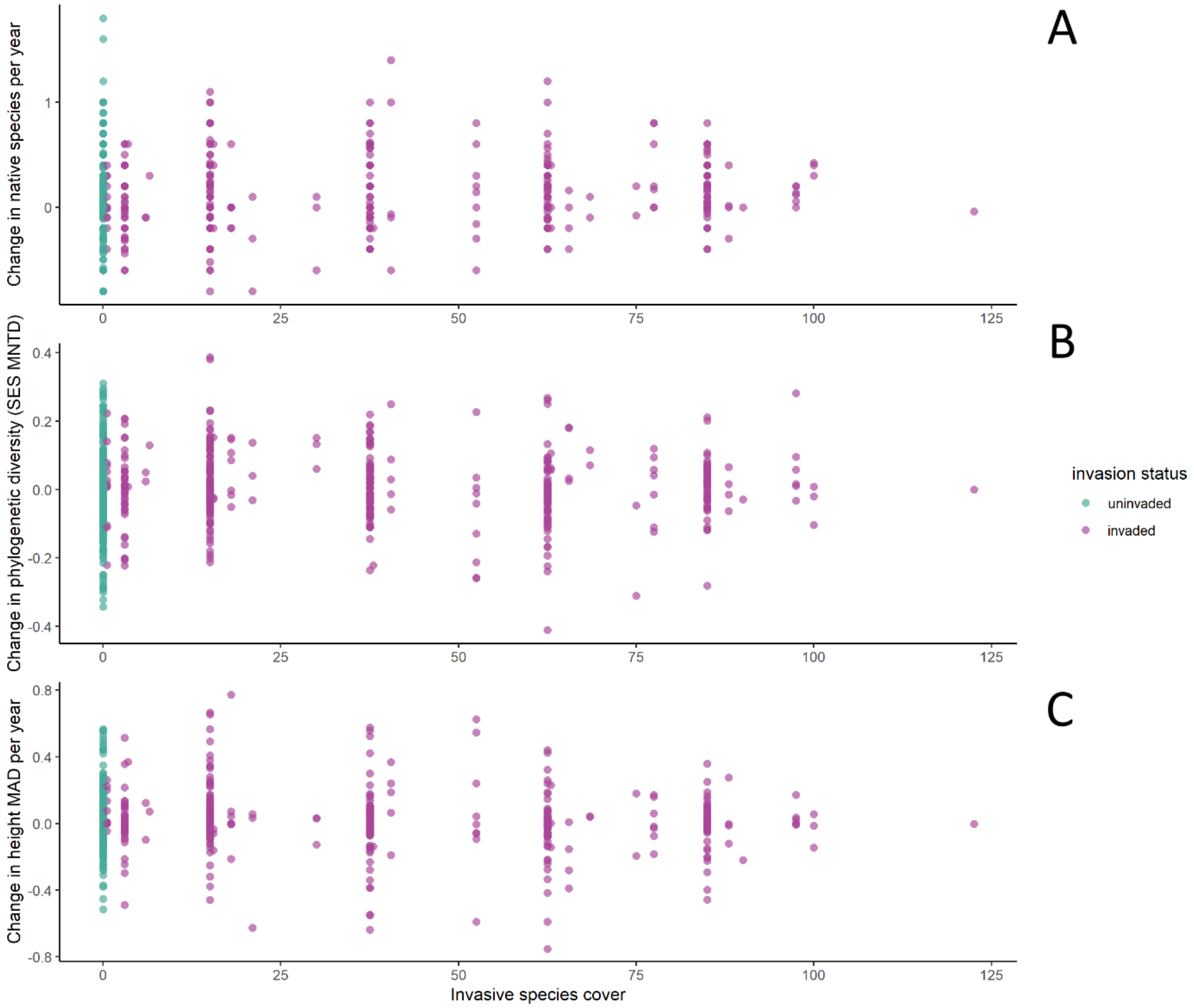

Figure 1.3: Relationship between change in native diversity and invasive species abundance. These three attributes of the native community, native species richness (A), phylogenetic diversity (B), and height weighted MAD (C), demonstrate high variability in uninvaded plots. Green dots indicate plots that were uninvaded and remained uninvaded throughout all surveys. Purple dots indicate plots that had become invaded. The y-axis indicates the observed change in each diversity metric at each plot over the surveys.

Table 2.1: Relative abundance of invaders by category. Percent of total invader biomass collected is listed by invader category.

Month	**Year**	**Invader Abundance**		
		Site-specific	**Native**	**Non-native**
June	2017	2.4%	18.7%	78.9%
September	2017	6.9%	73.0%	20.1%
June	2018	17.3%	42.1%	40.5%
September	2018	18.0%	59.5%	22.5%
September	2019	25.0%	67.2%	7.8%

Table 2.2: The five most common invaders in each plot, measured by total number of occurrences. Average biomass in grams listed in parentheses after each species.

Site-specific invaders	**Native invaders**	**Non-native invaders**
Symphyotrichum novae-angliae (19.0)	*Solidago altissima* (29.9)	Non-native grasses (10.1)
Oligoneuron rigidum (30.3)	*Oxalis stricta* (3.4)	*Medicago lupulina* (1.9)
Chamaecrista fasciculata (3.8)	*Symphotrichum pilosum* (12.3)	*Dipsacus laciniatus* (7.1)
Brickellia eupatorioides (2.8)	*Cornus racemosa* (0.4)	*Potentilla recta* (3.3)
Verbena stricta (4.6)	*Erigeron annuus* (5.4)	*Trifolium pratense* (2.1)

Table 2.3: Summary of linear models used to predict invasion.

Response	Plots included	Final model	Marginal R^2	Fixed effect	Standardized coefficient	Standard error
Summed biomass						
Site-specific invader biomass	71	Year + Initial site-specific invader biomass	0.15	Year	0.29	0.06
				Initial site-specific invader biomass	0.24	0.07
Solidago altissima biomass	71	Year + initial *S. altissima* biomass + Asteraceae biomass + Planted SES MNTD + Month	0.4	Year	0.49	0.05
				Initial *S. altissima* biomass	0.21	0.07
				Asteraceae biomass	-0.24	0.06
				Planted SES MNTD	0.1	0.05
				Month	0.41	0.13
Non-native invader biomass	71	Asteraceae biomass	0.1	Asteraceae biomass	-0.32	0.07
Total invader biomass	71	Year + initial invader biomass + planted SES MTND	0.33	Year	0.49	0.05
				Initial invader biomass	0.21	0.07
				Planted SES MTND	0.18	0.06
Individual species biomass models						
Site-specific invader species biomass	67	Month + Year	0.15	Month	0.22	0.07
				Year	0.15	0.07
Native invader species biomass	71	Year + Month + planted SES MNTD + Hierarchical SLA difference	0.13	Year	0.22	0.04
				Month	0.12	0.04
				planted SES MNTD	0.1	0.04
				Hierarchical SLA difference	-0.11	0.07
Non-native invader species biomass	59	Hierarchical height difference	0.11	Hierarchical height difference	0.29	0.11
All invader species	71	Year + Month + planted SES	0.08	Month	-0.10	0.03

biomass		MNTD + Hierarchical SLA difference		Year	0.13	0.03
				Planted SES MTND	0.06	0.03
				Hierarchical SLA difference	-0.10	0.05
Temporal trajectory models						
Change in site-specific invader biomass	70	Null				
Change in *Solidago altissima* biomass	70	Planted SES MNTD (aw)	0.13	Planted SES MNTD (aw)	0.36	0.11
Change in non-native invader biomass	70	Planted SES MNTD (aw)	0.06	Planted SES MNTD (aw)	0.25	0.11
Change in total invader biomass	70	Planted SES MNTD (aw)	0.18	Planted SES MNTD (aw)	0.43	0.11

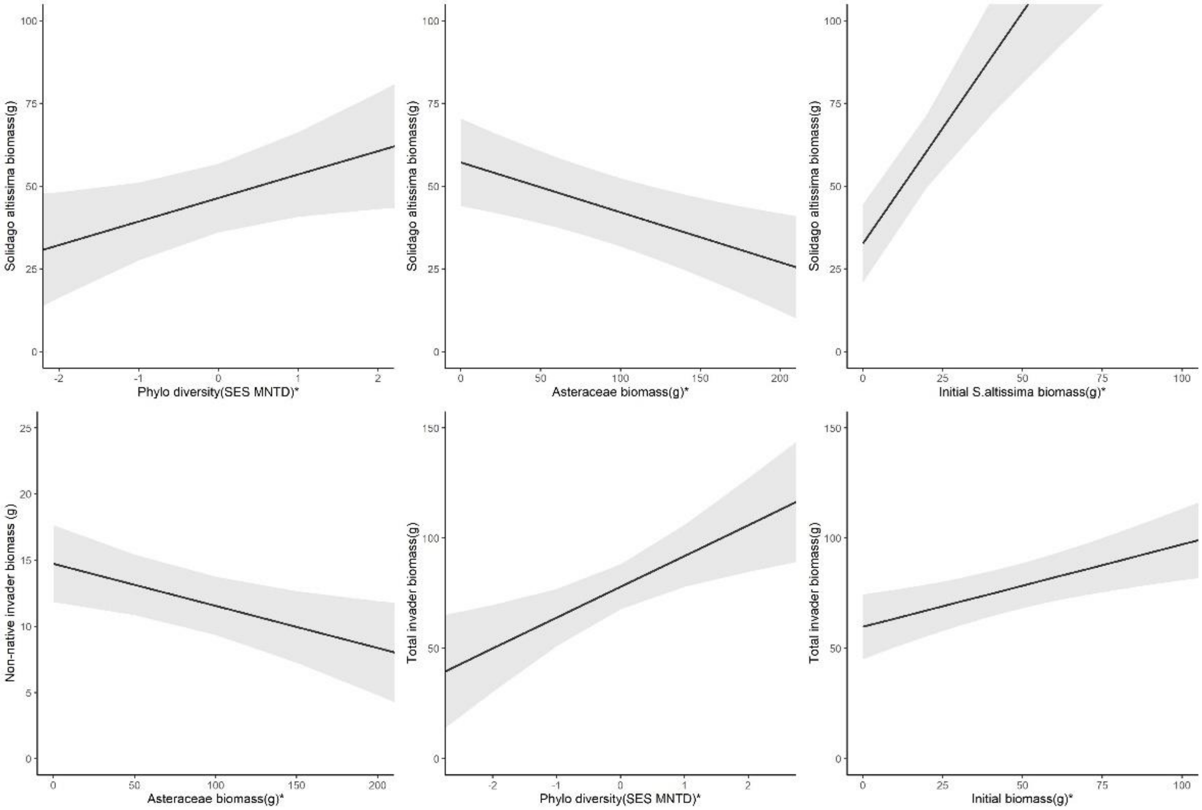

Figure 2.1: Partial effects plots depicting the effects of each predictor on summed invader biomass. For statistical models, we log-transformed biomass data and scaled and centered predictor values; however, plots show the raw values for ease of interpretation. The solid line represents the mean invader biomass predicted by the model and the ribbons represent the 95% confidence interval.

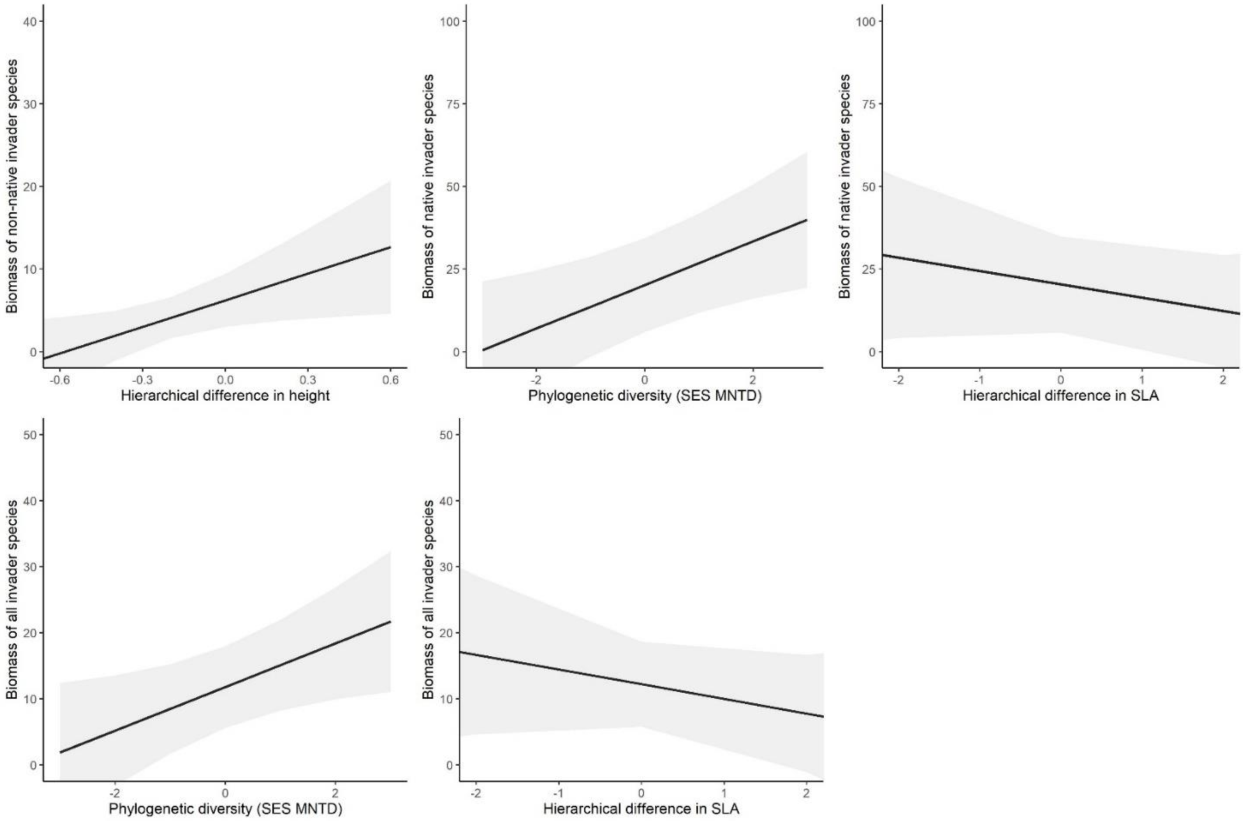

Figure 2.2: Partial effect plots reflecting the relationship of each predictor with biomass of individual invaders.

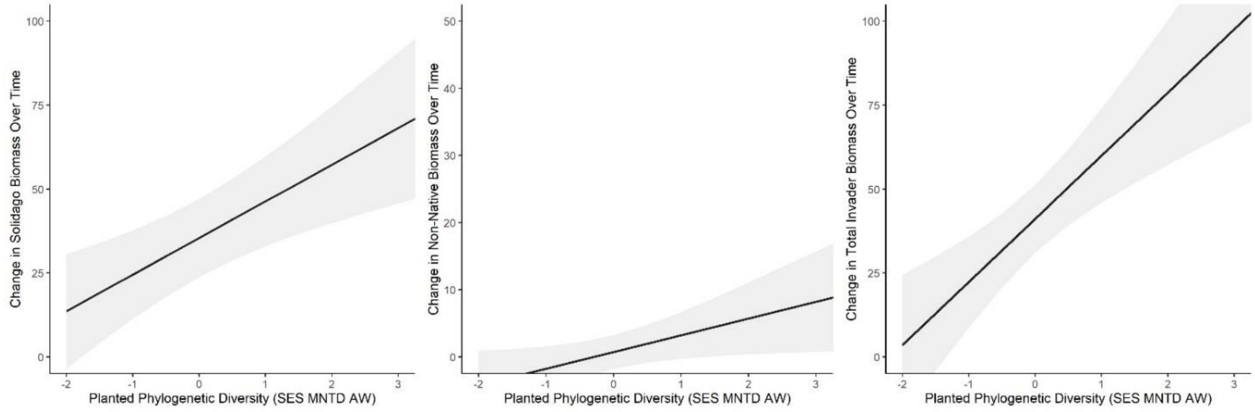

Figure 2.3: Partial effects plots depicting the effect of phylogenetic diversity on invader biomass over time. The solid line represents the mean predicted change in invader biomass over time while the ribbons represent the 95% confidence interval.

Table 3.1: Summary of the challenges encountered with each invader and observed effects of native characteristics. Each species had unique circumstances that complicated analysis, they are detailed below. These challenges meant that each species had a unique set of predictors considered. Significant relationships between invader responses and native species characteristics are noted, the direction of the relationship is indicated in parentheses after the response.

Species	Unexpected complication	Responses	PD		seed mass		height		LCC		LNC		SLA		phy distance	
			Div	Mono	Div	Mono	Div	Mono	Div	Mono	Div	Mono	Div	Mono	Div	Mono
O. biennis	Majority flowered in yr 1, only capsule count collected in yr 1	Capsule count (year one), survival (year one and two), biomass (year two)		NA	surv (-)	cap (+)	bio (-)	surv (-), cap (-)		cap (+)		bio (+)				
D. carota	Most plants killed by vole herbivory, too few survived in diversity plots for analysis	Survival and biomass	NA	NA	NA	bio (+)	NA		NA		NA	surv (+)	NA		NA	surv (-)
R. crispus	Many plants did not flower, biomass had to be separated by growth form (flowered vs basal)	Survival, basal biomass (monoculture and diversity), flowering biomass (monoculture only)	ba bio (-)	NA	surv (-)			surv (-), fl bio (-)		fl bio (+)		surv (+)	ba bio (+)		surv (-)	surv (-)

Table 3.2: Summary of linear mixed models for each invader. Marginal R^2 indicates the amount of variation explained by the fixed effects (rather than fixed effects + block).

Species	Plot Type	Response	Final model	Marginal R^2	Fixed effect	Std coefficient	Std error
Oenothera biennis	Diversity	Survival	seed mass + (1|block)	0.033	seed mass	-0.34	0.16
		Capsules	null				
		Biomass	height + (1|block)	0.266	height	-0.51	0.2
	Monoculture	Survival	height + (1|block)	0.014	height	-0.22	0.09
		Capsules	LCC + height + seed mass + (1|block)	0.062	LCC	0.1	0.04
					height	-0.21	0.04
					seed mass	0.13	0.04
		Biomass	LNC + (1|block)	0.049	LNC	0.22	0.09
Rumex crispus	Diversity	Survival	MPD + seed mass + (1|block)	0.07	MPD	-0.37	0.14
					seed mass	-0.35	0.15
		Biomass (basal)	SLA + PD + (1|block)	0.098	SLA	0.22	0.09
					PD	-0.2	0.09
	Monoculture	Survival	phy dist + height + LNC + (1|block)	0.052	phy dist	-0.21	0.08
					height	-0.27	0.08
					LNC	0.27	0.08
		Biomass (basal)	null				
		Biomass (bolted)	height + LCC + (1|block)	0.061	height	-0.07	0.03
					LCC	0.09	0.03
Daucus carota	Monoculture	Survival	LCC + phy dist + (1|block)	0.061	LCC	0.44	0.11
					phy dist	-0.23	0.12
		Biomass	seed mass + (1|block)	0.076	seed mass	0.27	0.1

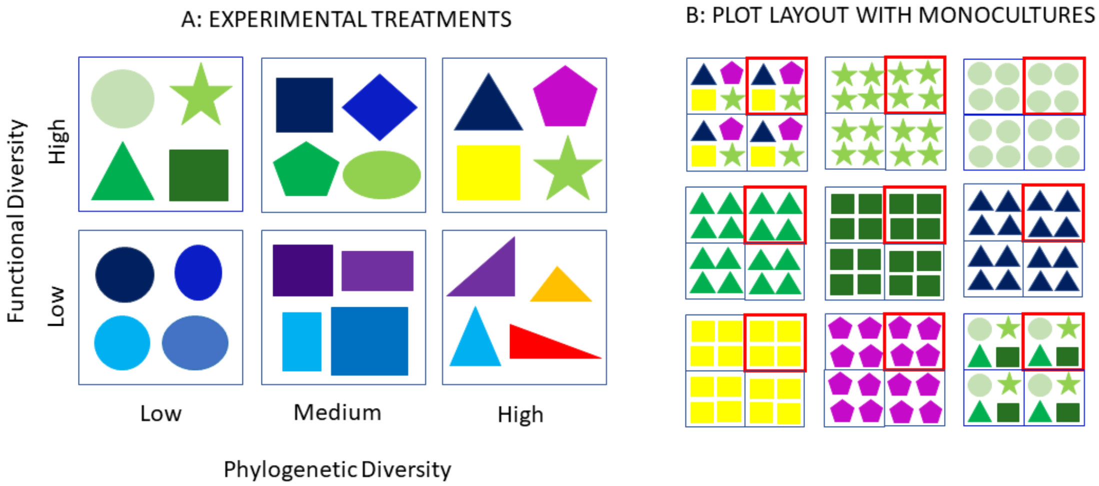

Figure 3.1: Conceptual figure of experimental design. Species are represented by shape and color. Phylogenetic diversity is represented by colors, species that are more similar in color are more closely related. Functional diversity is represented by shape, species that are more similar in their shape, are more functionally similar. A: The experiment has 15-species communities, depicted as four-species communities here for visual clarity. For each of the six diversity treatments, there were six different community compositions with each specific community replicated twice. B: Each species in the diversity treatments was established as a monoculture, with two monoculture plots of each species in the experiment. There was a total of 127 species in the experiment and 254 monoculture plots. There were 72 diversity plots with 36 distinct community compositions with 6 diversity treatments. Each 15-species community was replicated in each quarter of the 4m^2 plots. The invasion experiment happened in the northeast corner of each plot, represented by the red square in the figure.

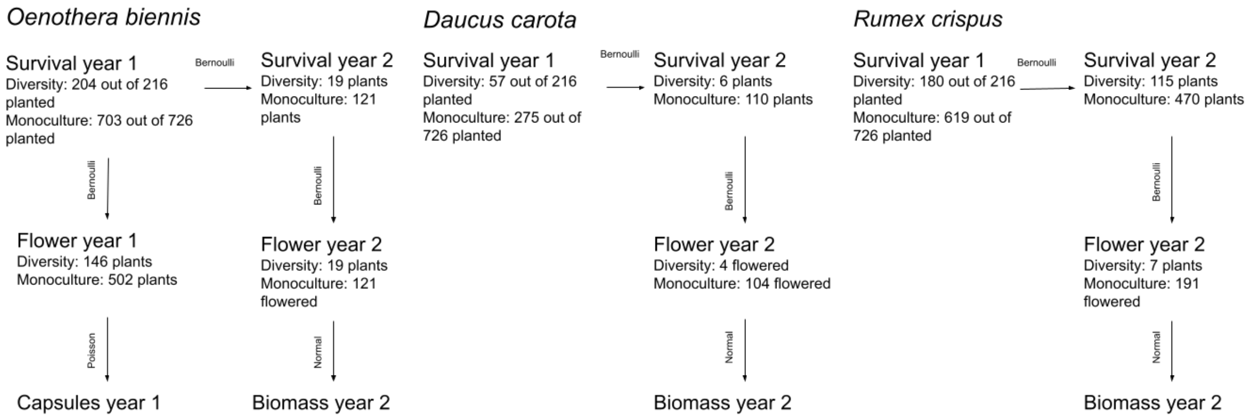

Figure 3.2: Graphical depiction of Aster model schemes. Arrows are labelled with the distribution used, either Bernoulli, Poisson, or normal distribution. Beneath each life stage is the number of plants that survived or flowered.

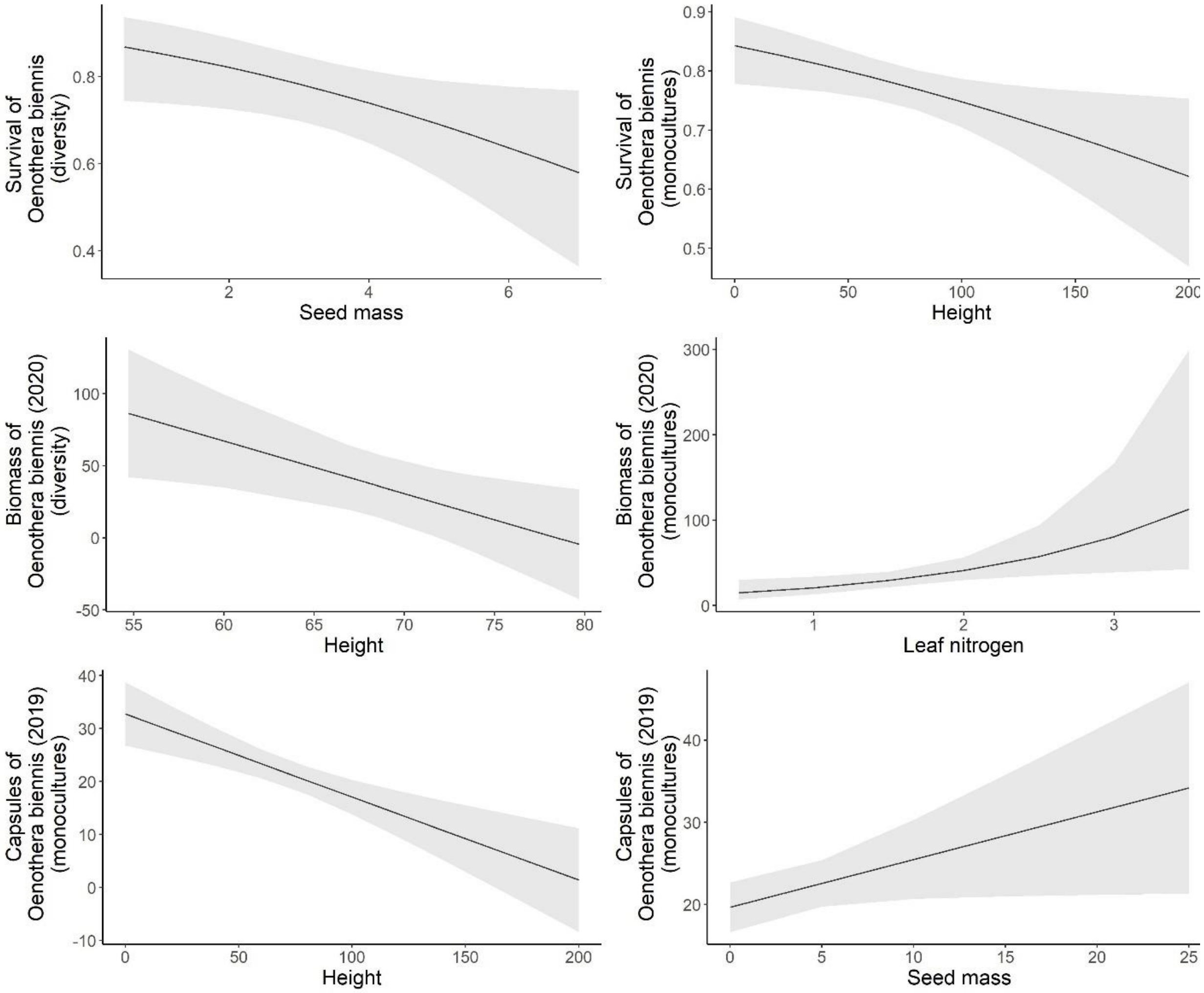

Figure 3.3: Partial effect plots for all predictors included in the final models for *Oenothera biennis*. Each plot represents the predicted partial effect of the predictor when all other predictors are held constant. The lines indicate the mean predicted by the GLMM and the ribbons indicate the 95% confidence intervals.

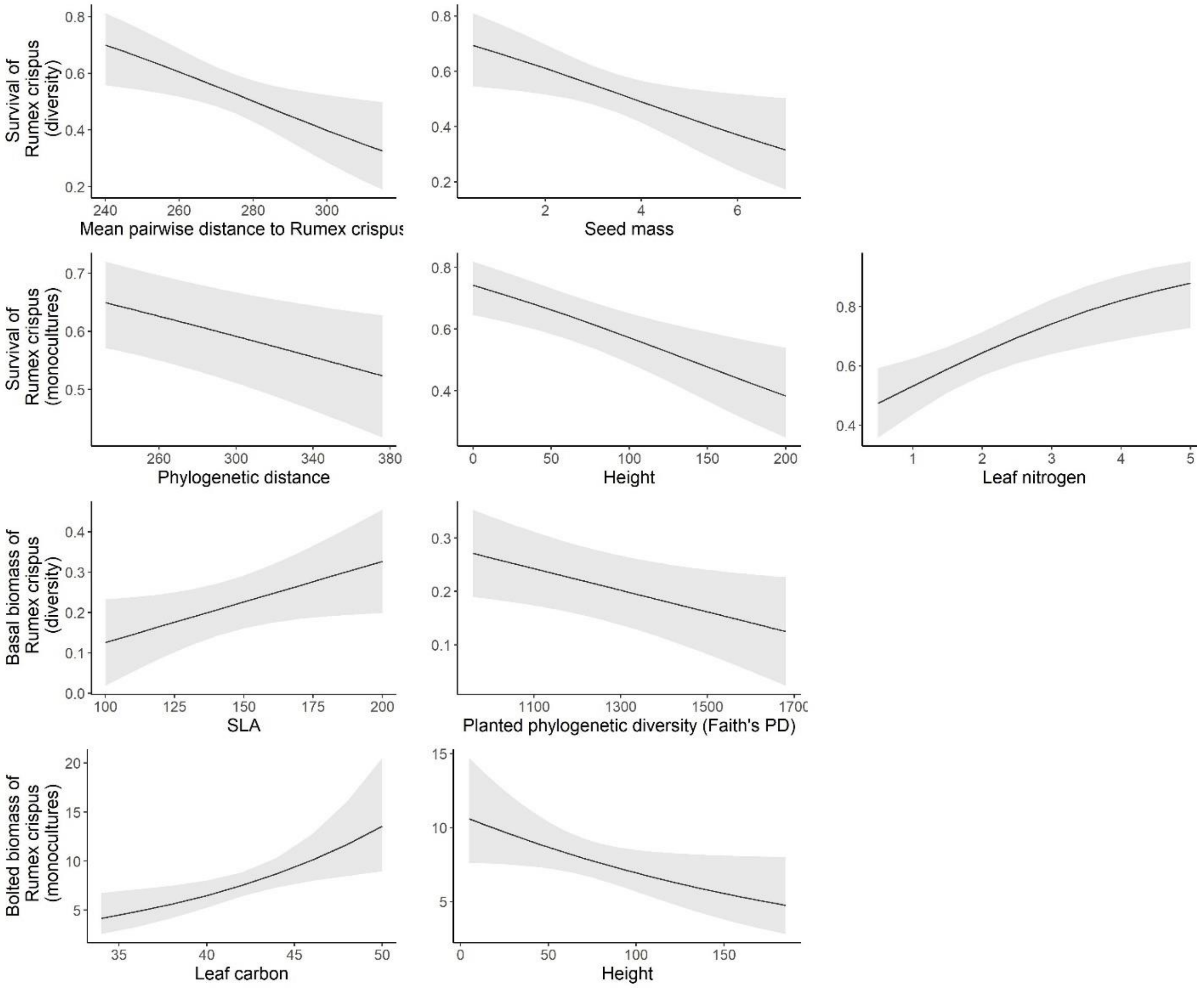

Figure 3.4: Partial effect plots for all predictors included in the final models for *Rumex crispus*.

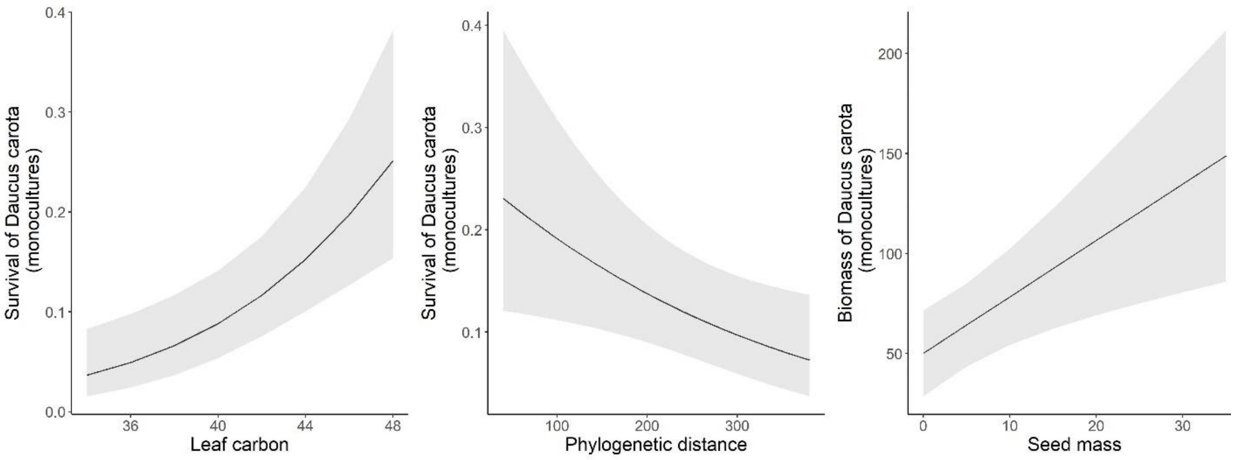

Figure 3.5: Partial effect plots for all predictors included in the final models for *Daucus carota*.

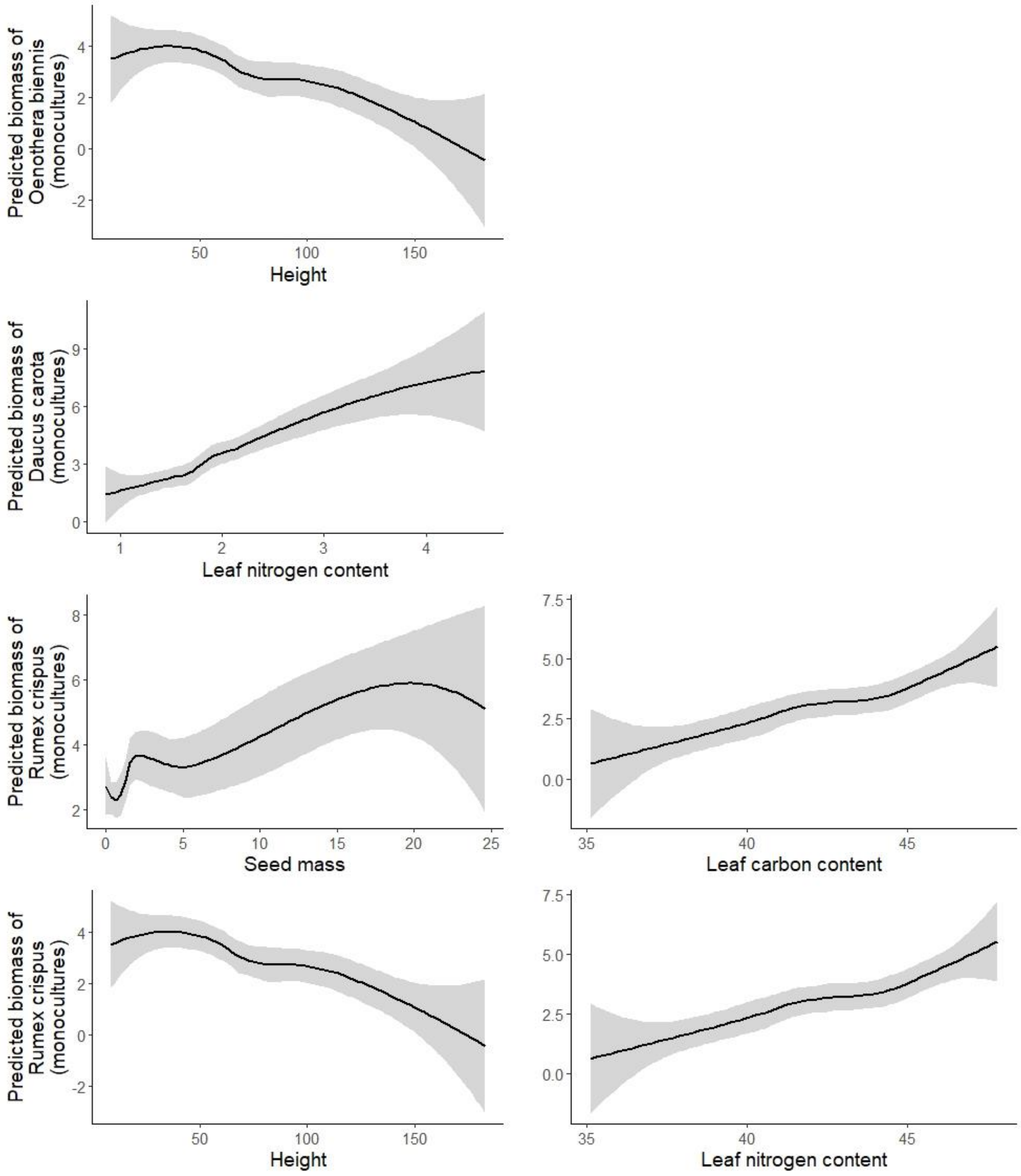

Figure 3.6 Predicted partial effects of native functional traits on biomass of *Oenothera biennis, Daucus carota,* and *Rumex crispus* from the Aster models.

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APPENDIX ONE

Supplementary material from chapter one

Table S1.1: Candidate functional traits. The following traits were considered for inclusion in the functional diversity analyses.

Specific Leaf Area (SLA)
Leaf Carbon Content (LCC)
Leaf Nitrogen Content (LNC)
Leaf Dry Mass Content (LDMC)
Photosynthetic capacity (A_{max})
Plant Height
Seed mass
CN Ratio
Root mass
Growth form
Flowering length

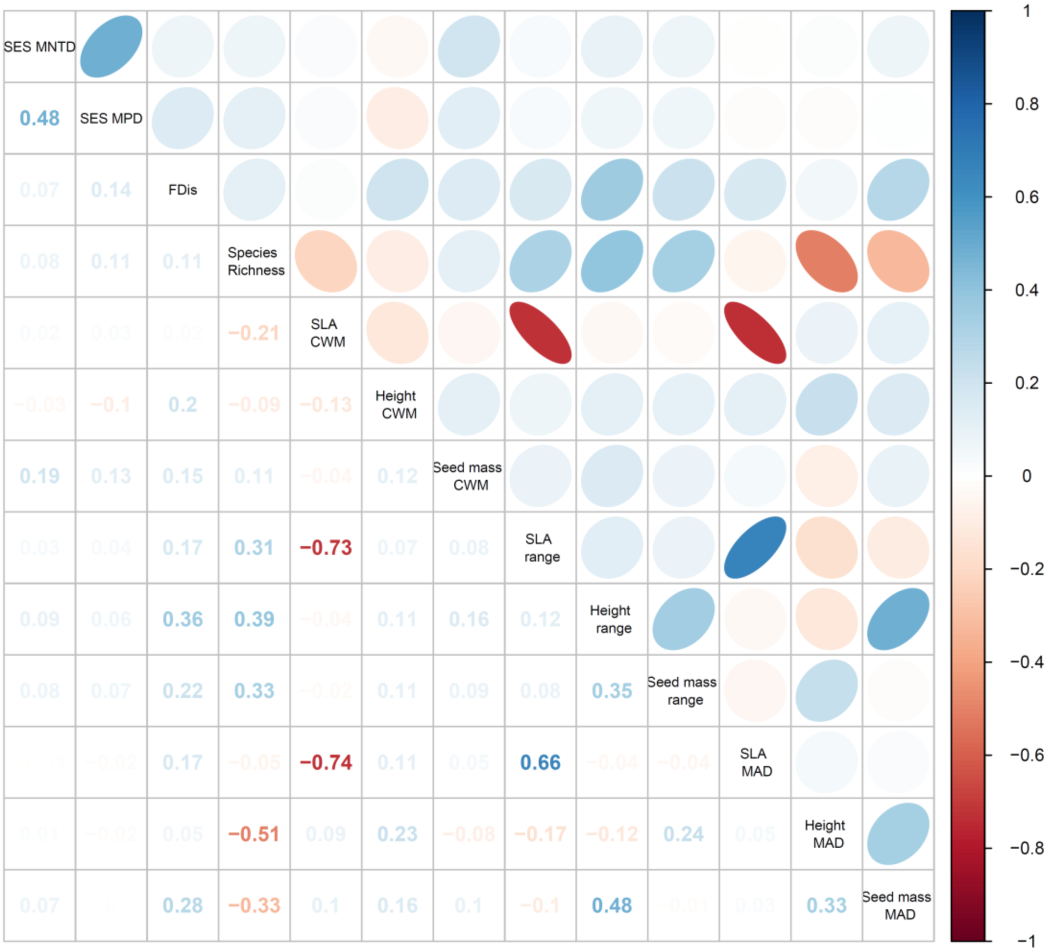

Fig S1.1: Pearson correlation coefficients for all diversity and single trait metrics considered.

APPENDIX TWO

Supplementary material from chapter two

Table S2.1: Weeds removed from plots following biomass collection. An "X" indicates that the species was weeded from the plots in that year.

Scientific name	**2017**	**2018**	**2019**
Alliaria petiolata	X		
Barbarea vulgaris	X	X	
Centaurea maculosa		X	X
Chenopodium album	X		
Cirsium arvense	X	X	
Convolvulus arvensis	X		
Cornus sp.		X	X
Daucus carota	X		
Dipsacus laciniatus	X	X	
Erigeron annuus	X		
Erigeron canadensis	X		
Lactuca serriola	X		
Lonicera sp.		X	X
Medicago lupulina	X		
Melilotus alba	X	X	
Melilotus officinalis	X		
Oenothera biennis	X		
Pastinaca sativa	X	X	
Prunus sp.		X	X
Rumex crispus	X		
Securigera varia	X	X	X
Senecio vulgaris	X		
Sonchus asper	X		
Thlaspi arvense	X		
Trifolium sp.	X		
Toxicodendron radicans	X	X	X

Ulmus sp.	X	X

Table S2.2: List of traits used to calculate functional diversity for the resident community.

Trait Type	**Functional Trait**
Continuous leaf traits	leaf dry matter content
	specific leaf area
	leaf nitrogen content
	leaf carbon content
	leaf phosphorus content
	stem dry matter content
	circularity
	vegetative height
	leaf length
	leaf thickness
	leaf width
	petiole length
Continuous traits	Seed mass
	Genome size
Categorical traits	lifeform
	life cycle
	habit
	flowering
	photosynthetic pathway
	nitrogen fixing
	habitat moisture trait
	adventitious
Binary root traits	bulbs
	corms
	fibrous
	primary
	rhizomes
	stolons
	tubers

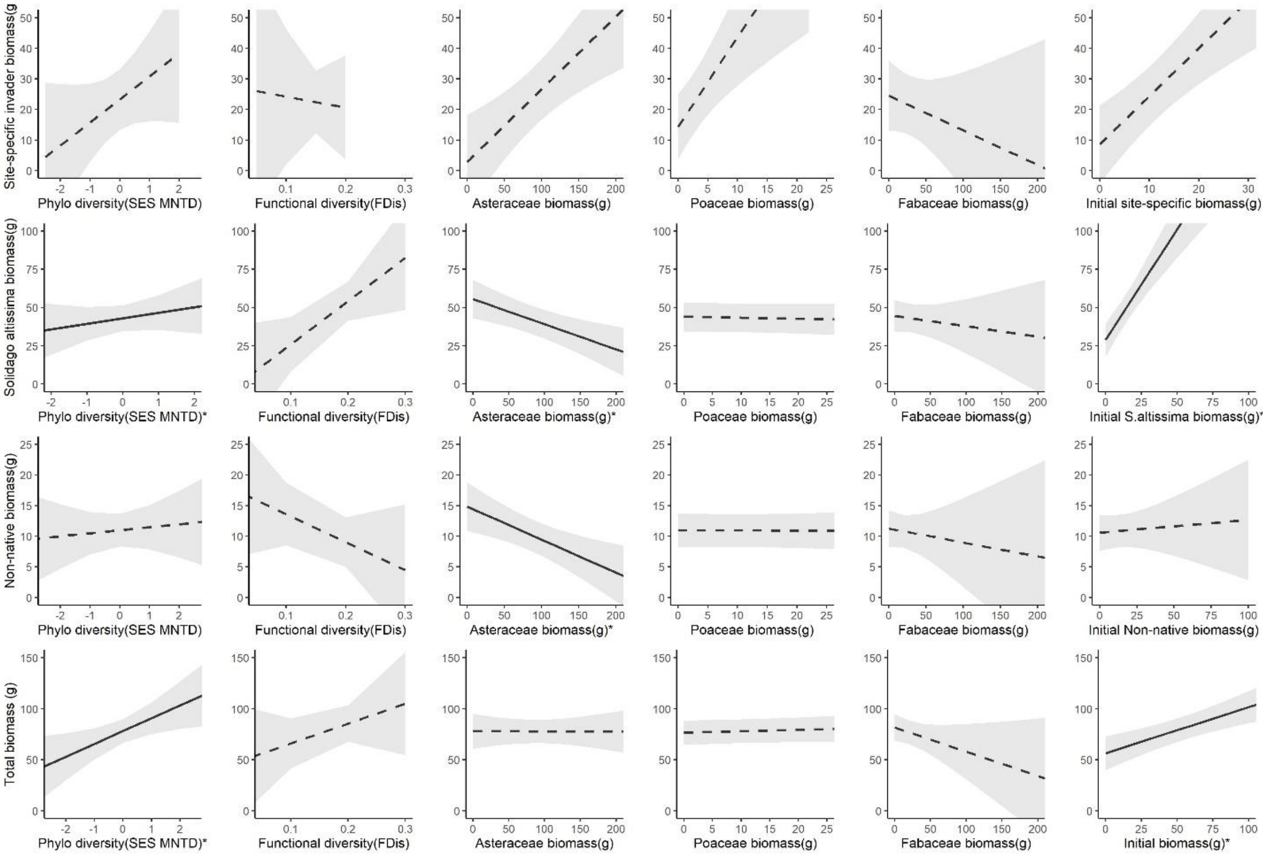

Figure S2.1: Partial effects plots depicting the effects of each predictor on invader biomass fitted to a global model. For statistical models, we log-transformed biomass data and scaled and centered predictor values; however, plots show the raw values for ease of interpretation. The solid line represents the mean invader biomass predicted by the model and the ribbons represent the 95% confidence interval. Dashed indicate predictor variables that were considered but were not included in the final model. Solid lines indicate predictor variables that were included in the final model which are also marked with an asterisk.

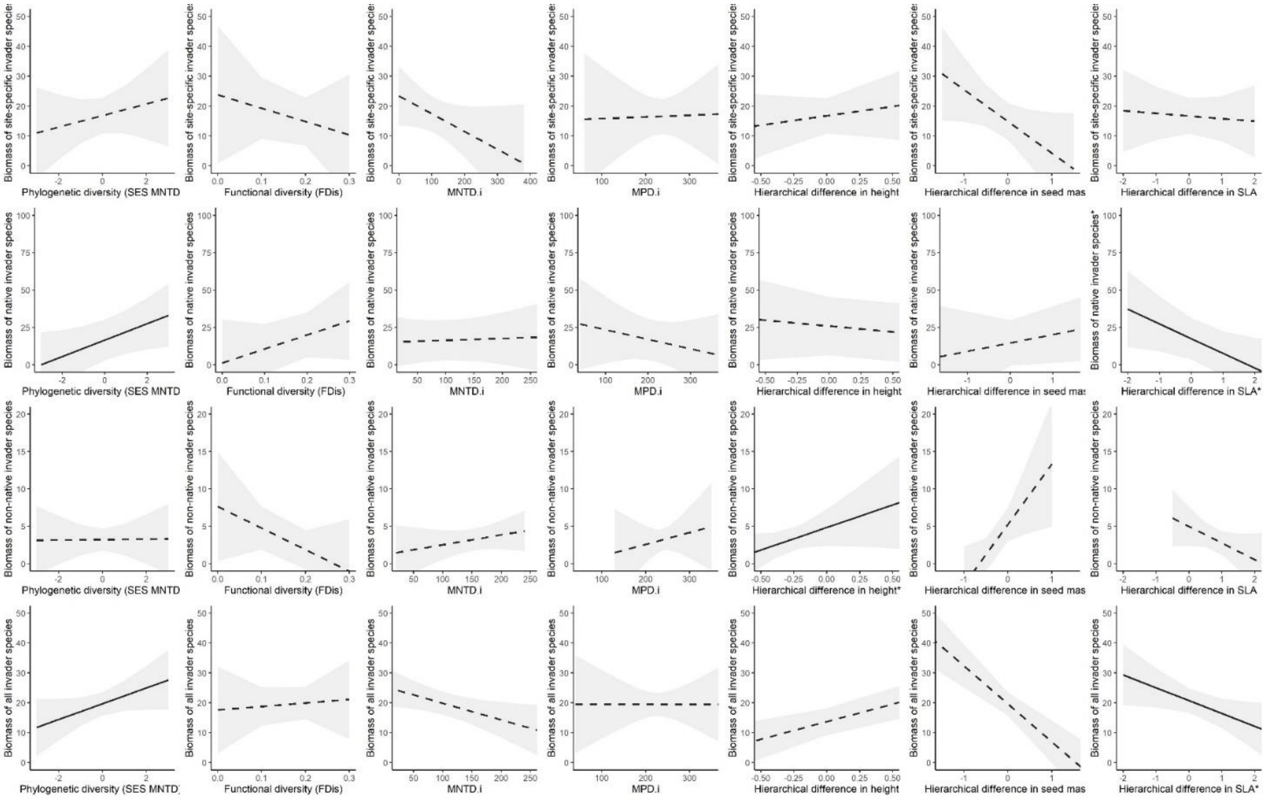

Figure S2.2: Partial effect plots of the global individual biomass models.

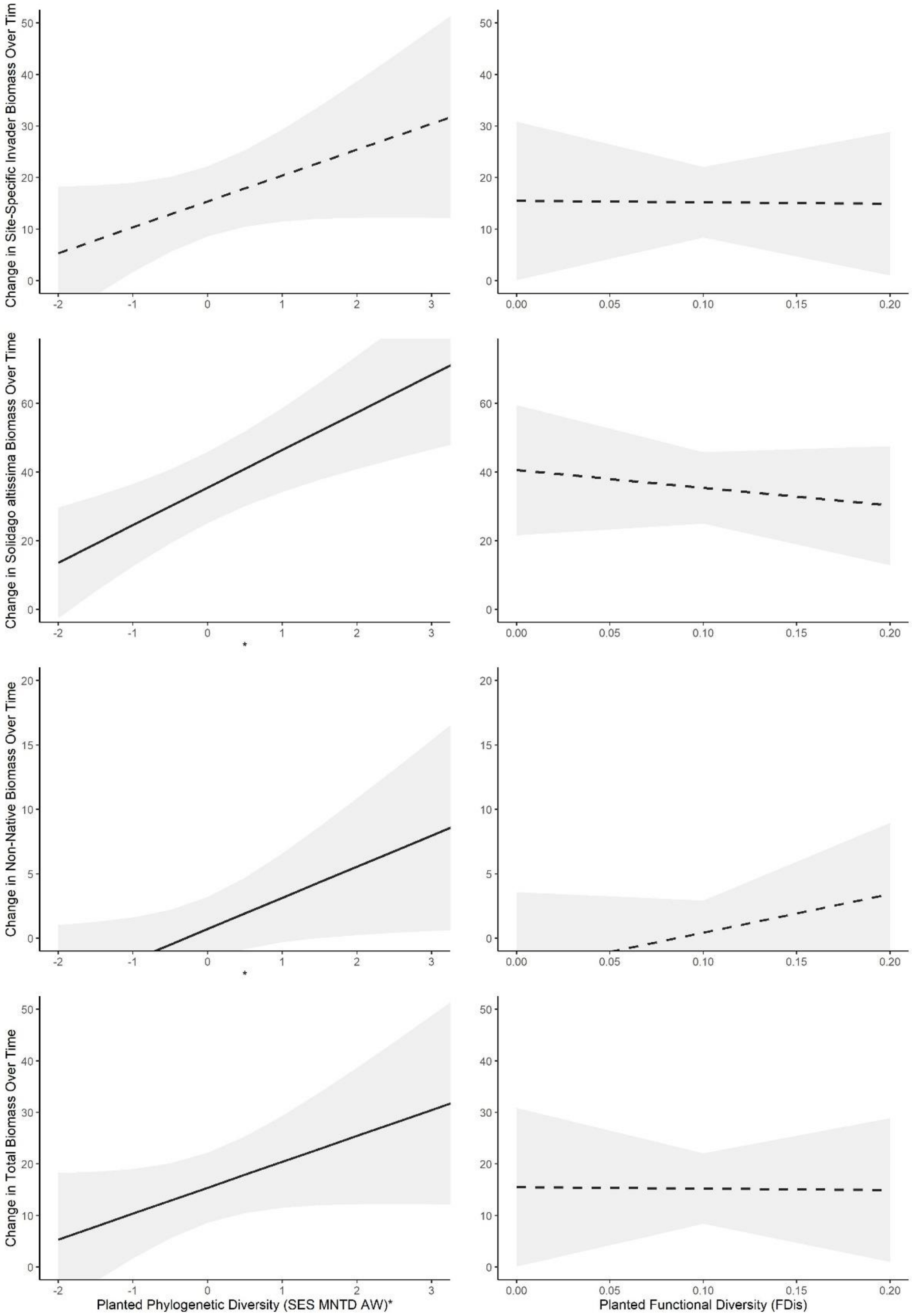

Figure S2.3: Partial effect plots of the global trajectory models.