INTERPRETING VARIATION IN RESTORATION OUTCOMES: FUNCTIONAL TRAITS SHAPE COMMUNITY ASSEMBLY AND ECOSYSTEM FUNCTIONING

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ABSTRACT

INTERPRETING VARIATION IN RESTORATION OUTCOMES: FUNCTIONAL TRAITS SHAPE COMMUNITY ASSEMBLY AND ECOSYSTEM FUNCTIONING

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Making sense of the mechanisms by which communities assemble and provide ecosystem functions is central to ecological research. The recovery of diversity and ecosystem functioning are also primary objectives of ecological restoration, yet these outcomes are often unpredictable. Restoration ecology has typically focused on reinstating particular sets of species; however, this focus on taxonomic composition limits generalization between restorations. Traits, due to their mechanistic and generalizable nature, may provide insights into community assembly mechanisms that move beyond this idiosyncrasy. That is, a better understanding of how traits vary among species may predict how their dispersal, establishment, and persistence affect species' distribution and abundance among sites that vary in environmental conditions. Trait-based approaches may shed light on a second major goal of restoration: understanding the functioning of ecosystems and how this is related to the diversity and composition of communities. Thus, functional traits hold great promise for interpreting, predicting, and linking the assembly and functioning of communities. This promise remains poorly realized, however, as tests linking environmental conditions, functional traits, and ecosystem functioning in restoration are rare. Restored systems offer a unique test of ecological theory at the scale of ecosystems. Here I use plant functional traits to study community assembly and ecosystem functioning in grasslands undergoing restoration. My first two chapters take a trait-based approach to studying processes such as invasion and species establishment that underlie community assembly using experimentally manipulated prairie restorations. I found that the extent to which a species' traits are adapted to the local environment, but not how much their traits overlap with species already residing at a site, influence a species' ability to invade a community. Likewise, trait-environment interactions play an important role in the invasion process, further supporting the idea that having traits that are adapted to a particular environment is important for invasion success. Furthermore, considering traits independent of their environmental context is inadequate for understanding community assembly processes and trait-environment interactions determine seedling establishment rates in recent prairie restorations. My last two chapters attempt to use functional traits to link community assembly and ecosystem functioning using a set of 29 restored prairies in southwestern Michigan. I found that environmental conditions predicted community weighted mean traits, showing the value of traits for studying community assembly. Also, both functional traits and environmental conditions play an important role in shaping ecosystem functioning during restoration, and the importance of traits and environment on functioning depends on the function of interest. Because of this, variation in environmental conditions will be necessary to promote multiple ecosystem functions across restored landscapes through management and by installing restorations in at sites with different environmental conditions. These results highlight the utility of functional traits for connecting community assembly and ecosystem functioning during restoration. Within this same system I also asked how different aspects of diversity (taxonomic, functional, phylogenetic) influence ecosystem functioning and an ecosystem’s ability to produce multiple functions simultaneously (ecosystem multifunctionality). I found that phylogenetic diversity and the landscape surrounding a restoration determine ecosystem multifunctionality, though the effect of landscape is much stronger than the effect of diversity. I also find no tradeoffs between ecosystem functions that contribute to multifunctionality across sites; instead, functions are independently affected by diversity, environmental, and landscape variables. In this case, the processes that increase many individual functions will increase multifunctionality. All of this work demonstrates that trait-based approaches to restoration can help improve our understanding of community assembly and ecosystem functioning at the ecosystem scale, explain variation in restoration outcomes, and show how restored systems can offer a unique test of ecological theory at the scale of ecosystems.

For Karissa Ann Propson, my partner, steady hand, motivation, love, and friend

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CHAPTER ONE

A TRAIT-BASED APPROACH TO RESTORATION

Introduction

Understanding the mechanisms by which communities assemble and provide ecosystem functions is a central goal in ecology (Díaz & Cabido 2001; Weiher & Keddy 2001, Mittlebach 2012). Community assembly affects the distribution and abundance of species through the processes of dispersal, establishment, and persistence at sites that vary in their abiotic and biotic conditions. The ways that these process play out across species, in turn, are related to the traits of species and, thus, the study of functional traits may provide insights into community assembly mechanisms (Weiher *et al.* 1999; McGill *et al.* 2006; Kraft, Valencia, & Ackerly 2008). Because species' functional traits are also related to ecosystem functioning (Díaz & Cabido 2001; Lavorel & Garnier 2002), functional trait-based approaches may additionally shed light on a second major goal of ecology: understanding the functioning of ecosystems and how this is related to the diversity and composition of communities (Tilman, Isbell, & Cowles 2014) Thus, functional traits hold great promise for interpreting, predicting, and forging a link between the assembly and functioning of communities and ecosystems.

In spite of this promise, we lack a robust understanding of how functional traits mediate community assembly and ecosystem functioning, in part because the vast majority of related studies have been observational or, when experimental, small-scale in nature (e.g. Fukami *et al.* 2005; Kraft, Godoy, & Levine 2015). While functional traits may provide insights into community assembly mechanisms, they do not replace the strong inference obtained through manipulative studies. As such, a promising way forward is to couple functional traits with experiments, providing cause-and-effect mechanistic understanding of how traits influence community assembly and ecosystem functioning . Yet, to date, virtually all manipulative studies of this nature have occurred on a small scale, which is problematic because assembly is influenced by processes operating at small to large spatial scales - e.g., dispersal influences assembly at landscape-scales and assembly is influenced by environmental conditions, which vary across space (Ackerly 2003; Brudvig & Haddad 2008; Helsen, Hermy, & Honnay 2013). To advance understanding of trait-based community assembly and its consequences for ecosystem functioning, we need manipulative studies that occur on scales relevant to the assembly of communities in the real world.

Ecosystems undergoing ecological restoration present such an opportunity. With a growing majority of the terrestrial Earth's surface transformed by human land use (Foley *et al.* 2005; Haddad *et al.* 2015), it is increasingly apparent that preservation alone will not maintain the biodiversity and functioning of natural ecosystems (Rodrigues *et al.* 2004). Because of this, restoration – active reinstatement of biological communities and ecosystem functionality– will be critical to conservation efforts (Dobson, Bradshaw, & Baker 1997; Young 2000; Hobbs & Harris 2001; Brudvig 2011; Suding 2011). Restored ecosystems offer unique opportunities to study community assembly and diversity-function relationships under realistic field conditions (Bradshaw 1987; Grman, Bassett, & Brudvig 2013; Zirbel *et al.* 2017) because: **1)** Seed sowing is used to manipulate dispersal and control the number of individuals and species arriving at a site. In many instances, sown species do not arrive naturally, providing the opportunity to link manipulated dispersal with establishment and persistence. **2)** Restoration actions (e.g. prescribed fire; grazing; mowing) directly influence environmental conditions that may affect assembly and ecosystem functioning. **3)** Restoration typically occurs at the ecosystem scale and is likely to capture processes that take place at the ecosystem scale (e.g. trophic dynamics).

In turn, consideration of functional traits may improve restoration success, which is of strong pragmatic importance as reinstating biodiversity, functioning, and services, underlain by biodiversity and functions, to degraded sites is the primary goal of restoration (Brudvig *et al.* 2017). Trait-based approaches hold promise for understanding both the assembly and functioning of restored ecosystems, yet - in spite of repeated calls - these ideas remain poorly tested (Temperton et al. 2004; Funk *et al.*

2008; Montoya, Rogers, & Memmott 2012; Perring *et al.* 2015). Moreover, we know very little about how actions taken during restoration to shape community composition favor species with particular traits that, in turn, determine function, as the effects of restoration on species composition/diversity and function have been typically studied separately (Montoya, Rogers, & Memmott 2012).

My dissertation confronts these knowledge gaps by coupling community assembly and biodiversity-ecosystem function theory with functional traits and restoration to address the core question:

How do plant functional traits structure the community assembly and ecosystem functioning of ecosystems undergoing restoration?

To answer this question my dissertation has focused on two main areas of research: **1)** Testing theory in trait-based community assembly and **2)** Building a link between community assembly and biodiversity ecosystem function theory using functional traits. All of this work has taken place using experiments and observational studies in restored tallgrass prairies in southwestern Michigan.

Trait-based community assembly

Understanding how a species' traits interact with its environment to determine performance is the conceptual underpinning for most trait-based community assembly research. However, the field has often struggled to move beyond simply correlating averaged trait values with environmental conditions to approaches that simultaneously consider functional traits, environmental conditions, and performance.

My work has attempted to push the field forward by using experimental manipulations in a restoration setting to: **1)** Understand whether similarity in functional traits between the current plant community and invaders or trait-environment matching mediates the success of the invading species, and **2)** Evaluate how trait environment interactions determine seedling establishment success in newly restored prairies.

Linking community assembly and ecosystem function

Plant functional traits have a great potential for linking the two major goals of ecological restoration, community assembly and ecosystem function. Yet, this potential has been poorly realized. In this dissertation, I have approached this connection in two ways: **1)** Using functional traits to link environmental conditions and ecosystem functions within a restoration to understand community assembly and the direct and indirect effect of environmental conditions on ecosystem functions, and **2)** Using restoration as a system to better understand diversity-ecosystem function relationships and apply this to real world systems by incorporating other metrics of biodiversity, considering landscape level variation in environmental conditions, and predicting multiple different ecosystem function across and within sites simultaneously.

Study system

My dissertation research focused on restored Tallgrass prairies in southwestern Michigan. Prairies in this region are generally dominated by perennial grasses and other graminoids along with a large diversity of long-lived forbs. These systems have relatively few shrubs and trees and have open canopies. The open structure of these systems is maintained through frequent disturbance from natural and man-made fires as well as grazing from large herbivores, primarily bison. Tallgrass prairie once stretched across much of central North America. Extensive conversion for agriculture and other human land use, has resulted in a loss of these habitats and today less than 0.1% of tallgrass prairie remains (Samson & Knopf 1994). The loss and fragmentation of tallgrass prairie habitat has resulted in the decline of many species and the ecosystem functions that rely on this ecosystem. Prairie restoration uses concepts from ecology to attempt to reconstruct lost prairie communities in the hope of returning native biodiversity and ecosystem functioning to degraded landscapes. Typically, tallgrass prairie restorations are initiated through sowing seeds of native prairie plants onto former agricultural lands and, subsequently managing them with prescribed fire and other approaches (Packard & Mutel 1997).

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CHAPTER TWO

TRAIT-ENVIRONMENT INTERACTIONS DETERMINE PLANT ESTABLISHMENT DURING RESTORATION

Abstract

Understanding how communities assemble is a major goal of ecology and of high pragmatic importance, for informing restoration management because of the strong conceptual ties to community assembly. Whether or not a species successfully establishes and persists at a site is determined by how its traits interact with the local environment to determine its performance (trait-environment interactions). Studies evaluating community assembly rarely consider all parts of this relationship. This can lead to unreliable estimates of how traits affect community assembly. We evaluated the importance of functional traits independent of environmental context versus trait-environment interactions for determining establishment success in a set of restored prairies in southwestern Michigan. To do this we selected 12 experimental prairie restorations, all sown with the same species at the same time but vary in their environmental conditions. At each site we measured a set of environmental variables that are expected to influence seedling establishment: soil water holding capacity (WHC), light availability, and herbivore pressure. We also counted the number of sown species that had established after the first growing season. For each of these species we compiled data on functional traits that might influence establishment including specific leaf area (SLA), seed mass, and root:shoot. We then compared environmental conditions and traits in our model along with trait-environment interactions including SLA by herbivore pressure, SLA by WHC, seed mass by light availability, and root:shoot by WHC. We found that none of the traits we measured influenced seedling establishment, but we did detect two trait-environment interactions that affected seedling establishment. While there was no main effect of SLA, low SLA species were more likely to establish in plots with higher soil water holding capacity; species with high SLA performed poorly overall, Also, low SLA species performed relatively better than high SLA species under high levels of herbivore pressure. Our work demonstrates that simply correlating

traits with measures of performance is inadequate for assessing assembly processes and that future community assembly studies should focus on trait-environment interactions. This work also has important pragmatic implications for restoration as these community assembly processes control the establishment of seeded species and the interaction between traits of sown species and environmental conditions at a restored site can determine what species are able to establish in a particular site.

Introduction

Trait-based approaches have been increasingly employed in community ecology to answer classic questions related to species' distributions and abundance along gradients, with particular focus on understanding patterns of community assembly (Ackerly & Cornwell 2007; Kraft, Valencia, & Ackerly 2008). Functional traits describe an individual's ability to disperse to, establish, and persist at a site (Violle *et al.* 2007), and have been lauded as a way for community ecology to take a more generalizable and mechanistic approach to studying community assembly (Weiher *et al.* 1999; McGill *et al.* 2006). Much of this work has considered how traits relate to performance or how traits are structured along gradients, but rarely have studies co-considered these two points (Ackerly 2003; Shipley, Vile, & Garnier 2006). This is important as species are likely distributed across space because of how performance is affected by the interaction between their traits and particular environmental gradients. Thus, there is a need to understand how interactions between traits and environment affect performance, yet such studies are rare in community ecology (Laughlin & Messier 2015).

How a species' traits interact with its environment affects key demographic rates, like establishment, which ultimately dictate species' distributions along gradients (Litchman & Klausmeier 2008). Trait data are typically correlated with measures of performance for individual species, spanning and averaged across locations (Messier, McGill, & Lechowicz 2010). Yet, this approach is overly simplistic as it assumes that the relationship between a trait value and performance is independent of the environment (Laughlin *et al.* 2018). For example, it is unlikely that a plant with high specific leaf area would perform equally well in both a wet and dry environment, but high specific leaf area may on average be associated with highly performing individuals. Taking into account how trait values correlate with and potentially tradeoff across locations spanning environmental gradients can create a better understanding of the importance of traits during establishment (Laughlin & Messier 2015).

Furthermore, virtually all trait-based community assembly studies use data collected from communities dominated by adult individuals and infer the process of assembly. However, much of the sorting that occurs during community assembly may take place early in the life history - germination, and seedling establishment, as seedling mortality rates can often be extremely high (Grubb 1977). Individuals that successfully disperse to a location may fail to establish if conditions are not conducive to germination and establishment (Myers & Harms 2011; Grman *et al.* 2015). Therefore, it is important to understand how the functional traits of seedlings interact with the local environment to determine their establishment success if we ultimately hope to better understand community assembly. Additionally, due to ontogenetic changes, seedling traits may be quite different from those of adults and measuring functional traits on adults to infer past assembly processes may be inadequate. Here we use trait data collected on seedlings to study the process of seedling establishment during the first year of an experimental restoration.

Finally, functional traits hold great promise for interpreting and predicting the assembly of restored communities. For example, by considering trait-environment interactions we may be able to inform decisions about seed mixes via matching species to sites conditions. However, this promise remains poorly realized as tests linking environmental conditions, functional traits, and plant performance in restoration are rare (Brudvig 2011). Additionally, restored systems can offer a unique test of ecological theory at the scale of ecosystems (Bradshaw 1987; Wainwright *et al.* 2018). Sites restored via seed sowing offer an ideal test of community assembly. After seeds are sown those species need to germinate and establish under the particular environmental conditions at a site. This variation in environmental conditions across sites leads to different species establishing based on their functional traits. Because seeded species are often absent in the surrounding landscape, we are able to make strong connections between the occurrence of seeded species and establishment. Furthermore, ecological restoration often occurs at the scale of ecosystems allowing for experimental tests of community assembly theory across large spatial scales and relevant environmental gradients.

Here, we test the hypothesis that species establishment within experimentally restored prairies is structured by trait environment interactions. To do so, we ask three specific questions:

1. Is seedling establishment structured by functional traits?
2. Is seedling establishment structured by local environmental conditions?
3. Is seedling establishment structured by interactions between traits and environment?

We focused on three functional traits (specific leaf area, seed mass, root:shoot) and three environmental gradients (soil water holding capacity, light availability, herbivore pressure) that we hypothesize to be important for plant establishment.

Methods

Our study took place within a set of experimentally restored prairies at the W.K. Kellogg Biological Station. Prior to restoration, these sites were old field communities which were former agricultural land. Herbaceous perennials dominated the vegetation at all 12 sites prior to restoration. The experimental restorations were established in fall of 2015 using a modified seed drill with half of each site receiving a 12 species mix and half receiving a 70 species mix. Seeding density of the different species ranged from 0.22 to 49 seeds per m^2. Sites range in size from ~0.2-3.5 hectares (totaling ~14 hectares). In the summer of 2016 all sites were mowed to a height of ~15cm to prevent weedy species from setting seed and reduce light competition with seeded species. In August of 2016 we counted the number of individuals of each of the sown species that had established in five 5x5m plots located at 1 meter intervals along a transect in the center of each half site.

Environmental conditions

At each site we measured a set of environment conditions thought to interact with plant traits and directly influence seedling establishment. These included: herbivore pressure, light availability, and soil water holding capacity. We used soil water holding capacity as this has been shown to inhibit the establishment of certain prairie species (Grman *et al*. 2015). To measure soil water holding capacity we took 10 cores along a 25m transect at each sites. We combined samples at the site level and by calculating the proportion of oven dried weight to saturated wet weight (Brudvig & Damschen 2011). Herbivory has been show to significantly impact species composition of prairies as herbivores selectively feed on certain species (Howe *et al.* 2006). To measure herbivore pressure we determined the percent leaf area missing on all leaves of 5 individual *Echinacea purpurea* plants in each 5x5m survey plot. We chose *E. purpurea* because it was abundant at each of the sites. This measure of herbivory likely represents pressure from generalist herbivores found across our study sites. Low light availability has also been shown to limit the establishment of seedlings (Foster 2001). To measure light availability we used a lightbar and measured the light levels above and below the plant canopy and then calculated the % light to get a measure of the amount of light reaching ground level.

Functional traits

We measured three functional traits of interest, we grew seedlings of all 70 species sown into the restoration sites in a greenhouse for ~3 months. We grew 5 individuals of each species. On each individual we measured root:shoot, specific leaf area (SLA,), and seed mass. We measured root:shoot as the total dried aboveground biomass divided by the total belowground dried biomass of an individual. Root:shoot is thought to be related to a species' drought tolerance (Grime 1977). We measured specific leaf area by measuring the area of a single leaf from each individual and dividing by the dry mass of the leaf. SLA is thought to be related to a species' nutrient use efficiency as well as total leaf nitrogen and therefore how attractive a species is to herbivores (Westoby *et al.* 2002). SLA is also related to water use efficiency and thus drought tolerance (Wright *et al.* 2004). Finally, we measured seed mass by taking the average mass of at least 50 oven dried seeds of each species. Seed mass is related to a seedlings ability to survive under competitive environments (Gross 1984).

Analysis

To understand how trait-environment interactions determine seedling establishment we used generalized linear mixed effects models. We included random effects of site, plot, and species to account for non-independence of samples. We used plot level counts for each sown species as our response variable and fit a zero-inflated Negative binomial error distribution. We included seeding rate for each species in the model to account for unequal seeding densities that may impact establishment rates. We included interactions between herbivory rate and SLA, root:shoot and soil water holding capacity, SLA and soil water holding capacity, and seed mass and light availability. We also included main effects for all interaction terms in the model. We centered all predictors in the model to have a mean of zero and scaled them by their standard deviations to help with model convergence. Variance inflation factors were all less than 2 suggesting that collinearity is not a problem in this model (Zuur, Ieno, & Elphick 2010).

Results

Seedling establishment rates were highly variable across sites. We found only marginal evidence for effects of environmental conditions on seedling establishment. Seedling establishment increased with increased soil water holding capacity (Figure 2.4, p=0.06, beta=0.13), but was unrelated to herbivore pressure or light availability (p=0.54, p=0.87).

We found no evidence for relationships between seedling establishment and the main effect of any of the functional traits we measured (Figure 2.1). The relationship between functional traits and seedling establishment were highly variable (Figure 2.1, root:shoot S.E.=0.26, SLA S.E.=0.27, seed mass S.E.=0.21).

We did detect evidence that seedling establishment was affected by two trait by environment interactions. The interaction between specific leaf area and soil water holding capacity (Figure 2.2a, p=0.02). Low SLA species performed better in plots with higher soil water holding capacity while species with high SLA performed poorly overall. Second, SLA and herbivore pressure interacted to structure seedling establishment (Figure 2.2b, p=0.05). We found that low SLA species performed relatively better than high SLA species under high levels of herbivore pressure.

Finally, we found that seeding density increased seedling establishment (Figure 2.3, p<0.0001, beta=0.93).

Discussion

Our results illustrate the importance of trait-environment interactions for seedling establishment. We found no significant main effects of any functional traits, and the effects of functional traits on seedling establishment had high variance suggesting a wide range of possible outcomes across different levels of a trait. We did however find two significant trait-environment interactions. Low SLA species performed better in plots with higher soil water holding capacity while species with high SLA performed poorly overall, and low SLA species performed relatively better than high SLA species under high levels of herbivore pressure. The combination of no main effects of any functional traits and significant trait-environment interactions cautions against trait-based community assembly studies that simply correlate functional traits with measures of fitness and demonstrates the importance of focusing on how characteristics of a species interact with the local environment to determine establishment.

We found no main effects of any functional traits on seedling establishment and only a marginally significant effect of soil water holding capacity. Furthermore, we found that effect of functional traits on seedling establishment had high variance, higher than any other effects in the model (Figure 2.1). It is likely this is because at high or low levels of a functional trait we do not see high or low levels of establishment but instead these traits interact with environmental conditions to determine establishment. While we do see a trend towards lower SLA species establishing better overall, this relationship is highly variable and depends on both herbivore pressure and soil water holding capacity. Correlating traits or community weighted mean traits with environmental conditions and assuming that the average trait value of a community reflects the value of a trait that is best suited for a particular environment may inaccurately assess the relationship between the environment, functional traits, and performance as we show here. Future trait-based assembly work should avoid the assumptions made by approaches that utilize community average trait values (Laughlin & Messier 2015).

Trait-environment interactions offer an approach to studying assembly that avoids the assumptions of correlating traits with environmental conditions or performance. Here we find two significant trait-environment interactions on seedling establishment. First, low SLA species performed better in plots with higher soil water holding capacity while species with high SLA performed poorly overall. This is the opposite of what we expected because high SLA species should perform better on wetter sites than those with low SLA (Westoby 1998). More work needs to be done to investigate whether or not other correlated traits or environmental conditions might underlie this unexpected relationship. Second, low SLA species performed relatively better than high SLA species under high levels of herbivore pressure. This may be because high SLA species often have high nitrogen content per unit mass (Reich, Walters, & Ellsworth 1997) and are often poorly defended against herbivores (Westoby *et al.* 2002). These results demonstrate that simply correlating traits with measures of performance is inadequate for assessing assembly processes. Recent work from Laughlin *et al.* (2018) has shown that approaches such as these can give unreliable estimates of how traits affect assembly processes. Moving forward our work here and others suggests that trait-based assembly work should consider how trait-environment interactions affect species establishment and persistence (Edwards, Litchman, & Klausmeier 2013; Laughlin & Messier 2015).

Our work also illustrates the merits of considering trait-environment interactions in context of ecological restoration. Restored ecosystems have been lauded for their capacity as testing grounds for community assembly concepts; we show these merits for the study of trait-environment interactions. Additionally, our results have pragmatic importance for restoration. We find a large effect of seeding density on establishment. Grman *et al.* (2015) found this same result in an observational study of tallgrass prairie restorations. Both studies show the importance of overcoming dispersal limitation during restoration and sowing adequate amounts of seed can improve establishment. However, even after controlling for differences in seeding density we still find an effect of trait-environment interactions on establishment. This suggests that considering seed mix composition to match particular environmental conditions at a site is important . We also show that species with a particular set of traits are not necessarily better than others due to the fact that we find no significant main effects of traits, but the suitability of species is context dependent.

Over the past two decades trait-based approaches have shown their utility for addressing core questions in community ecology (Weiher *et al.* 1999; McGill *et al.* 2006). However, we show here that without co-considering functional traits, environmental conditions, and performance we may be making incorrect estimates of community assembly processes. Here we show that it is necessary to consider functional traits within a particular environmental context to understand species establishment. We also demonstrate the utility of restoration for making experimental tests of community assembly processes at the scale of ecosystems, and show how our finding might have important pragmatic implications for restoration.

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APPENDIX

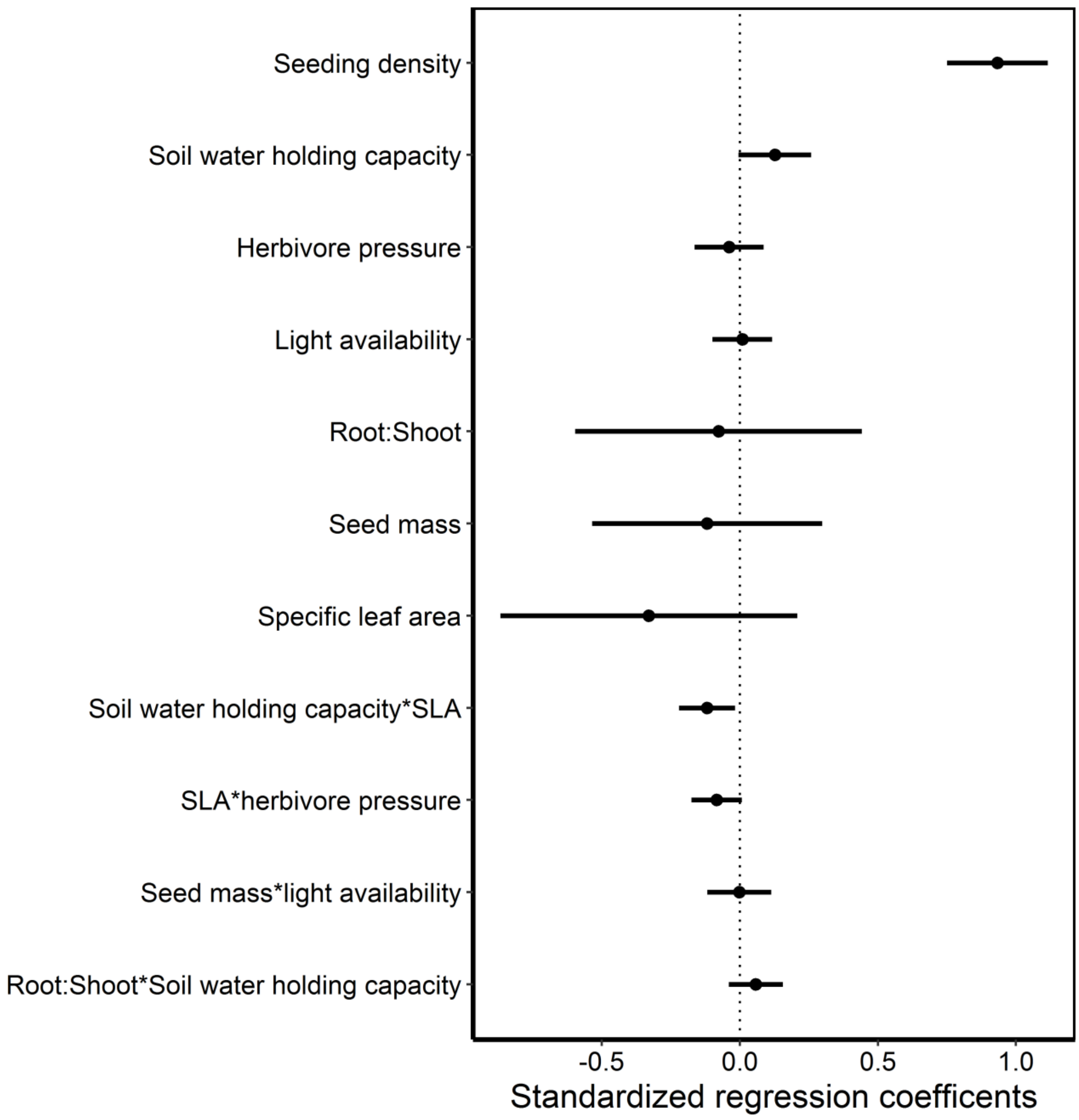

Figure 2.1. Standardized effect of each of the predictors on seedling establishment from our model. Bars represent 95% confidence intervals.

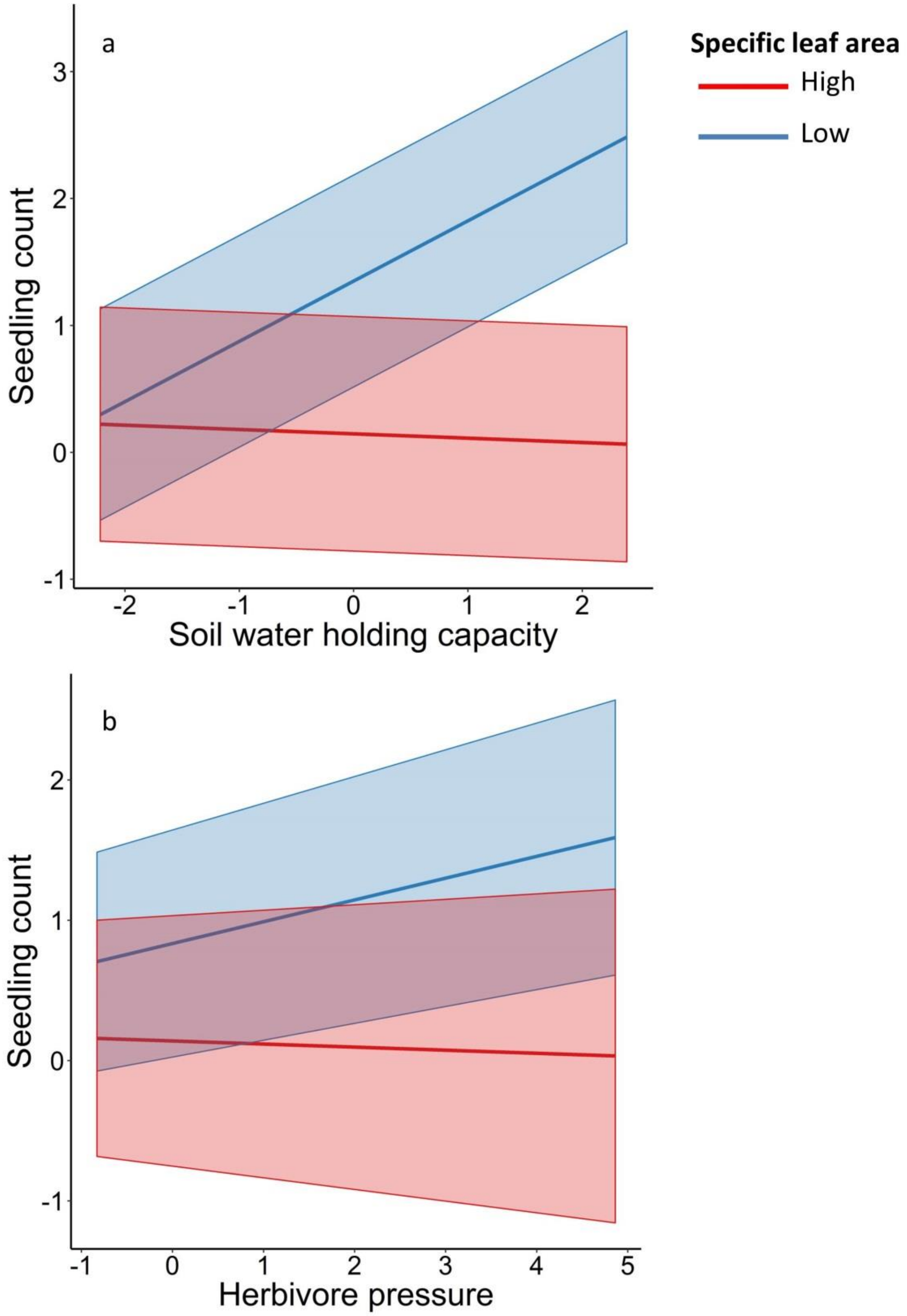

Figure 2.2. SLA interacted with (a) soil water holding capacity and (b) herbivore pressure to determine seedling count. The shaded region represents 95% confidences intervals.

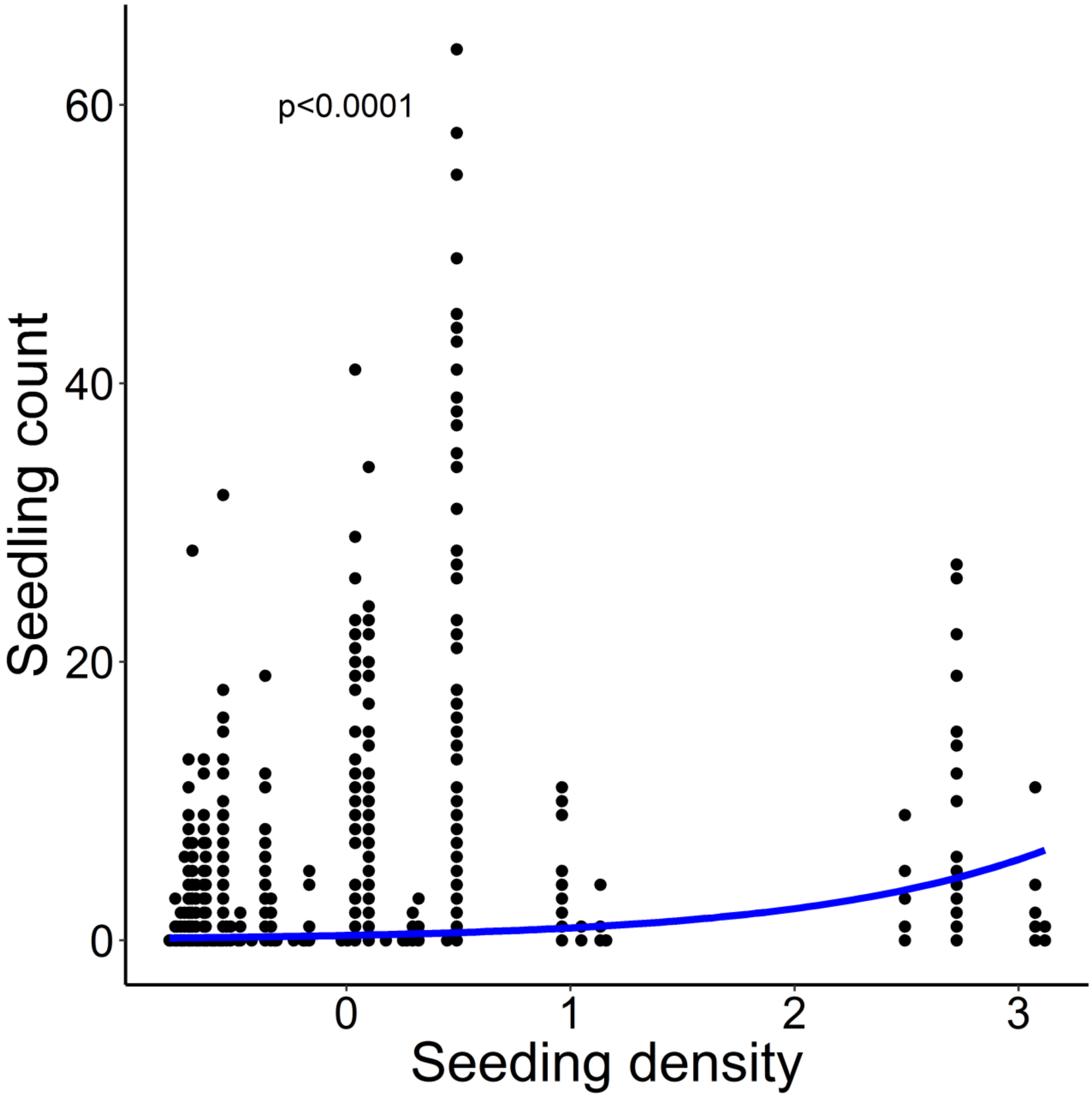

Figure 2.3. Relationship between seeding density and seedling count. Each point represents plot level counts of a single species.

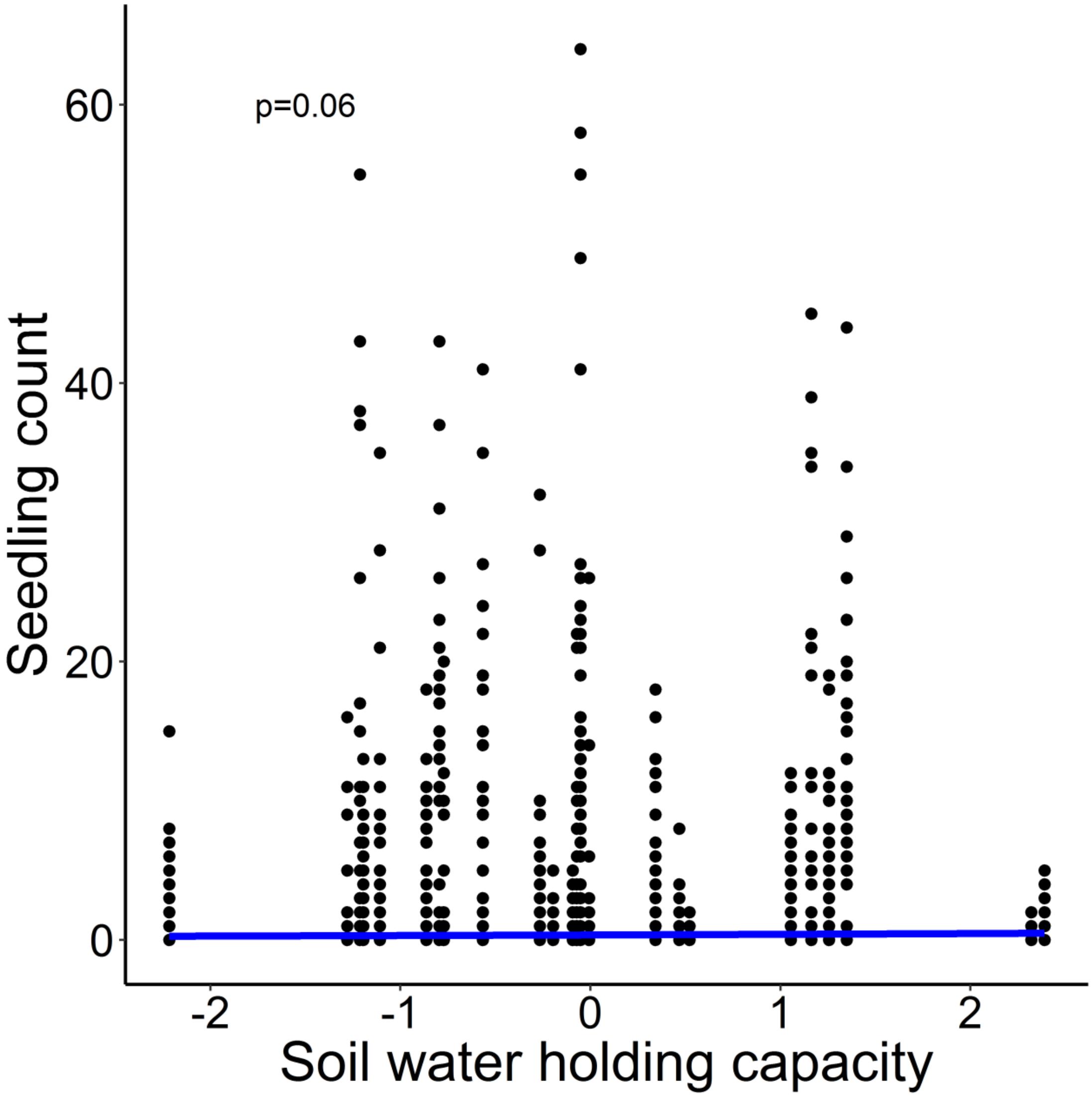

Figure 2.4. Relationship between soil water holding capacity and seedling count. Each point represents a plot level count of a single species.

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CHAPTER THREE

ENVIRONMENTAL FILTERING, NOT LIMITING SIMILARITY, DETERMINES INVASION SUCCESS

Abstract

Understanding a species ability to invade a novel community is a central goal of community ecology. While many theories have been proposed to explain the process of invasion, few studies have evaluated these theories simultaneously. The ability of a species to invade a locality is dependent on how the traits of the invader interact with the environmental conditions (biotic and abiotic) and the resident community. Furthermore, these relationships may be context dependent, where the importance of different processes depend on the environmental conditions a species is invading. Because these processes of invasion are not mutually exclusive, and may determine invasion success concurrently, it is important to consider each simultaneously.

Here we ask whether the degree of overlap between the traits of the invader and the resident community (limiting similarity) and how well the traits of the invader allow it to survive local environmental conditions (environmental filtering) determines invasion success and if these relationships are context dependent. To do this we experimentally invaded ten prairie restorations, which differed in both environmental conditions and community composition. None of the 22 prairie species introduced occurred at these sites. Six seed addition plots were established at each site, and within each plot we counted the number of seedlings of each species that successfully invaded. The results showed a negative relationship between trait dissimilarity and invasion success We do not find any evidence that this relationship was context dependent as the relationship between trait dissimilarity and invasion success did not vary with sand content. We did find significant trait by environment interactions: sand content and seed mass and sand content and growth rate. Together these results show that how well a species' traits allow it survive local environmental conditions and not how much their traits overlap with those of the resident community determines invasions success. This suggests

that environmental filtering and not limiting similarity is an important factor determining invasion success by native species into these restored systems.

Introduction

A species' ability to invade is central to core areas of research in ecology including community assembly and co-existence theory (Weiher, Clarke, & Keddy 1998; Chesson 2000) . Understanding a species' ability to invade also has strong pragmatic importance as these same processes should determine a non-native species' ability to invade a community as well as a manager's ability to establish new native species into a community through seeding (Lockwood & Samuels 2004; Funk *et al.* 2008). Many different hypotheses have been proposed to explain whether or not a species will successfully invade a new locale (Keddy & Shipley 1989; Keddy 1992; Funk *et al.* 2008). Because the processes that control invasion are not mutually exclusive and may determine invasion success concurrently it is important to consider each of these processes simultaneously. Some theories suggest that a species' interactions with its environment and the community present at a site should determine whether or not it is able to successfully invade. Furthermore, some of these relationships may be context dependent where the importance of the overlap between a species traits and those of the community it is invading will depend on the environment conditions a species is invading. We still have a poor understanding of how these different processes determine a species' ability to successfully invade a locality.

At its core, a species' ability to invade a community is dependent on how the traits of the invader interact with the environmental conditions and the traits of the resident community at a site. Many theories have been put forward to describe the conditions for which a species should successfully or unsuccessfully invade. These include limiting similarity, environmental filtering, and competitive hierarchies (Keddy & Shipley 1989; Keddy 1992; Funk *et al.* 2008). Limiting similarity predicts that a species that disperses into a community will be less likely to establish if its traits closely match those of the species that are already present (Funk et al. 2008).This is because species that are similar in their traits are expected to utilize similar niches and compete strongly. In contrast, environmental filtering predicts that species that are successful in invading a community will have traits that are adapted to the local environmental conditions (Kraft et al. 2015). As a result, environmental filtering would lead to the prediction that having traits similar to species that are already present may be beneficial because those traits are able to persist in the current environment. A third hypothesis - competitive hierarchies - assumes that individuals with the best set of traits will successfully invade (Keddy & Shipley 1989). These ideas are non-mutually exclusive and may act simultaneously on species invading a community. Yet, even with the large body of work on this topic we still lack studies that consider these ideas simultaneously, and this limits our ability to understand the relative importance of each of these processes (Dukes 2000; Fargione, Brown, & Tilman 2003; Turnbull, Rahm, & Baudois 2005; Emery 2007).

To test the predictions of each of the processes thought to determine a species' likelihood of invading we need a metric that quantitatively approximates how species interact with each other and their environment. Functional traits can be used to characterize a species' ability to disperse to, establish, and persist at a site (Violle *et al.* 2007), and provide a mechanism for how species interact with their environment allowing for strong tests of how species invade a community. We expect the aforementioned processes, limiting similarity, environmental filtering, and competitive hierarchies, to predict certain patterns in the traits of the invaders. Limiting similarity predicts that the traits of the invader should be dissimilar from those of the community already present to avoid niche overlap. Environmental filtering predicts the opposite pattern because the traits of the successful invaders will be those that are best adapted to the local environmental conditions and the community already present likely possesses this same set of traits. If limiting similarity and environmental filtering operate simultaneously, we would expect a quadratic relationship between trait dissimilarity and invasion success where species perform poorly at both low and high levels of trait dissimilarity. Environmental filtering also predicts that trait-environment interactions should structure invasion success as species with certain traits will best invade some environmental conditions, but species with different traits will best invade other environments. Finally, competitive hierarchies predict that functional traits on their own, not interacting with environmental conditions, will predict invasion success. This potential for trait-based approaches to provide insights into processes structuring invasion remains unrealized due to a lack of experimental studies evaluating this suite of processes from a functional trait perspective.

We also expect that the relationship between traits, the resident community, and environment to be context dependent. The strength of each of the above processes may vary based on the environmental conditions at a site. For example, the degree to which we see trait dissimilarity between the invader and standing community may depend on environmental conditions where harsher sites might see stronger evidence of environmental filtering due to the strong effect of environmental conditions (Chase 2007). Whereas on more benign sites limiting similarity may be more important as competition between species is expected to be stronger (Dickson *et al.* 2014). Context dependencies can also help explain disparities between the different theories put forward to explain invasion success. While competitive hierarchies predicts that individuals with the best set of traits will successfully invade (Keddy & Shipley 1989), it is unlikely that the best set of traits will be the same across environmental gradients. Instead, the traits best adapted to certain environmental conditions should be the most likely to succeed, which is the same prediction made by environmental filtering. To date there are few studies that attempt to understanding how context dependencies shape invasion success will be important for determining which processes might be most important under varying abiotic conditions and to remedy discrepancies between processes that predict invasion success.

To better understand a species ability to invade a novel community we must test multiple theories put forth to explain patterns of invasion and understand the degree to which these relationships are context dependent. To do this we added seeds of 22 native prairie species, including grasses and forbs, into restored grasslands to which these species did not occur or occur infrequently. Ecological restoration provides a rich testing ground for community assembly and invasion theory (Funk *et al.* 2008), through the intentional addition of species by seed and manipulation of environmental gradients and community composition. Species composition and environmental conditions also vary widely across restorations allowing us to test both limiting similarity and environmental filtering within the same system. This also has pragmatic importance for restoration as these same processes control a non-native species' ability to invade and a manager's ability to establish new species within a restoration via inter-seeding. Here we address four research questions:

1. Does the overlap between a species' traits and the traits of the current community determine invasion success (limiting similarity)?
2. Does the relationship between a species' traits and the local environment determine invasion success (environmental filtering)?
3. Do trait hierarchies or a best set of functional traits determine invasion success (competitive hierarchies)?
4. Are these relationships dependent on the harshness of a site?

Methods

Study sites

This experiment was conducted in 10 tallgrass prairie restorations in southwestern Michigan which had formerly been agricultural fields. Sites ranged in age from 7-10 years since planting and varied in their environmental conditions and community composition (Grman, Bassett, & Brudvig 2014). At each site we established six 1x1 m plots and placed a 0.5x0.5 m plot in the center for the seed addition and in spring of 2015, we cleared litter from this area to create good seed to soil contact and each plot was sown with 22 native prairie species. Seeded species are not present in the landscape and were either never seeded into any of the restorations or were seeded but only occurred at <2% mean cover across our 10 sites, or found in <1 plot on average across sites during a previous sampling (Grman et al. 2014). This allowed us to be able to make strong connections between the occurrence of seeded species and invasion.

Community composition and seedling counts

In the fall of 2015 we recorded the percent cover of all species not sown in this experiment in each of the 1x1m plots to quantify local community composition. In 2015 and 2016 we counted all seedlings of each sown species in each 0.25m^2 plot to quantify rates of invasion of each sown species. Not all species were able to establish, and for these analyses we only focus on species that established in at least 1 plot across the study; this resulted in 15 of the 22 species being used.

Environmental conditions

At each site we took ten 20 cm by 3 cm^2 soil cores distributed across the sampling area We aggregated soil cores at the site level and analyzed these for sand content which is related to both nutrient content and soil water holding capacity. Water availability, especially on sandy soils, can limit species invasion by selecting for drought adapted traits (Padilla & Pugnaire 2007). Sand content also relates to the harshness of a site which is expected to create context dependencies in how invasion processes occur (Chase 2007).

Functional traits

We compiled a database of functional traits for species present during plant composition surveys and seedling counts using standard methods (Pérez-Harguindeguy *et al.* 2013). For this analysis, we focused on four continuous traits (growth rate, vegetative height, specific leaf area (SLA), and seed mass) and six categorical traits taken from the literature (life history, clonality, photosynthetic pathway, root morphology, and nitrogen fixing). We selected these traits because they represent different aspects of a species niche and that describe how a species might interact with the current community and local environmental conditions when invading. For all continuous traits except growth rate, we collected traits from healthy, flowering adults growing in full sun (Pérez-Harguindeguy et al. 2013) located at least

10 m away from a site edge. We measured vegetative height as the distance between the ground and highest photosynthetic structure on 20 individuals. We measured SLA by collecting 2 leaves from each of 10 individuals. We kept leaves turgid and stored for <10 hours until area was determined with a leaf area scanner and then dried leaves at 65°C for 48 hours before weighing. We calculated SLA as leaf area divided by dry mass. We determined seed mass by taking the average of at least 50 seeds from at least 5 individuals for each species dried at 80°C for 48 hours before weighing. When necessary, we supplemented seed mass data from the KEW seed information database (Royal Botanic Gardens Kew, 2016). We measured growth rate by growing 10 individuals of each of the seeded species in the greenhouse for approximately 4 months. We calculated growth rate as the total dry mass of the plant divided by the number of days it was allowed to grow. For the categorical traits, we compiled data from online trait databases and floras (Flora of North America Editorial Committee, eds. 1993, Iverson et al. 1999, Royal Botanic Gardens Kew 2016, National Plant Data Team 2017). We classified life history as annual, biennial, or perennial. We classified whether a species had the ability to reproduce vegetatively (clonal spread) or whether reproduction was only by seed. We classified root morphology as fibrous (small to no differentiation in root size classes), primary (clear differentiation in root size classes, including taproots), or rhizomatous (underground stems producing adventitious roots) (ILPIN). We classified photosynthetic pathway using either C3 or C4 photosynthesis. Finally, we described whether or not a species was able to fix nitrogen through symbiotic relationship with bacteria.

Analysis

We conducted these analyses using R v.3.3.0 (R Development Core Team 2013). We calculated trait dissimilarity for each invader within each plot by first using the FD package to calculate Gower dissimilarity between each species across all of the traits mentioned above, except for growth rate, where zero represents complete trait overlap between two species and 1 represents no overlap in traits between two species (Gower 1971; FD package). We then calculated the average dissimilarity between each invader and all species present in the plot it was added to, weighted by the abundance of the species present and dividing by the total number of species in a plot. We used generalized linear mixed effects models with seedling counts of each species in each plot as the response variable. We included site, plot, species, and year as random effects, and used a zero inflated Poisson distribution to account for overdispersion due to a large number of zero counts. We also included seeding rate in the model because not all species were sown at the same density.

To test question 1, whether trait overlap determines invasion success, we included trait dissimilarity between the invader and resident community in the model. We also included the quadratic trait dissimilarity term to test whether or not trait overlap and trait-environment matching co-determine invasion success. To test question 2, whether how closely traits match environmental conditions determines invasion success, we included trait-environment interactions in the model. We included sand content by SLA because SLA is related to both nitrogen and water use efficacy (Wright *et al.* 2004). We predict that high SLA species will invade poorly and sandier sites. We included sand content by growth rate because growth rate is related to competitive ability (Weiher *et al.* 1999). We predict that fast growing species will invade better on sites with lower sand content. Finally, we included sand content by seed mass as larger seeded species have more stored resources allowing them to survive on harsher sites (Westoby 1998). We predicted that larger seeded species would invade better on sandier sites. We also included the main effect of sand content. To test question 3, trait hierarchies, we included the main effects of each of these functional traits. Finally to test question 4 we included an interaction between trait dissimilarity and sand content to see if the effect of trait dissimilarity was dependent on environmental harshness. Interactions between traits and the environment to test context decencies of competitive hierarchies were already included to test whether how well a species' traits are adapted to environmental conditions determines invasion success.

All terms were included in the same model. We centered all predictors in the model to have a mean of zero and scaled them by their standard deviations to help with model convergence. Variance inflation factors were all less than 2 indicating multicollinearity was not a concern (Zuur, Ieno, & Elphick 2010).

Results

Functional trait dissimilarity between the invader and the resident community explained invasion success. As species became more functionally distinct they were less likely to successfully invade (Figure 3.2, beta=0.45, $p<0.001$). We found no evidence for a quadratic effect of trait dissimilarity. This suggests that environmental filtering and not limiting similarity determine invasion success in these sites.

For the three functional traits we focused on - growth rate, SLA, and seed mass - to determine if environmental filtering was important in determining invasion, we only found an effect of seed mass. We found that smaller seeded species were more likely to establish than larger seeded species (beta=-1.11, p=0.003). We did find a marginally significant effect (Figure 3.3, beta= 0.51, p= 0.09) of growth rate with faster growing species being more likely to invade

We did not find any evidence that the effect of trait dissimilarity on invasion success varied with environmental conditions (Figure 3.1, p=0.91). We did however find a significant interaction between sand content and growth rate (Figure 3.4a, p=0.002) with fast grow species invading better on sandier sites and slow growing species invading more poorly on sandier sites. We also found a significant interaction between sand content and seed mass (Figure 3.4b, p=0.02) with small seeded species preforming worse on sandier sites and large seeded species invading better on sandier sites.

Discussion

Here we evaluated whether or not the interactions between a species traits and the environment or with the traits of a community already present at a site affects its ability to successfully invade and if this relationship is context dependent. To our knowledge, no other studies have simultaneously considered the importance of limiting similarity, environmental filtering, and competitive hierarchies for invasion success and whether or not these relationships are context dependent. We found a negative relationship between trait dissimilarity and invasion success, supporting a role of environmental filtering and not limiting similarity for invasion at our sites. We also found evidence for competitive hierarchies, as invasion success was higher among smaller seeded species. There was some evidence that competitive hierarchies are context dependent, as we detected two different trait-environment interactions contributed to invasion success: seed mass by sand content and growth rate by sand content. These trait-environment interactions are also further evidence that environmental filtering determines invasion success. While we did find that the relationship between invasion success and individual traits is context dependent we did not find evidence for context dependency in limiting similarity (trait dissimilarity). Together, our findings show that in these prairies, invasion success is determined more by how species' traits determine the ability to establish in particular local environmental conditions and not by whether species possess unique traits from the community to which they are invading.

The negative relationship between trait dissimilarity and invasion success and the trait-environment interactions we found both suggest that environmental filtering and not limiting similarity is influencing invasion success during the first two years in our system. This result matches what was found in a meta-analysis on invasion experiments by Price and Pärtel (2013) which found no evidence for limiting similarity across invasion experiments done in natural communities. In our system, there initially seems to be strong selection for species with traits that allow them to survive local environmental conditions. After this initial filtering it is possible the competitive dynamics between species will become more apparent and limiting similarity will become important.

These results provide insights into the process of invasion in restored prairies. We found significant effects of one functional trait and two trait-environment interactions. Species with higher seed mass were less likely to invade than those with lower seed mass. While species were sown at different densities we controlled for this in our models and found no effect of seeding density on invasion success. Small seeded species were less likely to invade on sites with sandier sites while larger seeded species were slightly more likely to invade on sites with sandy soil than sites with soil containing more clay and silt. This could be because larger seeds have greater energy stores and are able to better invade sites with low nutrient and water soils such as sandy sites. Leishman and Westoby (1994) found a similar result where larger seeded species had higher survival rates than smaller seeded species under dry soil conditions when grown in the greenhouse. We also found a significant interaction between sand content and growth rates with faster growing species invading better than slower growing species on sandier sites. This may be because faster growing species produce more root mass (Figure 3.6) which increases their survival on sandier soils. These significant trait-environment interactions show that competitive hierarchies are context dependent as whether or not a species successfully invades is not only based on its traits but their environmental conditions into which it is invading.

While we did find that evidence that competitive hierarchies are context dependent, we did not find evidence that the relationship between trait dissimilarity and invasion success was dependent on the environment. Other work has found evidence that under harsh conditions deterministic processes such as environmental filtering and competition should be more pronounced (Chase *et al*. 2007). We however do not see this pattern in our system where we do not find a significant interaction between trait dissimilarity and sand content.

Our results have pragmatic importance for both restoration ecology and invasive species management. First, our results suggest that restoration managers should select species with traits that will allow them to survive a site's environmental conditions. Matching functional traits to environmental conditions would likely improve the establishment of native species. In the absence of known trait-environment relationships, our results suggest that inter-seeding species that are similar to the resident community may be an effective way to increase diversity. Second, our results suggest that planting species with traits similar to those of invaders or planting a diverse set of traits to increase trait overlap between invasive species and native species may not be an effective way to control invasive species. Altering environmental conditions, if possible, so that they favor native rather than non-native species may be a more viable alternative to invasive species control. For example, if potentially problematic non-native species share a particular set of traits it might be possible to alter environmental conditions in a way that disfavors these traits. Other work has also suggested that native species that have a competitive advantage over invasive species in a given environment may be a better option than picking species that overlap in traits with invasive species (Funk & Wolf 2016). In this case planting competitively dominant species may be an effective way to prevent invasion by non-native species.

Community assembly and species coexistence rely on a species' ability to successfully invade a community. By evaluating multiple invasion theories simultaneously we show that across a set of restored prairies the successful invasion of species is primarily determined by how a species' traits interact with the local environment but not with the traits of the community present at a site. Here a trait-based approach is necessary to help understand mechanism for how species interact with their environment and the traits of resident species allowing for strong tests of how species invade a community. Future work should continue to utilize functional traits to simultaneously test the multiple determinates of invasion success especially under different environmental conditions as well as how the relative importance of each of these processes might change through time.

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APPENDIX

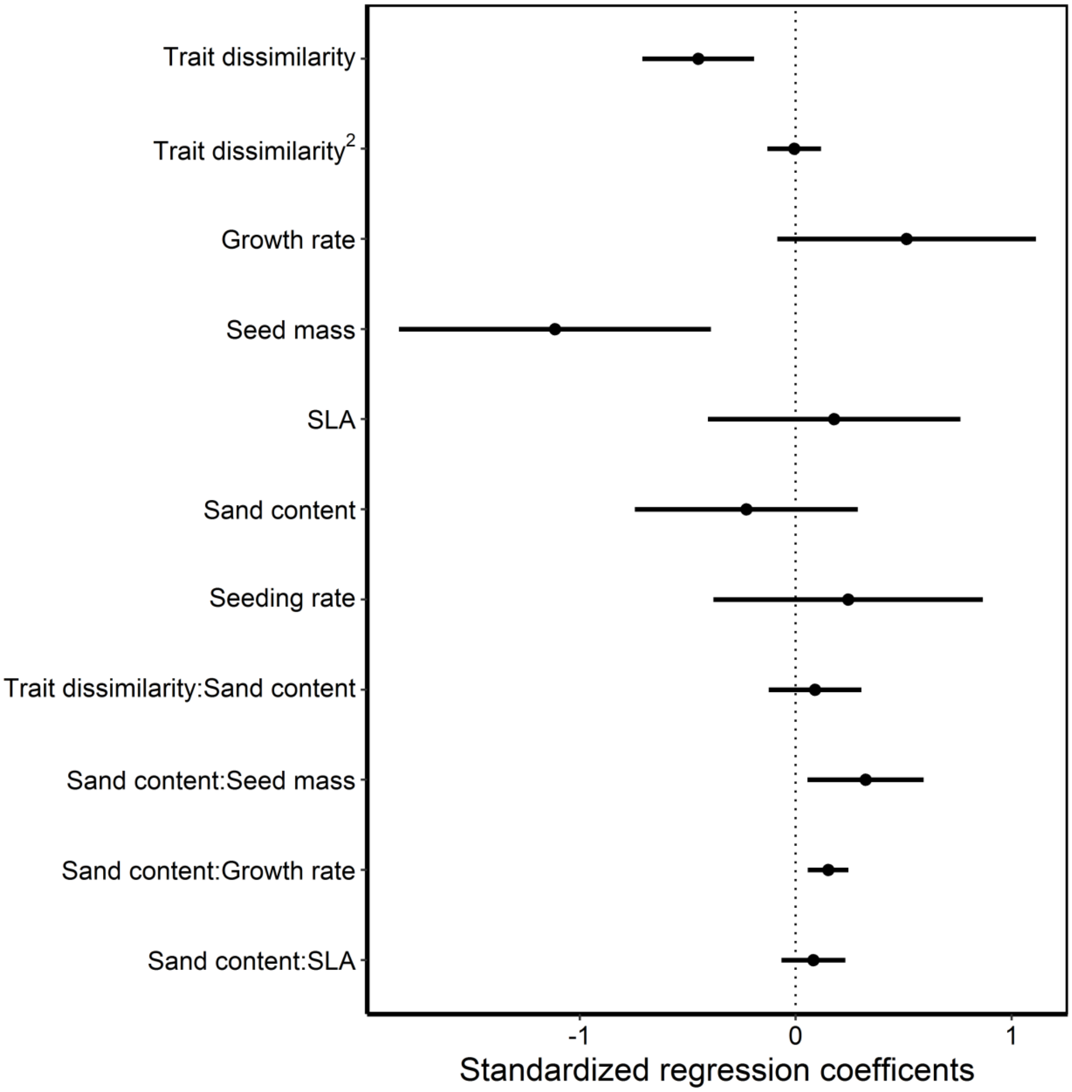

Figure 3.1. Standardized effect of each of the predictors on invasion success from our model. Bars represent 95% confidence intervals.

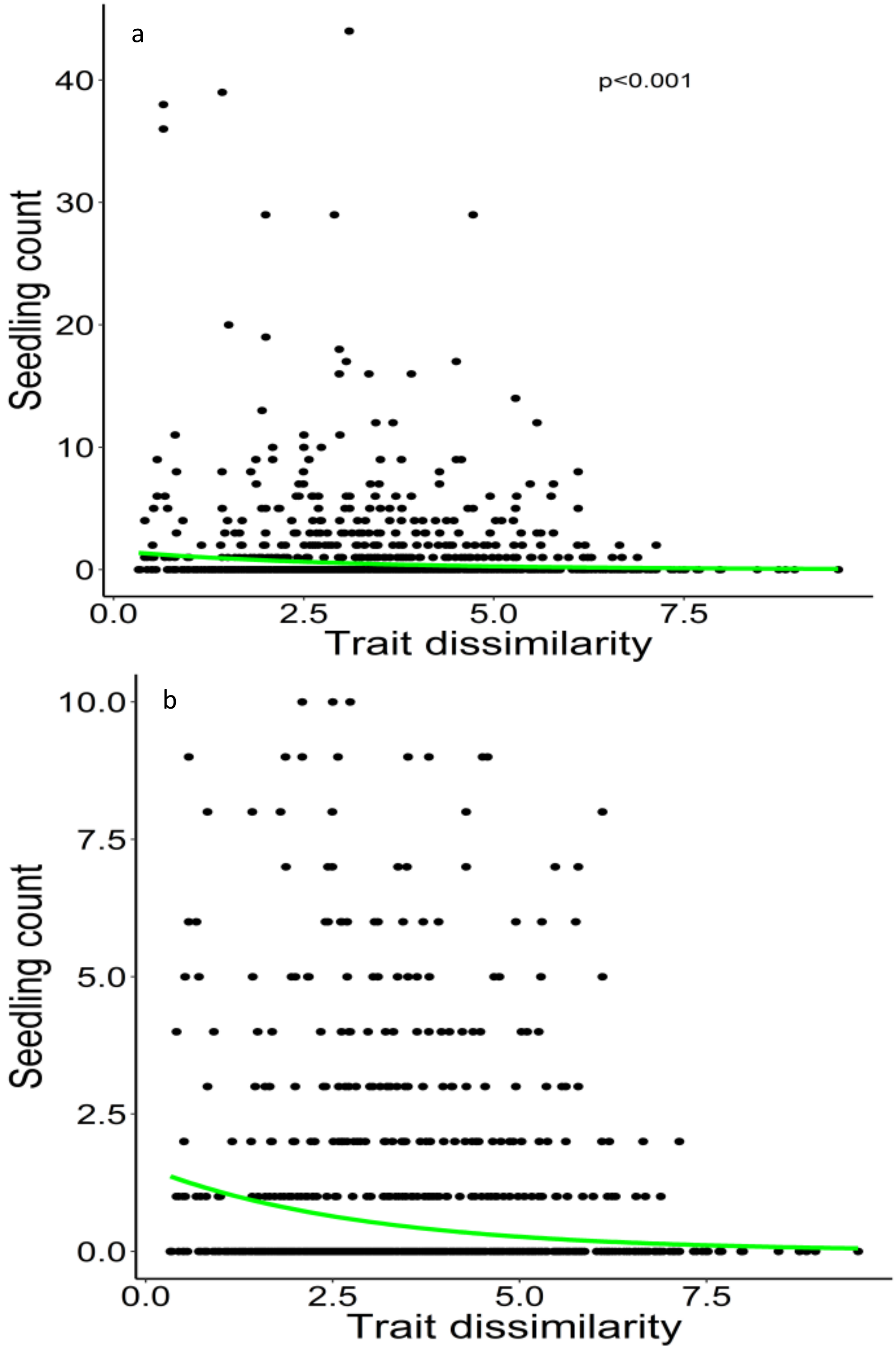

Figure 3.2. Relationship between trait dissimilarity and seedling count. Panel a shows the full result while panel b shows a zoomed in portion of panel a to better visualize the relationship. Each point is the count of a species in each of the plots.

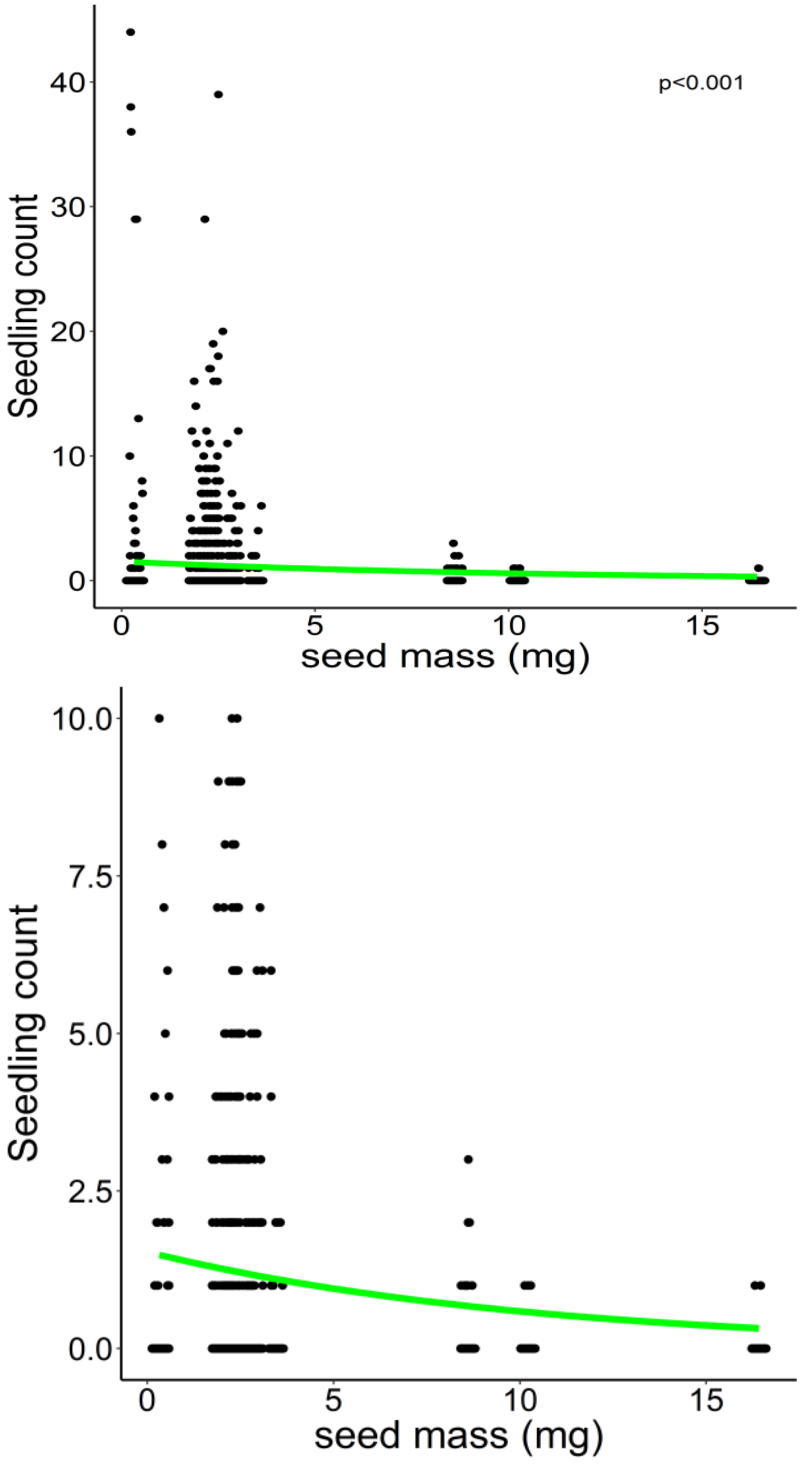

Figure 3.3. Relationship between seed mass and seedling count. Panel a shows the full result while panel b shows a zoomed in portion of panel a to better visualize the relationship. Each point is the count of a species in each of the plots.

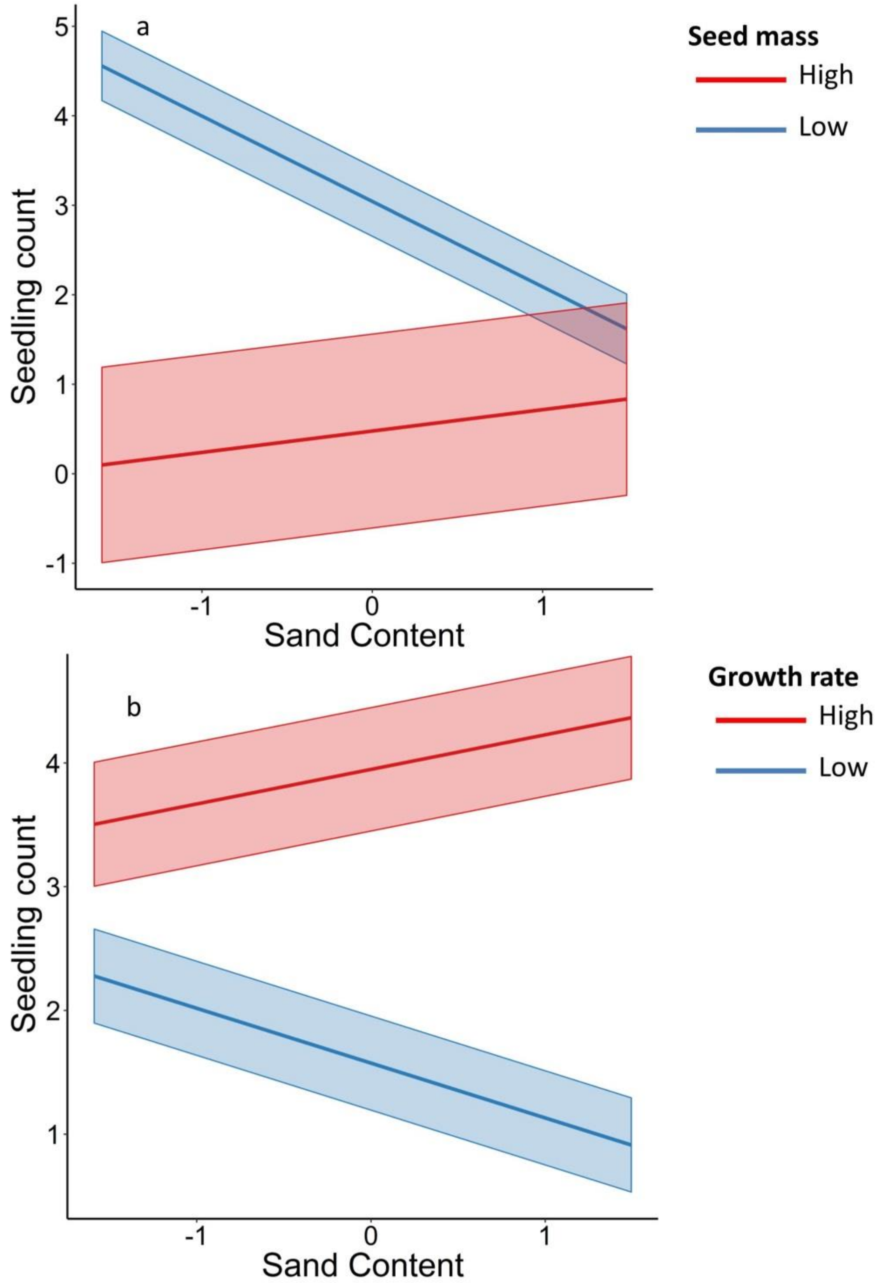

Figure 3.4. Panel a shows the interaction between sand content and growth rate and their relationship with seedling count. Panel b shows the interaction between sand content and seed mass and their relationship with seedling count.

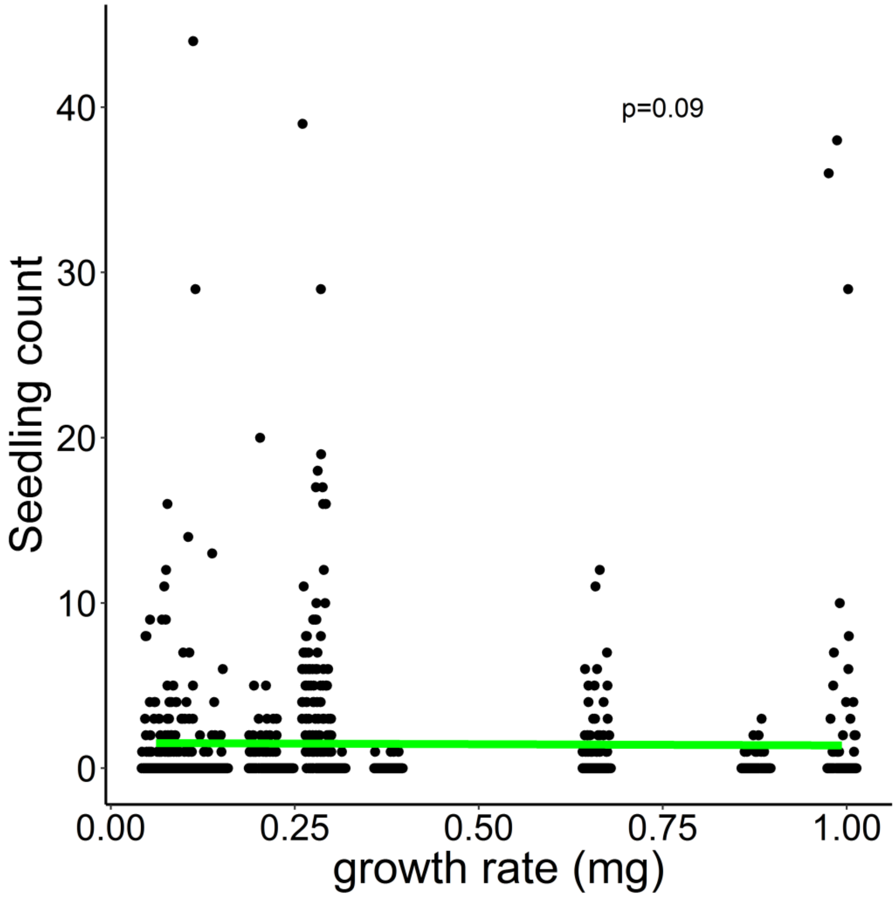

Figure 3.5. Relationship between growth rate and seedling count. Each point is the count of a species in each of the plots.

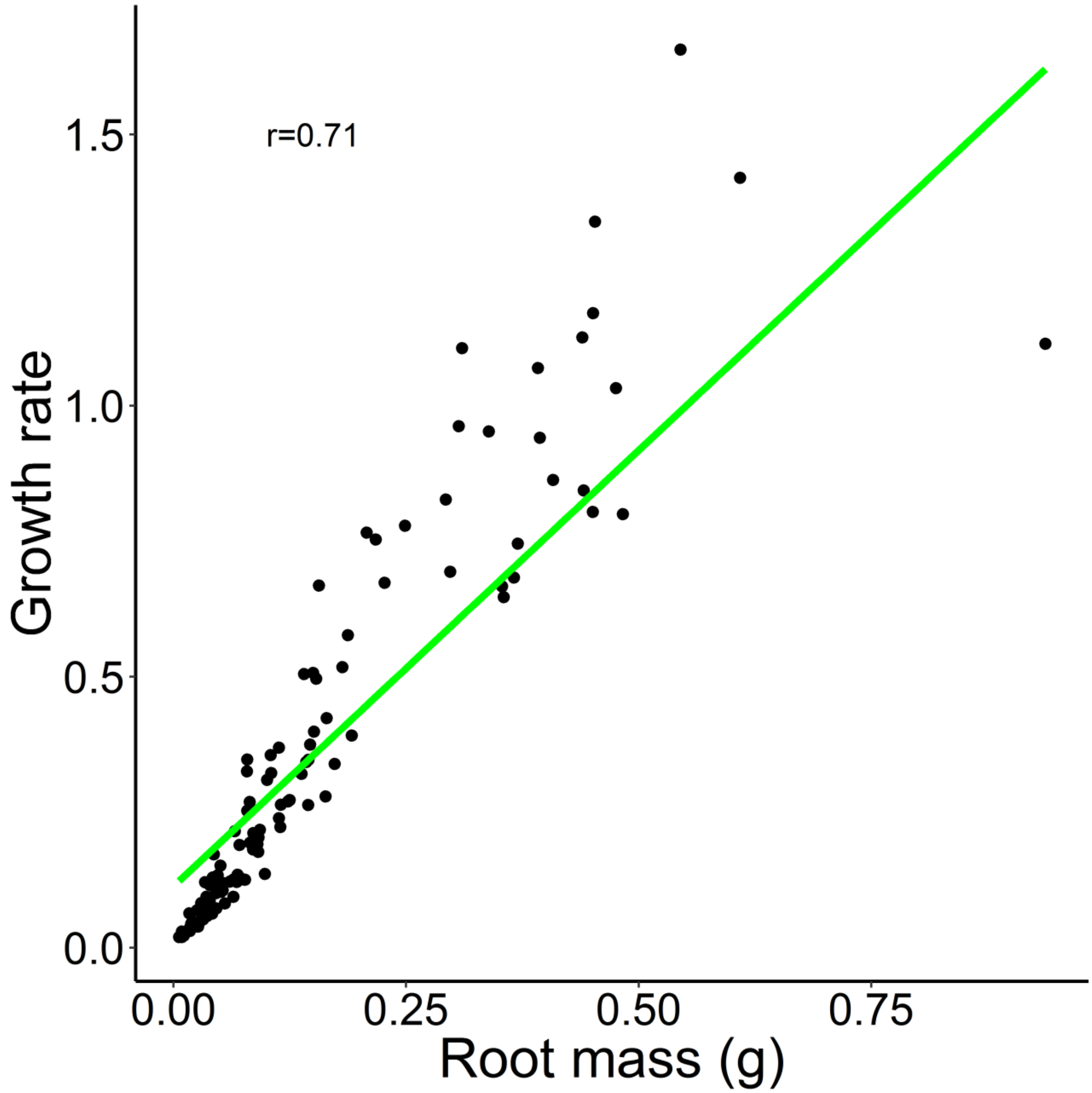

Figure 3.6. Relationship between root mass and growth rate for each of the sown species. Each point is an individual. Ten individuals of each species were included in the model. Species was included as a random effect to account for non-independence. This relationship is statistically significant at $p<0.05$.

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CHAPTER FOUR

PLANT FUNCTIONAL TRAITS AND ENVIRONMENTAL CONDITIONS SHAPE COMMUNITY ASSEMBLY AND ECOSYSTEM FUNCTION DURING RESTORATION

Abstract

1. Recovering biological diversity and ecosystem functioning are primary objectives of ecological restoration, yet these outcomes are often unpredictable. Assessments based on functional traits may help with interpreting variability in both community composition and ecosystem functioning because of their mechanistic and generalizable nature. This promise remains poorly realized, however, because tests linking environmental conditions, functional traits, and ecosystem functioning in restoration are rare.
2. Here, we provide such a test through what is to our knowledge the first empirical application of the 'response-effect trait framework' to restoration. This framework provides a trait-based bridge between community assembly and ecosystem functioning by describing how species respond to environmental conditions based on traits and how the traits of species affect ecosystem functioning.
3. Our study took place across 29 prairies restored from former agricultural fields in southwestern Michigan. We considered how environmental conditions affect ecosystem functioning through and independently of measured functional traits. To do so, we paired field-collected trait data with data on plant community composition and measures of ecosystem functioning and used structural equation modelling to determine relationships between environmental conditions, community-weighted means of functional traits, and ecosystem functioning.
4. Environmental conditions were predictive of trait composition. Sites restored directly from tillage (as opposed to those allowed to fallow) supported taller species with larger seeds and

higher specific leaf area. Site age and fire frequency were both negatively related to specific leaf area. We also found a positive relationship between soil moisture and specific leaf area.

5. Both trait composition and environmental conditions predicted ecosystem functioning, but these relationships varied among the measured functions. Pollination mode increased and fire frequency decreased floral resource availability, seed mass had a negative effect on below-ground biomass production, and vegetative height increased decomposition rate. Soil moisture and fire frequency both increased while site age decreased above-ground biomass production, and site age and soil moisture both increased decomposition rate.
6. *Synthesis and applications.* Our results suggest that both trait composition and environmental conditions play a role in shaping ecosystem function during restoration, and the importance of each is dependent on the function of interest. Because of this, environmental heterogeneity will be necessary to promote multiple ecosystem functions across restored landscapes. A trait-based approach to restoration can aid interpretation of variable outcomes through insights into community assembly and ecosystem functioning.

Introduction

Human land uses have modified a large proportion of natural ecosystems, causing a loss of biodiversity and alterations to the biological, geochemical, and physical processes that comprise the functioning of ecosystems (Foley *et al.* 2005; Cardinale *et al.* 2012; Haddad *et al.* 2015). In response, ecological restoration – active reinstatement of biological communities and ecosystem functionality – has been widely lauded for its potential to promote conservation success by increasing habitat area and quality (Dobson, Bradshaw, & Baker 1997; Young 2000; Hobbs & Harris 2001; Brudvig 2011; Suding 2011). Yet, the notorious unpredictability of restoration outcomes challenges the potential success of restoration (Suding 2011). Promoting more predictable outcomes, in terms of biodiversity and ecosystem functioning, is a major goal of restoration ecology (Choi 2007; Rey Benayas *et al.* 2009;

Matthews & Spyreas 2010). Considering the mechanisms by which communities assemble and thereby determine ecosystem functioning during restoration would provide insights into restoration outcomes, more predictable success, and transferability of findings among restoration efforts (Hobbs & Norton 1996; Palmer, Ambrose, & Poff 1997; Brudvig 2011; Montoya, Rogers, & Memmott 2012).

Functional trait-based approaches may be useful for understanding both community assembly and ecosystem functioning during restoration. Restoration ecology has typically focused on reinstating particular sets of species (Brudvig 2011) and this focus on taxonomic composition may limit generalization between restorations (Palmer, Ambrose, & Poff 1997; Temperton *et al*. 2004). Traits may provide insights into community assembly mechanisms to move beyond this idiosyncrasy. That is, a better understanding of how traits vary among species may predict how their dispersal, establishment, and persistence affect distribution and abundance among sites that vary in abiotic and biotic conditions (Weiher *et al.* 1999; McGill *et al.* 2006; Kraft, Valencia, & Ackerly 2008). Species' functional traits are also related to ecosystem functioning (Díaz & Cabido 2001; Lavorel & Garnier 2002), and because of this, functional trait-based approaches may shed light on a second major goal of restoration: understanding the functioning of ecosystems and how this is related to the diversity and composition of communities (Tilman, Isbell, & Cowles 2014). Thus, functional traits hold great promise for interpreting, predicting, and linking the assembly and functioning of communities and ecosystems.

The 'response-effect trait framework' integrates functional traits and restoration by incorporating two ideas: (1) community assembly is mediated by how functional traits respond to environmental conditions (response traits), and (2) ecosystem functioning is influenced by the trait composition of the community (effect traits) (Lavorel & Garnier 2002; Suding *et al.* 2008). Response and effect traits may be independent, correlated to one another, or one-and-the-same (i.e. the same trait responds to environmental conditions and determines function), depending on the assembly mechanism and function of interest (Lavorel & Garnier 2002). Correlations between traits have often been considered at the level of the individual in the context of life-history trade-offs (Westoby 1998; Weiher *et al.* 1999), but traits may also be correlated at the community level if suites of species possessing similar functional traits respond to the same assembly processes. For example, plant height and specific leaf area may be uncorrelated within species, but if both traits respond to a site level factor, such as nutrient availability, there may be a correlation in site level averages of these traits. Understanding the correlations or trade-offs among functional traits at both within-species and community levels is important for linking the processes that determine composition and function. Finally, site-to-site variation in environmental conditions - either modified by or independent of restoration actions - might also affect ecosystem functioning through processes not mediated by functional traits (Fig. 1). In spite of its promise for interpreting restoration outcomes and linking environmental conditions (including those manipulated through restoration), community assembly, and ecosystem functioning (Perring *et al.* 2015), no tests, to our knowledge, have evaluated the response-effect trait framework in restoration. Instead, restoration ecology has generally focused on how environmental conditions determine species composition or diversity and diversity-ecosystem function relationships independently (Montoya, Rogers, & Memmott 2012).

Here, we evaluate the trait response-effect framework within tallgrass prairies in southwestern Michigan, which have been restored by sowing native prairie seeds onto former agricultural lands. We employ structural equation modelling (SEM; Grace 2006) to consider the relationships among site conditions and actions taken during restoration, plant functional trait composition, and aspects of ecosystem functioning within these sites. We address three questions: (1) In what ways do environmental conditions affect plant functional trait composition? (2) What are the relationships between environmental conditions and ecosystem functioning and how are these mediated through plant functional traits? (3) Are response and effect traits correlated, uncorrelated, or one-and-the-same, and what insights do these relationships provide for interpreting the response-effect trait framework?

Methods

Study system

We addressed these questions within a set of 29 tallgrass prairies in southwestern Michigan, restored from former agricultural fields through seed sowing. Tallgrass prairie was once a dominant ecosystem across much of central North America, but this area has been reduced to less than 0.1% due to conversion to agriculture and other human land uses (Samson & Knopf 1994). Today, tallgrass prairie restorations are typically initiated through sowing seeds of native prairie plants onto former agricultural lands and, subsequently, the resulting grasslands are managed with prescribed fire and other approaches (Packard & Mutel 1997).

The 29 sites were located across four counties and ranged in size from <1 to >38 hectares and were 5 to 9 years old at the time of sampling. Sites were managed with prescribed fire and were burned 0-4 times. We expected fire to affect plant communities through species' traits by promoting species with fire adaptations, such as having low specific leaf area to conserve nutrients (Cornelissen *et al.* 2003; Cavender-Bares & Reich 2012). Sites varied in their land-use history. After cessation of row-crop agriculture, some sites were immediately restored, while others were managed for hay, or allowed to fallow for one or more years before being restored. Previous land use influences plant community composition (Grman, Bassett, & Brudvig 2013) and likely alters trait composition. The landscape surrounding each site also varied. We analysed the surrounding landscape using ArcGIS, to calculate the total amount of the landscape covered by forest, grassland, wetland, agriculture, or urban area within a 500m radius (9.3.1, ESRI, Redlands, CA, USA; Grman, Bassett, & Brudvig 2014). The surrounding landscape can influence composition of the plant community based on which species are able to disperse from different landscape types and through trophic interactions.

Field data collection

We determined plant species composition and abundance (% cover) within ten 1x1 m plots at each site along a 45 m transect during August 2013. We took eight 3 cm^2 by 20 cm deep soil cores around each plot and combined them to form a composite sample for each site which we analysed for soil organic matter, soil texture (sand, silt, and clay content), Mehlich-III phosphorus, Bray-II phosphorus, and pH (Brookside Laboratories, New Knoxville, OH, USA). Separately, we assessed soil water holding capacity at the plot level by calculating the proportion of oven dried weight to saturated wet weight and used site means for analysis (Brudvig & Damschen 2011). We expected these soil components to influence trait composition based on species nutrient uptake strategies and drought stress capabilities.

We also measured six ecosystem functions at each site: aboveground biomass production, belowground biomass production, decomposition rate, floral resource availability, and two aspects of trophic dynamics: seed predation and arthropod predation. We measured aboveground biomass production by clipping all plant material at the end of the 2013 growing season in each 1x1 m plot. We sorted samples to remove litter and oven dried at 65°C for at least 48 hours before weighing. To measure belowground biomass, we took 3 cm^2 by 20 cm deep soil cores from the corner of each plot at the end of the growing season. We passed soil cores through a 2 mm sieve to collect all roots which were then washed and dried at 65°C for 48 hours before weighing. We measured decomposition rate adjacent to each 1x1 m plot by placing 3.80±0.01 g of cellulosic fibre paper inside a sealed 15.5 x 15.5 cm mesh bag (mesh size 2 mm^2) at the soil surface, beneath the litter layer. We collected mesh bags after 108-123 days and dried at 65°C for 48 hours before weighing. We calculated decomposition rate by subtracting final mass from starting mass and dividing by the time they remained in the field. We measured floral resource availability by estimating the percent cover of showy flowers likely pollinated by animals within each 1x1 m plot in June, July, and September 2013. We calculated total floral cover by summing across all three sampling periods. We measured seed predation, which can have important bearing on seedling recruitment during restoration (Germain *et al.* 2013), by placing 20 seeds per species for each of four prairie species common across our sites (*Sorghastrum nutans, Desmodium canadense, Monarda fistulosa*, and *Rudbeckia hirta*) within 12 x 12 x 5.5 cm plastic containers with two 6.5 x 4.5 cm openings cut from adjacent sides of each container to allow access to arthropod and mammalian seed predators. Because we covered containers to prevent seed loss during rainstorms, this design excluded birds that may also function as seed predators in this system (Howe & Brown 1999). We placed seeds on a small amount of sand within each container to mimic soil surface conditions. We placed one container at ground level adjacent to each plot and collected after 13 days. We calculated seed predation rate as the total number of seeds removed from each trap. Finally, we measured arthropod predation rate by securing four wax worms (*Galleria mellonella*) to a petri dish and then covering worms with a small amount of sand to reduce desiccation but allow visibility. We placed the petri dishes at ground level adjacent to each plot and covered them with a wire cage, with 1.27 cm wide holes, to prevent predation from birds and mammals, owing to concerns of uniformly high predation. After 24 hours we counted the number of wax worms removed from each plate by arthropod predators.

Trait collection

We collected trait data for species that were present during surveys using standard methods (Pérez-Harguindeguy *et al.* 2013). We focused on four traits - vegetative height, pollination mode, specific leaf area (SLA), and seed mass - because these are thought to affect community assembly through the processes of dispersal, establishment, and persistence and/or are related to the functions we quantified (Weiher *et al.* 1999; Díaz & Cabido 2001). We obtained most trait data from individuals at one of our 29 sites. While we recognize the important role that intraspecific trait variation can play in community assembly (Jung *et al.* 2010*;* Laughlin *et al.* 2012), it was infeasible to meaningfully quantify intraspecific variation across the 170 species in our dataset. We collected traits from haphazardlyselected healthy, flowering adults in full sun (Cornelissen *et al.* 2003), located at least 10 m away from a site edge. Vegetative height is related to a species' competitive ability with taller species better adapted to compete for light (Weiher *et al.* 1999). We measured vegetative height as the distance between the ground and highest photosynthetic structure on 20 individuals. Specific leaf area (SLA) is also related to competitive ability, as species with low SLA are better competitors for limiting resources such as nitrogen (Weiher *et al.* 1999). SLA also relates to growth rate and stress tolerance with faster growing and less stress tolerant species having higher SLA (Wright *et al.* 2004). We measured SLA by collecting 2 leaves from each of 10 individuals. We kept leaves turgid and stored on ice for <10 hours until area was determined with a leaf area scanner. We then dried leaves at 65°C for 48 hours before weighing. We calculated SLA as leaf area divided by dry mass. Seed mass is related to dispersal and establishment, with smaller-seeded species producing more seeds per reproductive effort, increasing the chance of dispersal; while species with larger seeds are more likely to establish in competitive environments (Westoby 1998). Smaller seeded species are also more likely to form persistent seed banks (Thompson & Grime, 1979) allowing them to establish after disturbance. We determined seed mass by taking the average of at least 50 seeds for each species dried at 80°C for 48 hours before weighing. When necessary, we supplemented seed mass data from the KEW seed information database (Royal Botanic Gardens Kew, 2016). Pollination mode is related to whether or not a species produces flowers meant to attract pollinators. We determined pollination mode by classifying whether or not each species produces showy flowers likely to be attractive to pollinators. Because trait data were missing only for some uncommon species and our trait analyses were weighted by species abundances (see below), missing trait data likely had little impact on our results. In sum, across traits, we acquired vegetative height, and SLA trait data for species representing 90% of abundance in our surveys and pollination mode on 100% of species; we collected 78% of seed mass data in the field and 17% from Kew.

Analysis

We conducted analyses in R v.3.0.2 (R Development Core Team 2013). We first calculated community weighted means (CWM) for each functional trait at each site. We did this by weighting the trait value of each species by its total percent cover at each site (summed across plots) to calculate a mean value for each trait at each site. Because of correlations among soil variables and among landscape context variables (Grman, Bassett, & Brudvig 2013), we used principle components analysis (PCA) to create one variable describing soil conditions and one describing landscape context. The soil PCA included soil organic matter, soil texture (sand, silt, and clay content), Mehlich-III phosphorus, Bray-II phosphorus, pH, and water holding capacity. The first PC axis described 56% of variation in soil variables and was positively related to silt, clay, soil organic matter, pH, and water holding capacity and negatively related to sand and both measures of phosphorus. The landscape context PCA included the total amount of land covered by agriculture, forest, wetland, grassland, or development. The first PC axis described 59% of variation in landscape variables and was positively related to forest, grassland, and wetland cover and negatively related to agriculture and development. Finally, we logit transformed the floral resource availability variable to meet normality assumptions (Warton & Hui 2011).

We then developed structural equation models (SEM) using the Lavaan package in R (Rosseel 2012) based on hypothesized relationships between environmental conditions, functional traits, and ecosystem functions (see Appendix S1). SEM is a useful tool for understanding the direct and indirect effects of predictors in complex multivariate systems (Grace *et al.* 2012). To test question 1 and determine how traits responded to the environmental conditions, we predicted CWM trait values for vegetative height, SLA, and seed mass with site age, soil moisture (first soil PC axis), fire return interval, landscape context (first landscape PC axis), and land-use history. To test question 2 we predicted each ecosystem function based on CWM traits and the environmental conditions, using a separate model for each ecosystem function: aboveground biomass production, belowground biomass production, decomposition rate, floral resource availability, seed predation rates, and arthropod predation rates. We allowed all environmental conditions to covary with each other, and we also allowed all CWM trait means to covary with one another. We expected these covariances because of un-modelled common causes (i.e. environmental conditions within the same site or functional traits on the same species). We examined modification indices to determine whether there were paths missing from the models that significantly improved model fit based on the single-degree-of-freedom chi-square criterion of 3.84 (equivalent to $P<0.05$) (Grace 2006). We added paths that met this criterion and were biologically plausible. We tested for deviation from multivariate normality using the psych package in R (Revelle 2016). Only floral resource availability had significant kurtosis. For this model we calculated Sartorra-Bentler adjusted χ^2. All SEM meta-models are shown in Figs.4.5-4.10.

To test question 3 and address possible correlations among response and effect traits, we used the Hmisc package in R to test for significant Pearson's correlations between all pairwise CWM trait values and all functional traits at the species level (Harrell 2014).

Results

The SEMs fit the data well (minimum P=0.40 for χ^2 goodness of fit; P> 0.05 indicates good fit; Grace 2006) and accounted for differing amounts of variation in ecosystem function (R^2= 0.09–0.46). All path coefficients reported below (r) have been standardized, so their values can be compared to assess their relative effect sizes.

Community assembly

SEMs for each of the six ecosystem functions had the same community assembly paths; i.e., those between environmental conditions and trait CWMs (Fig. 4.2). Only land-use history explained variation in CWM seed mass (R^2=0.17), where seed mass was higher on sites that were restored directly from tillage (P=0.03, r=0.39). Similarly, only land-use history explained vegetative height (R^2=0.23), with higher values on sites restored directly from tillage (P =0.01, r=0.45). Vegetative height was slightly higher on sites with higher soil moisture, but this relationship was only marginally significant (*P* =0.064, r=0.25). Finally, SLA was explained by fire frequency, land-use history, site age, and soil moisture (R^2=0.42). Older sites or those that burned more frequently had species with lower SLA (*P* =0.02, r=-0.34; *P* =0.02, r=-0.37). Sites restored directly from tillage contained species with higher SLA (*P* =0.002, r=0.49). Drier sites had species with higher SLA (*P* =0.04, r=0.30).

Ecosystem Functioning

Environmental conditions influenced ecosystem functioning, both directly and indirectly through their influence on traits. Below we report the total standardized effect (TSE) or the sum of all direct and indirect standardized path coefficients between a predictor and response variable. Subsequently, we report the proportion of the TSE explained by the direct relationship between environmental conditions and each ecosystem function and the proportion mediated by functional traits.

Floral resources were influenced by trait composition and environmental conditions (Fig. 4.2.a, R^2=0.32). Communities supporting more animal-pollinated species produced more floral resources (*P* =0.002, r=0.53). There was a negative TSE of fire frequency on floral resource availability (Fig. 4.3, TSE=-0.19). This effect was largely driven by a direct negative effect of fire on floral resources (*P* =0.05, r=-0.31). There was also a negative TSE of soil moisture on floral resource availability (TSE=-0.2), largely due to a marginally significant direct effect of soil moisture on floral resource availability as drier sites had higher floral resource availability (*P* =0.08, r=-0.29).

Aboveground biomass production was influenced by environmental conditions, but not traits (Fig. 4.2.b, R^2=0.41). There was a positive effect of fire frequency on biomass production (Fig. 4.3, TSE=0.29), largely due to a direct positive effect of fire on biomass production (*P* =0.04, r=0.29). There was also a positive TSE of soil moisture on biomass production (TSE=0.44), resulting from a direct effect of soil moisture on biomass production. Aboveground biomass was greater on wetter sites (*P* =0.01, r=0.39). Modification indices suggested including a path between site age and biomass; the negative effect (TSE=-0.32) was due to a direct relationship where older sites produced less aboveground biomass (*P* =0.025; r=-0.33).

Belowground biomass production was influenced by trait composition, but not directly by environmental conditions (Fig. 4.2.c, R^2=0.28). A negative effect of land-use history on belowground biomass (Fig. 4.3, TSE=-0.14) was largely related to a small indirect effect with sites being restored directly from tillage having higher seed mass and in turn less belowground biomass (*P* =0.02, r=-0.50). Modification indices suggested including the path between seed mass and belowground biomass. This path is likely due to seed mass being correlated with an unmeasured trait that influences belowground biomass.

Decomposition rate was influenced by both trait composition and environmental conditions (Fig. 4.2.d, R^2=0.44). Decomposition rate increased with site age (Fig. 4.3, TSE=0.42) because of a direct effect, with older sites having higher decomposition rates (*P* =0.004, r=0.40). Decomposition also increased with soil moisture (TSE=0.38) because of a direct effect, where wetter sites had higher decomposition (*P* =0.03, r=0.31), and an indirect effect, where wetter sites had taller species and decomposition rate was faster within taller communities (*P* =0.03, r=0.31).

Arthropod predation was not influenced by trait composition or environmental conditions (no significant relationships; Fig. 4.2.e, R^2=0.16). However, arthropod predation did increase with site age (figure 4.3, TSE=0.30) because of a marginally-significant (*P* =0.1) direct effect where older sites had more predation (r=0.29).

Seed predation rate was weakly influenced by environmental conditions (Fig. 4.2.f, R^2=0.09), but we found no evidence for an influence of trait composition. Seed predation varied with landscape context (Fig. 4.3, TSE=0.31) because of a marginally-significant (*P* =0.09) direct effect. Sites surrounded by forest and grasslands had higher seed predation rates than sites surrounded by developed and agricultural areas (r=0.31).

Trait correlations

We found varying degrees of correlation between CWM trait values across our sites (Fig. 4.4). Sites with more cover of tall species had less cover of animal-pollinated species (r=-0.40, *P* =0.03) and greater seed mass (r=0.65, *P* =0.0001). Sites with more animal-pollinated species had higher SLA (r=0.41, *P* =0.03). We found that correlations between traits occurred primarily because of community level processes at our sites and not because of correlations among traits at the species level, as we found no significant correlations between traits at the species level (Fig. 4.11).

Discussion

Understanding how ecological communities assemble and how species assemblages determine ecosystem functioning are major goals of ecology broadly and restoration ecology specifically. Here, we provide what is, to our knowledge, the first application of the response-effect trait framework to restoration, integrating these two concepts (Lavorel & Garnier 2002). Ecological theory suggests that interpreting restoration through the lens of trait-based approaches to community assembly (Weiher *et al.* 2011) and ecosystem functioning (Diaz & Cabido 2001) will confer greater predictability and more generalizable outcomes (Suding 2008). Real-world tests of these ideas are important but rare (Cardinale *et al.* 2012). By providing such a test, our work leads to four key insights. First, by applying a trait response-effect framework, we show the relationships among environmental conditions, plant functional traits, and ecosystem functioning. Second, prairie communities assembled based on how traits responded to environmental conditions, including those influenced by restoration. Third, traits and environmental conditions together influenced ecosystem functioning, yet these relationships varied among functions and no one environmental condition or set of traits impacted all functions. Finally, we illustrated how functional traits are correlated across sites, which may have important implications for connecting community assembly and the provisioning of ecosystem function. Together, these results demonstrate the utility of applying the response-effect framework to restoration.

Our models did a good job of explaining community assembly, relating environmental conditions to trait composition across sites, and providing insights into mechanisms of assembly. For example, sites that were burned more frequently supported a community with lower SLA, likely because fire clears litter and volatilizes nutrients which reduced competition for light and increased nutrient competition (Knapp & Seastedt 1986; Cavender-Bares & Reich 2012). Species with lower SLA are considered poor light competitors but may be better competitors for limiting soil nutrients (Grime 1977; Westoby 1998). Additionally, land-use history - whether or not a site was allowed to fallow following tillage agriculture - predicted vegetative height, SLA, and seed mass. Previous land use can affect the composition of weedy species, and potentially residual soil nutrient levels, during prairie restoration from agriculture (Grman, Bassett, & Brudvig 2013). We found that sites restored directly from tillage, rather than being allowed to fallow, contained taller species with larger seeds and higher SLA. This suggests that shorter, low SLA weedy species may be important drivers of trait composition during prairie restoration either through their establishment or how they affect the establishment of other species through competition. If land-use legacy, fire disturbance, and other mechanisms of community assembly are generalizable through traits (Laughlin 2014), our community assembly findings have important bearing on how sites are selected for restoration, subsequent management decisions, and predicting restoration outcomes more broadly.

We also showed that ecosystem functions responded to both environmental conditions and traits and that no single environment or plant community maximized all functions. Consequently, variability in environmental conditions and management practices will be necessary to promote multiple ecosystem functions across a restored landscape. For example, sites with low soil moisture supported higher levels of floral resources and belowground production, but lower levels of aboveground production and decomposition (Fig. 4.3). As a result, maximizing levels of these functions will require restoring areas with both high and low soil moisture. Other studies have also shown that heterogeneous landscapes lead to variable levels of multiple ecosystem functions across a landscape (Lavorel *et al.* 2011). We recognize that the use of standardized materials across sites may have affected the relationships we observed between functional traits and this ecosystem function. For example, we observed no relationship between SLA and decomposition, yet use of site-specific leaf material might have yielded a relationship between high SLA leaf litter and high decomposition rates (Garnier *et al*. 2004). We recognize that our ability to explain variation in ecosystem functioning ranged widely (R^2=0.09 to 0.44), and were often independent of core traits used in community ecology, suggesting the need for better models (e.g., more robust trait or environmental data). Alternatively, there may be inherent variation in predictability among functions. Both non-mutually exclusive possibilities suggest the need for more tests of how traits and environmental conditions affect ecosystem functioning among sites during restoration.

Our results illustrate the utility of the response-effect trait framework by showing how the relationships between response and effect traits are important for linking environmental conditions to levels of ecosystem functions and the processes of community assembly and ecosystem functioning. We showed that this is because response and effect traits can be the same trait, traits that are correlated with one another, or uncorrelated and that this is dependent on the environmental conditions, functional traits, and ecosystem functions being measured. One example of response and effect traits being one-and-the-same in our system is vegetative height, which responded to land-use history and affected decomposition rate. There were also situations where a trait affected ecosystem function, was not directly influenced by environmental conditions, but correlated with one or more other traits that did respond to environmental conditions. For example, although land-use history did not affect pollination mode or floral resources directly, it may have done so indirectly via the correlation between pollination mode and vegetative height. The correlation between pollination mode and vegetative height is not a species-level trade-off with shorter species producing animal pollinated flowers (Fig. 4.11) but instead a site-level trade-off (Fig. 4.4). One potential explanation is that vegetative height increases with C4 grass abundance, which also causes a reduction in animal pollinated species (Fig.4.12). Dominance of C4 grasses during prairie restoration has been shown to cause strong competition for resources and the loss of forb species (Dickson & Busby 2009). Correlations between response and effect traits are important for understanding how the assembly process can indirectly influence ecosystem functioning. Situations where response and effect traits are one-and-the-same or correlated confer predictability based on relationships between assembly and functioning. In these instances, restoration practitioners may be able to choose sites with certain environmental conditions or use management techniques to alter these conditions to promote ecosystem functions of interest. However, response and effect traits can also be uncorrelated, which could limit our ability to predict functioning. For instance, we detected no effect traits that predicted seed predation, and modification indices did not suggest any other trait associations with seed predation that could be correlated with unmeasured effect traits. In such cases, we may be unable to predict levels of function based on commonly measured functional traits or the assembly mechanisms to which traits respond. It will be important for future work to determine correlations between traits that respond to environmental conditions and have an effect on ecosystem function.

Despite these complications, our results illustrate the value of the response-effect trait framework for conducting restoration. Our work informs decisions about restoration site selection and management practices within sites undergoing restoration. Certain site conditions, such as soil moisture and landscape context, cannot be easily manipulated but can have large impacts on trait composition and ecosystem functioning. Within our sites, drier sites contained species with higher SLA. These sites also produced higher floral resources but lower levels of aboveground biomass and had lower decomposition rates (Fig. 4.3). We also found that sites surround by forests and grasslands had higher seed predation rates than those surrounded by agriculture and development. In these situations, decisions about which sites to restore will be important if we have particular composition or function goals. Other environmental conditions, such as fire frequency, are also important for trait composition and ecosystem functioning and can be directly manipulated during restoration. Prescribed fire is a powerful restoration tool for shaping species composition and functioning, such as aboveground biomass production (Briggs & Knapp 1995; Spasojevic *et al.* 2010). Our results suggest an important mechanism for this process, by which increasing fire frequency decreases SLA across our sites. Increased fire frequency also alters the provisioning of ecosystem functions across our sites, decreasing floral resources and increasing aboveground biomass production (Fig. 4.3). Our results also suggest that actions taken to compensate for land-use history (such as depleting a weedy seed bank) can have major implications for trait composition and ecosystem function. Our results show that fallowing prior to restoration resulted in markedly different trait composition with lower vegetative height, SLA, and seed mass, compared to sites restored directly from tillage. This change in trait composition impacted function, with fallowed sites having more floral resources and belowground biomass but less aboveground biomass and lower rates of decomposition. Future work should consider additional functional traits that might influence community assembly and ecosystem functioning during restoration. For example, root traits, such as specific root length or rooting depth, might influence functions such as belowground biomass production.

There is a strong pragmatic need to apply ecological theory to restoration, to increase predictability and decrease idiosyncrasy between restorations (Palmer, Ambrose, & Poff 1997; Young, Chase, & Huddleston 2001; Choi 2007). Our results provide an important empirical bridge between the theory and applied utility of functional traits for interpreting how individuals respond to environmental conditions, affect interactions within and between trophic levels, and influence the ways that ecosystems function during restoration (Weiher *et al.* 1999; Lavorel *et al.* 2013; Kraft, Godoy, & Levine 2015). In turn, our work illustrates the utility of restored ecosystems for testing theory in trait-based ecology because they inherently manipulate assembly (e.g., through seed sowing) and environmental conditions that modify assembly (e.g., prescribed fire). In doing so, we illustrate how understanding relationships between environmental conditions, functional traits, and ecosystem functions can guide restoration practice to meet composition and ecosystem function goals within a restored landscape.

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Data Accessibility

Data and R code available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.2175q (Zirbel *et al.* 2017).

APPENDIX

Figures

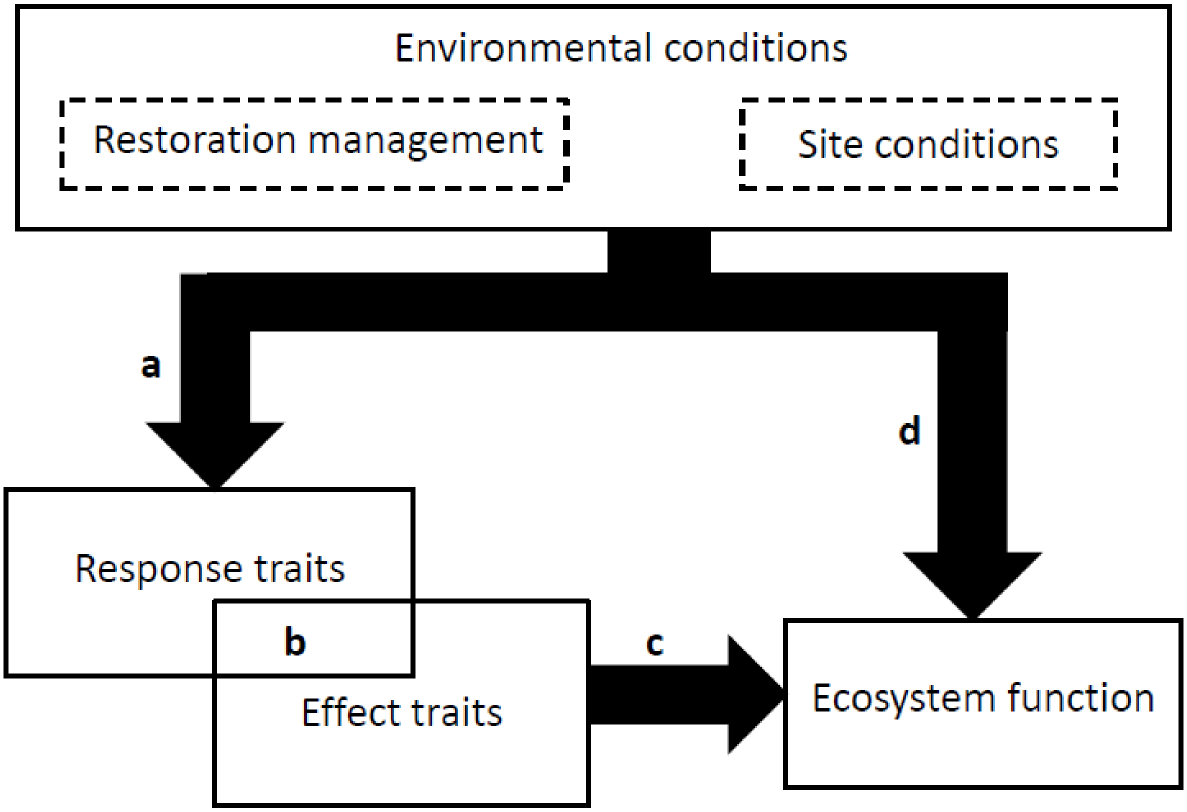

Figure 4.1. Conceptual diagram illustrating: (a) community assembly, the processes by which environmental conditions (both site conditions and restoration management) determine response trait composition. (b) The possible relationship between response and effect traits. (c) The process by which effect traits produce ecosystem function. (d) The independent effect of environmental conditions on ecosystem function, not mediated by functional traits.

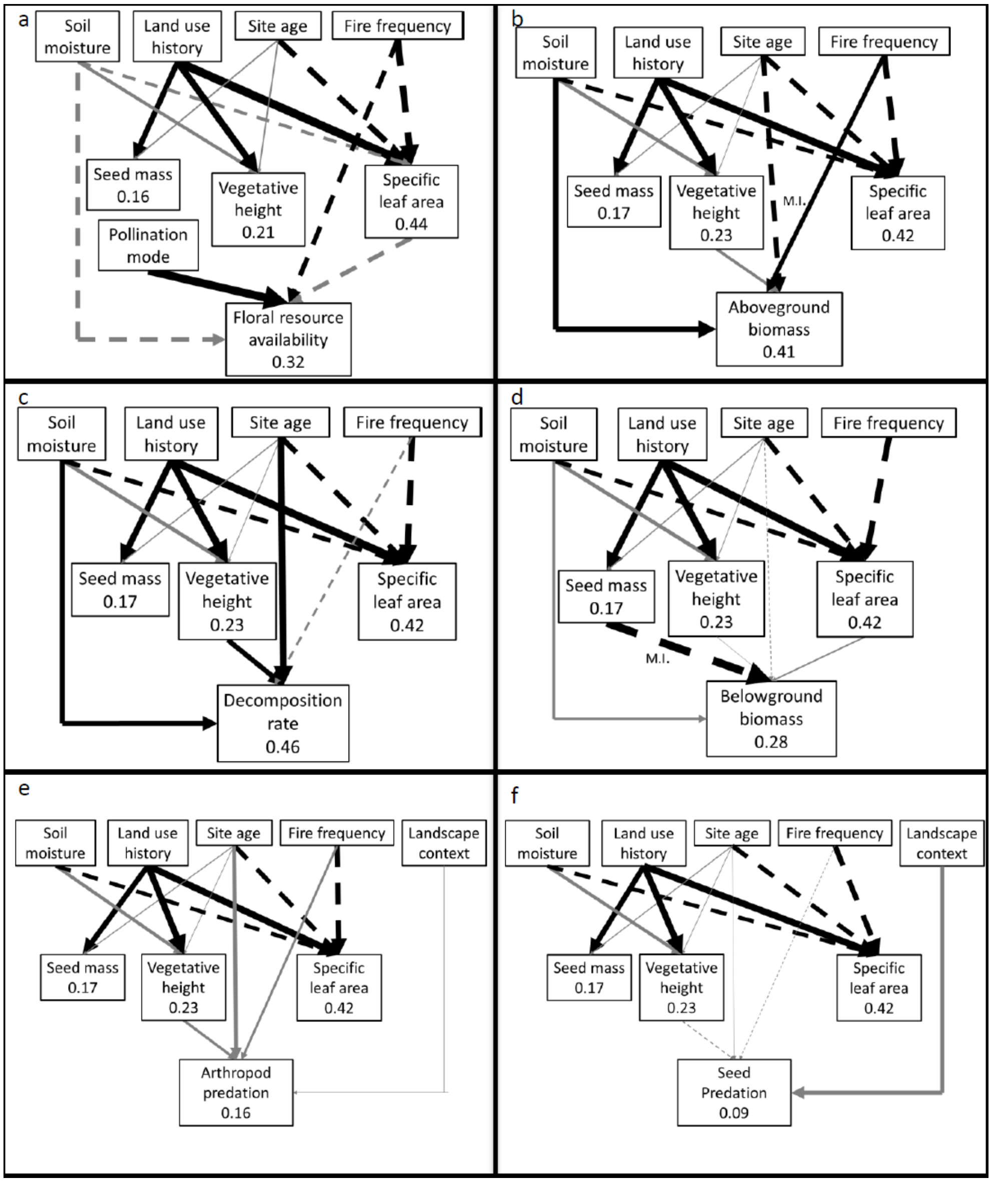

Figure 4.2. Structural equation models for each ecosystem function. Reasoning for each path is listed in the Appendix Black paths represent significant relationships ($p<0.05$). Grey paths represent non-significant relationships. Paths labelled M.I. show relationships added based on suggestions from modification indices. Solid lines represent positive relationships and dashed lines negative relationships. Paths are weighted by standardized path coefficients. Values inside of the box are the R^2 values for that response variable. All environmental conditions covary with one another as do all CWM trait values (not shown). Meta-models for each SEM are shown in Figs. 4.5-4.10.

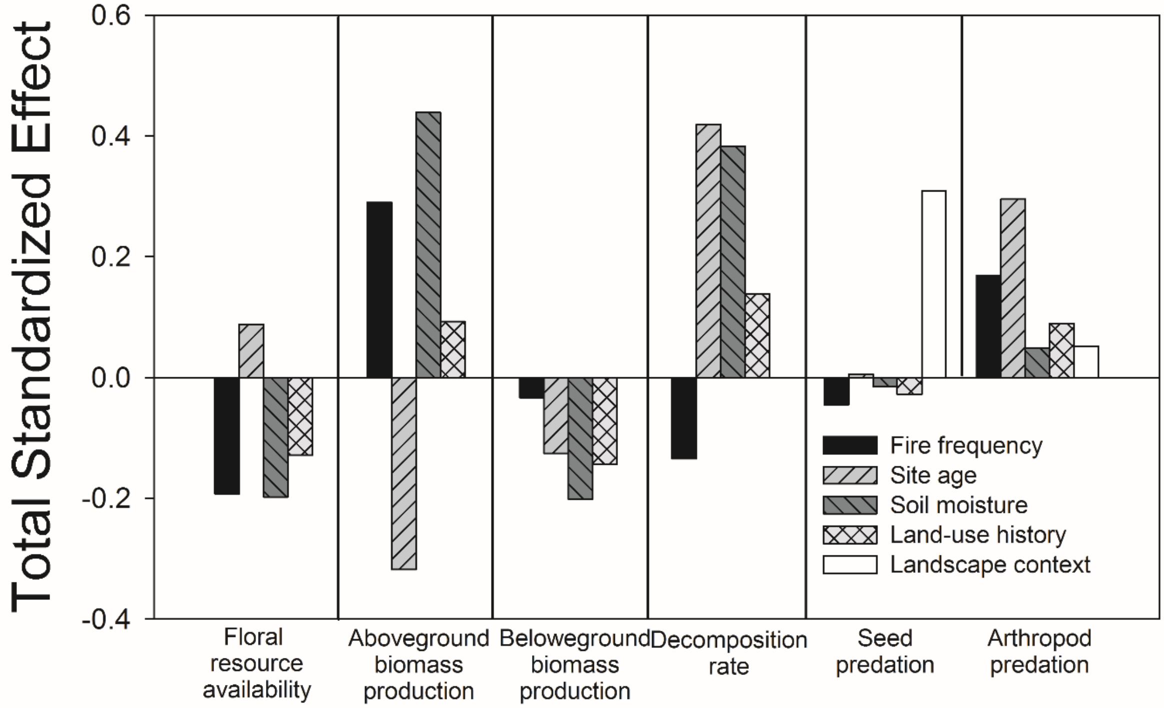

Figure 4.3. Total standardized effect of each environmental condition on each ecosystem function. Landscape context was only included in the seed predation and arthropod predation models.

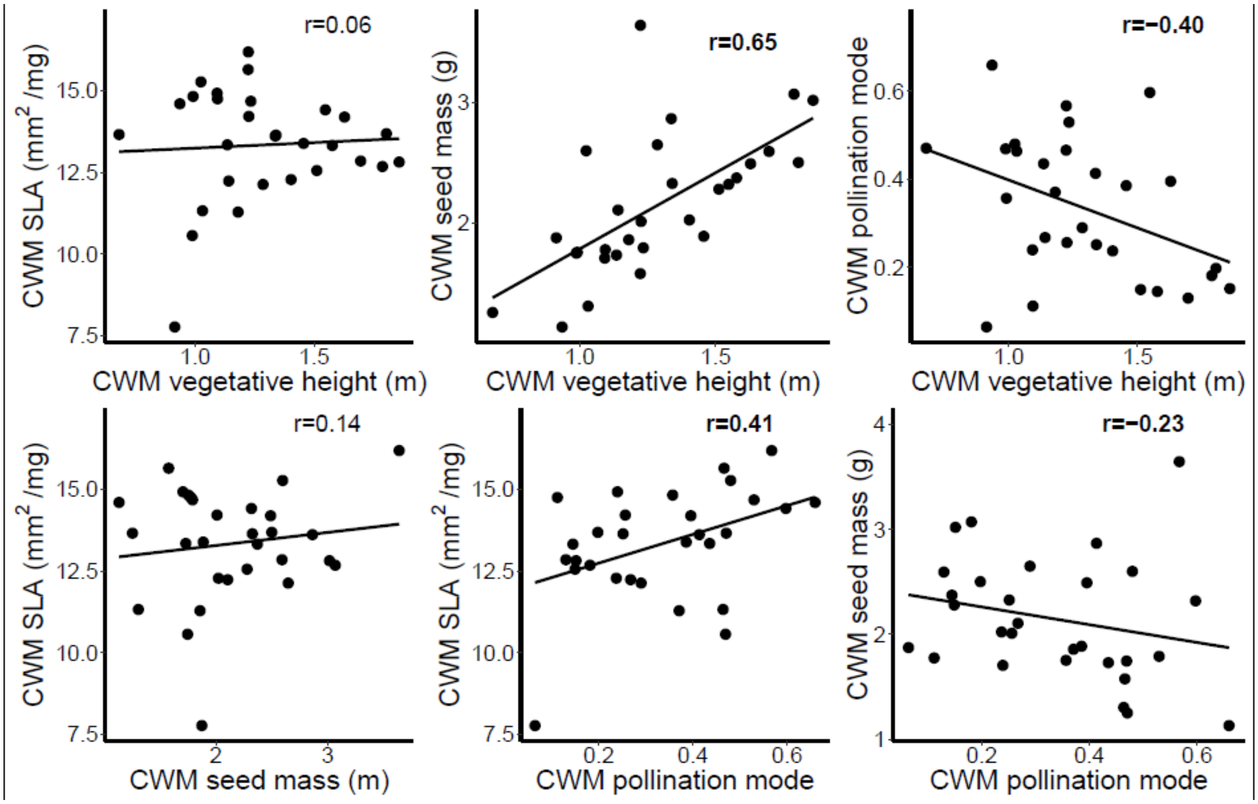

Figure 4.4. Bivariate correlations between all pairwise CWM traits. Bolded r values represent significant Pearson's correlations ($p<0.05$). Each point represents a study site. Plots of species level trait correlations are shown in Fig. 4.11.

Supplemental material

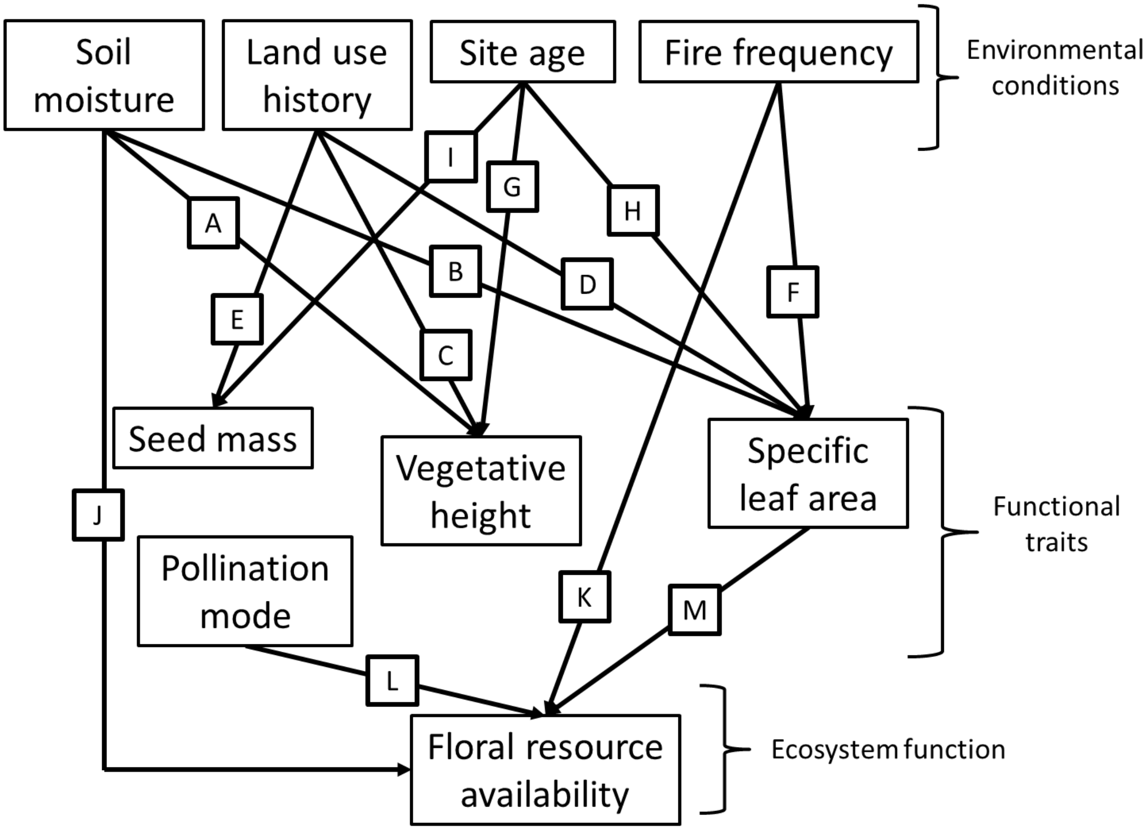

Figure 4.5. Meta-model representing the relationships between environmental conditions, functional traits, and floral resource availability. All environmental conditions covary with one another as do all CWM trait values (not shown). Letters represent hypothesized relationships.

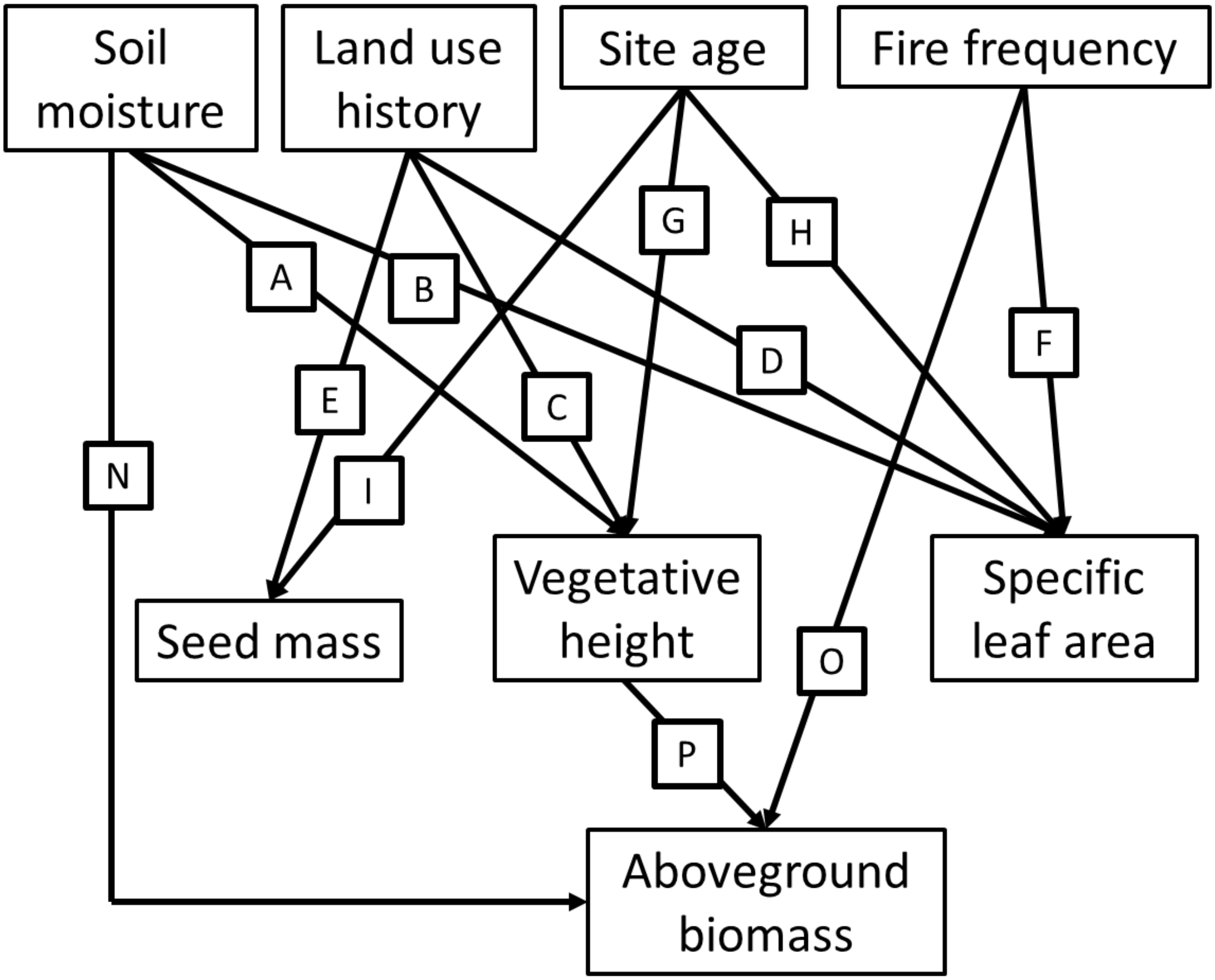

Figure 4.6. Meta-model representing the relationships between environmental conditions, functional traits, and aboveground biomass production. All environmental conditions covary with one another as do all CWM trait values (not shown). Letters represent hypothesized relationships.

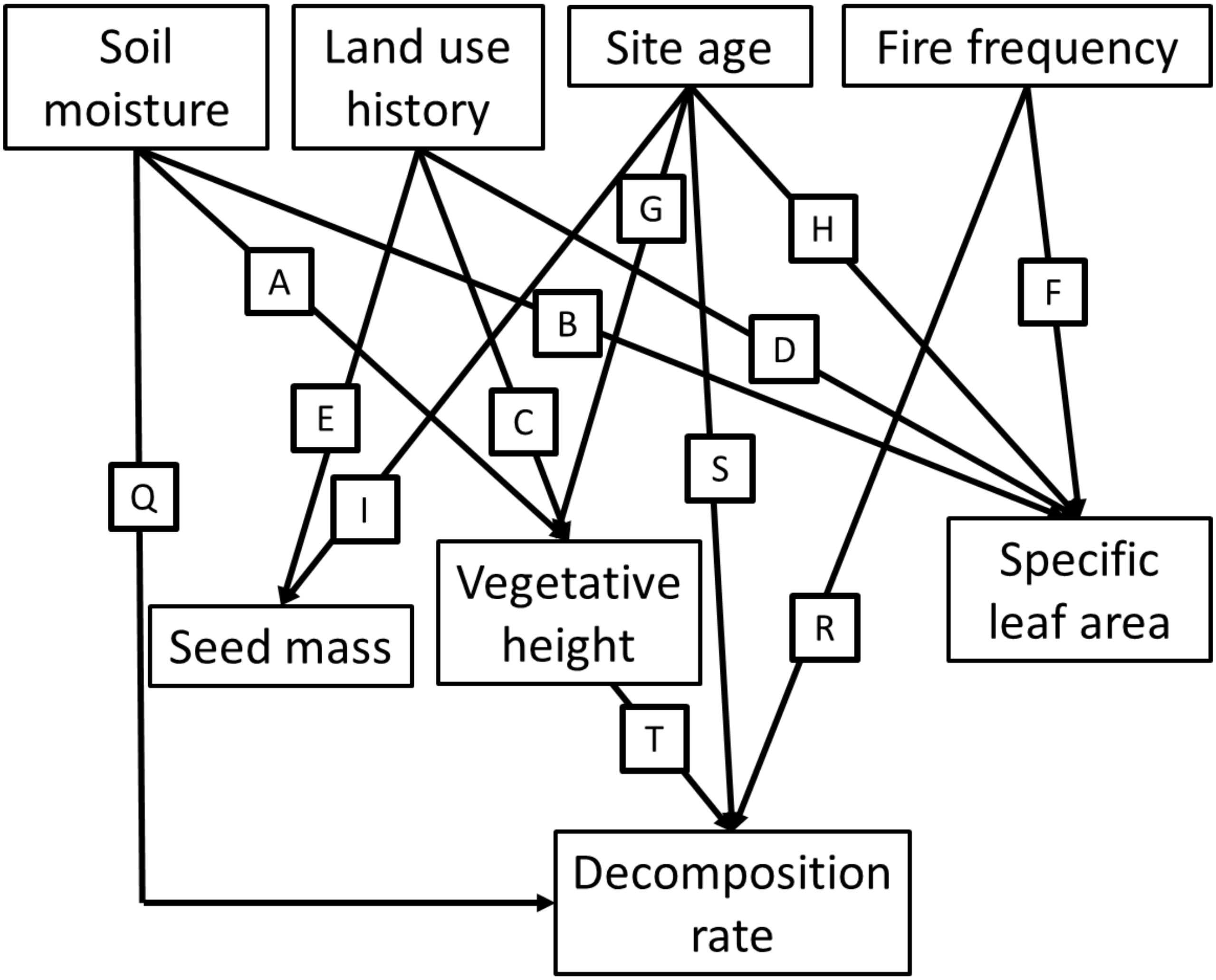

Figure 4.7. Meta-model representing the relationships between environmental conditions, functional traits, and decomposition rate. All environmental conditions covary with one another as do all CWM trait values (not shown). Letters represent hypothesized relationships.

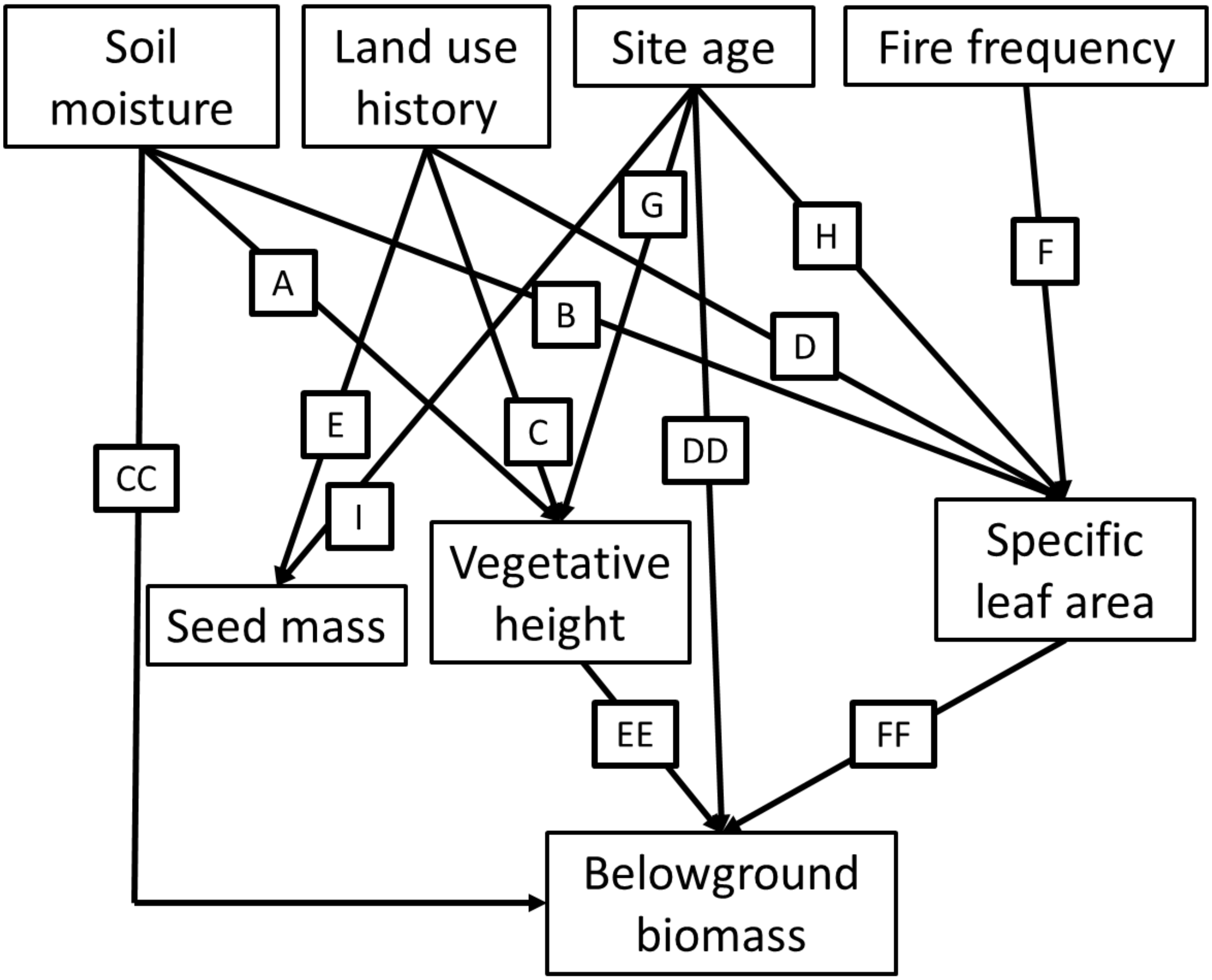

Figure 4.8. Meta-model representing the relationships between environmental conditions, functional traits, and belowground biomass production. All environmental conditions covary with one another as do all CWM trait values (not shown). Letters represent hypothesized relationships.

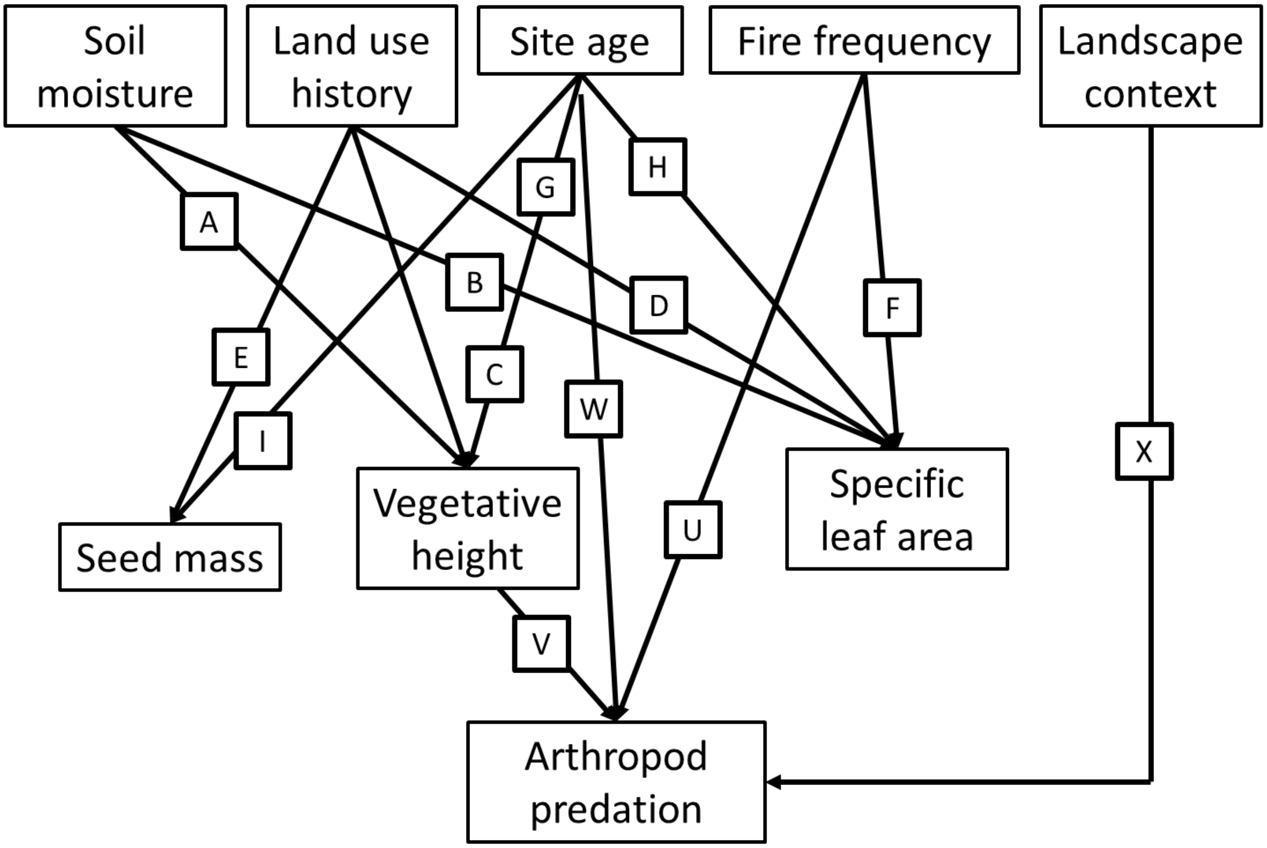

Figure 4.9. Meta-model representing the relationships between environmental conditions, functional traits, and arthropod predation. All environmental conditions covary with one another as do all CWM trait values (not shown). Letters represent hypothesized relationships.

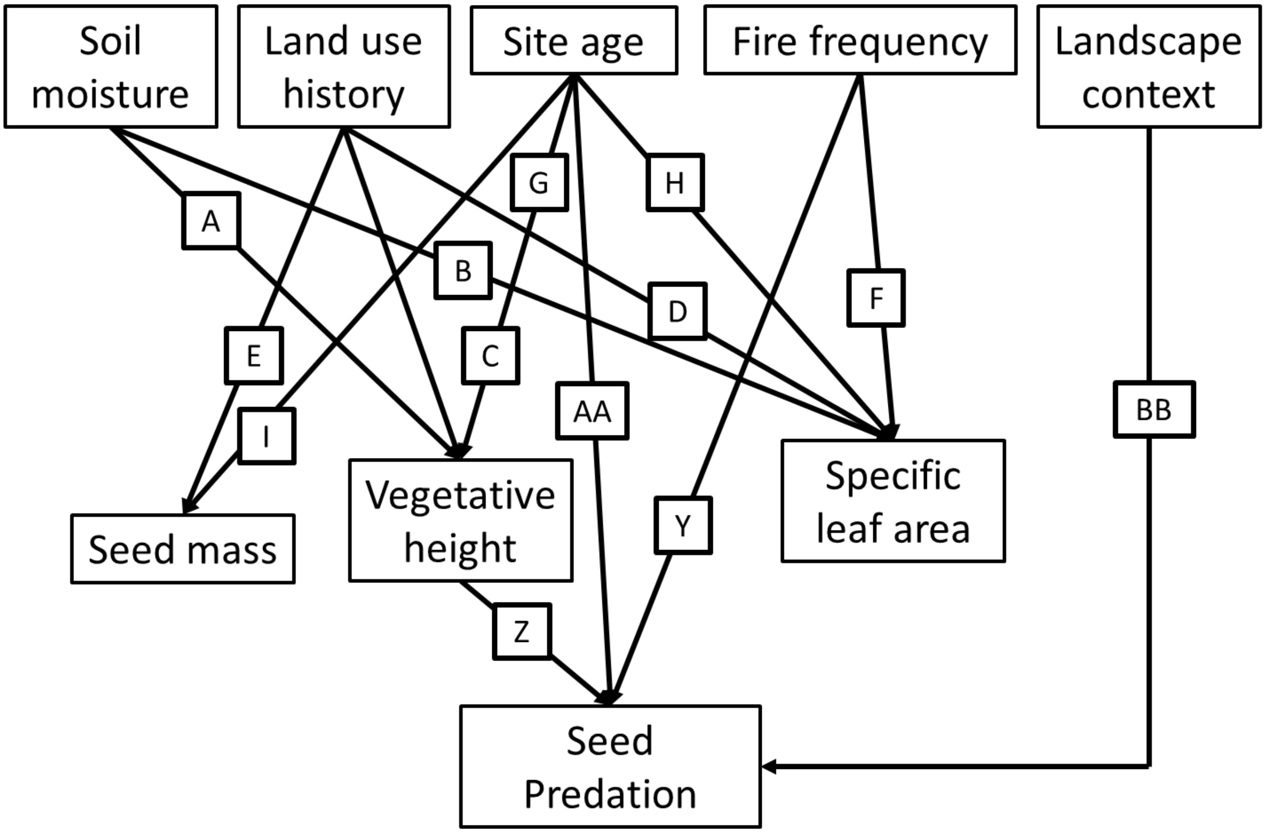

Figure 4.10. Meta-model representing the relationships between environmental conditions, functional traits, and seed predation. All environmental conditions covary with one another as do all CWM trait values (not shown). Letters represent hypothesized relationships.

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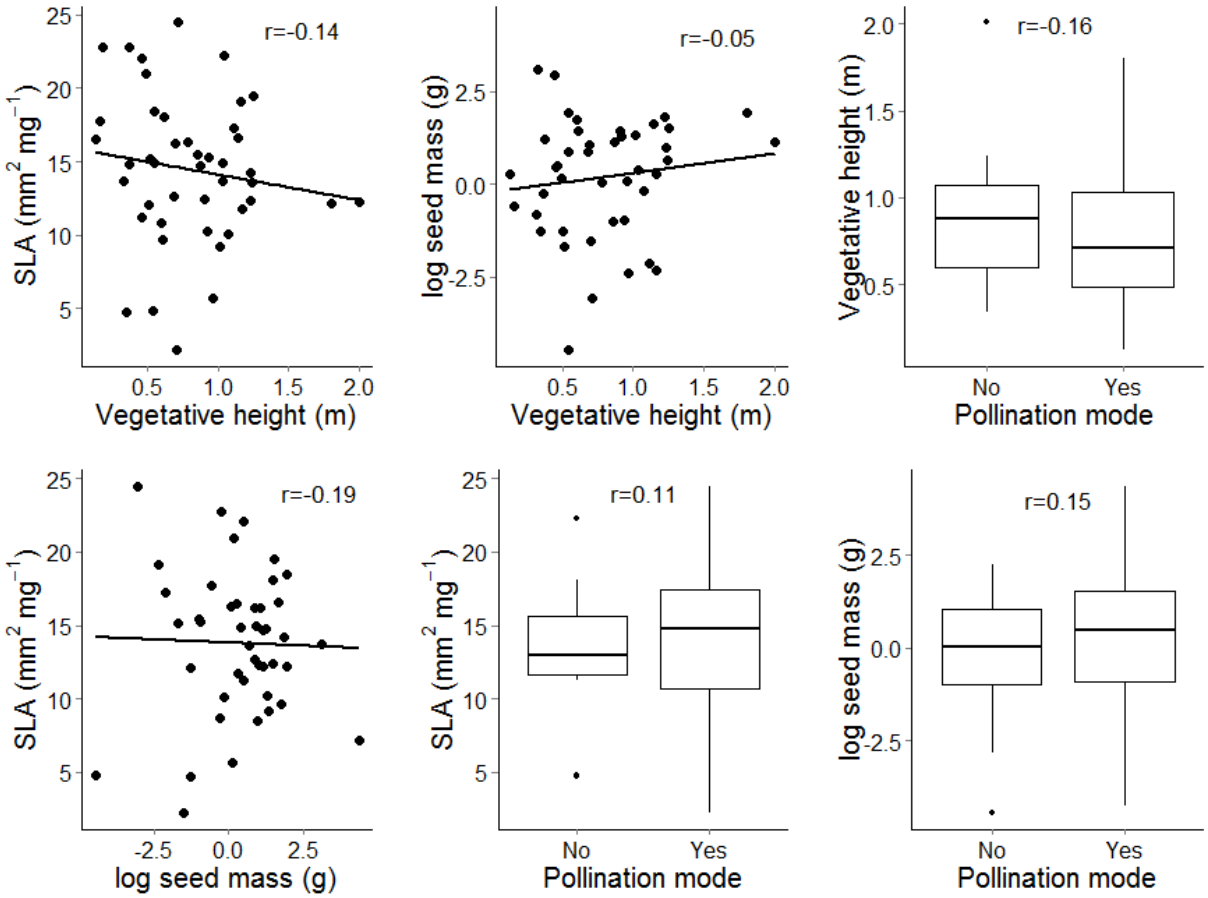

Figure 4.11. Bivariate correlations between all pairwise species traits. No r values had significant Pearson's correlations ($p<0.05$). Each point represents a species.

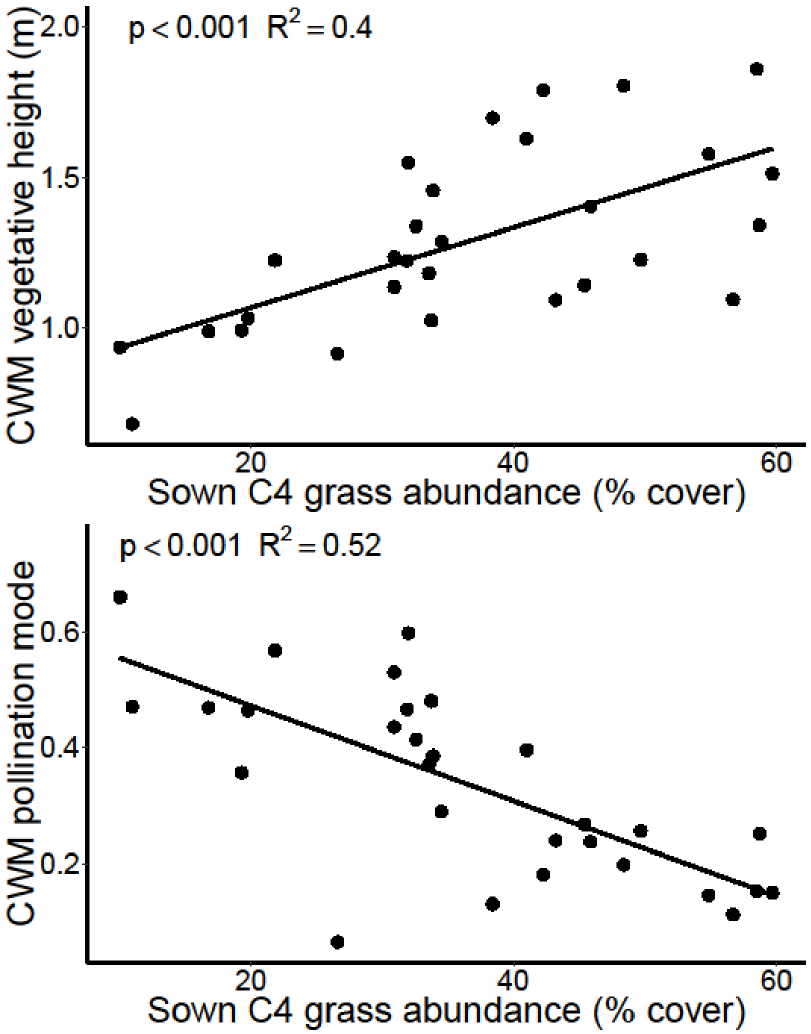

Figure 4.12. Relationships between sown C4 grass abundance and (a) CWM vegetative height and (b) CWM pollination mode. Each point represents a study site. Linear regression was used to calculate p-values and R^2 for each relationship.

Theoretical basis for the hypothesized relationships in the structural equation models. Letters correspond to the path labels in Fig. 4.5-4.10

Community assembly

A. Soil moisture →Vegetative height: Sites with wetter soils (higher silt/clay content/higher water holding capacity) will support communities comprised of species with taller vegetative height (Dickson *et al.* 2014) because taller species are better competitors under high nutrients (Gaudet & Keddy 1988; Goldberg & Landa 1991).

B. Soil moisture→SLA: Sites with wetter soils (higher silt/clay content/higher water holding capacity) will support communities comprised of species with higher SLA values (Laliberté *et al.* 2012) because species with high SLA-leaves have less conservative resource use strategies (Garnier 1992; Reich, Walters, & Ellsworth 1992).

C. Land use history→Vegetative height: Sites allowed to fallow before restoration, rather than being restored directly from tillage, will support communities comprised of species with shorter vegetative height. Sites with a land-use history of fallowing have a higher abundance of ruderal non-prairie species (Grman, Bassett, & Brudvig 2013) and ruderal species are commonly short statured (Westoby *et al.* 2002).

D. Land use history→SLA: Sites allowed to fallow before restoration, rather than being restored directly from tillage, will support communities comprised of species with higher SLA values. Sites with a land use history of fallowing have a greater abundance of ruderal non-prairie species (Grman Bassett, & Brudvig 2013) and ruderal species are commonly fast growing with, high SLA values (Knapp & Smith 2001).

E. Land use history→Seed mass: Sites allowed to fallow before restoration, rather than being restored directly from tillage, will support communities comprised of species with smaller seed masses. Land-use history can affect seed bank composition, including an increased abundance of ruderal species (Corbin & D'Antonio 2012) and ruderal species commonly have small seeds (Grime 1977).

F. Fire frequency→SLA: Sites burned more frequently will support communities comprised of species with lower SLA values. Increased fire frequency reduces competition for light and increases nutrient competition which decreases SLA (Cavender-Bares & Reich 2012).

G. Site age→Vegetative height: Older sites - those sown further in the past - will support communities comprised of species with greater vegetative height. Resource (light) competition becomes stronger with successional time (Goldberg 1990) and taller plants are better competitors for light (Gaudet & Keddy 1988).

H. Site age→SLA: Older sites - those sown further in the past - will support communities comprised of species with lower SLA values. Average SLA of the community decreases with age (Laliberté *et al.* 2012). This is likely because nutrient limitation increases during succession and species with low SLA values may have advantages under low nutrient conditions due to the ability to limit nutrient losses to herbivory (Grime 2002).

I. Site age→Seed mass: Older sites - those sown longer in the past - will support communities comprised of species with larger seed mass. Resource competition, including for light, becomes stronger over successional time (Goldberg 1990). Species with larger seed mass perform better under competition (Reader 1993; Westoby 1998) and in low light environments (Gross 1984).

Ecosystem Function

J. Soil moisture→Floral resource availability: Sites with wetter soils (higher silt/clay content/higher water holding capacity) will have greater floral cover, independent of plant community composition effects. Higher nutrient availability will allow individuals to invest more resources in flowering (Muñoz *et al.* 2005).

K. Fire frequency→Floral resource availability: Increased fire frequency will increase floral cover. The amount of floral resources decreases with time since fire (Vogel, Koford, & Debinski 2010).

L. Pollination mode→Floral resource availability: Sites supporting communities of species that produce flowers attractive to pollinators will support a greater abundance (cover) of floral resources. Planting species attractive to pollinators increases the total area covered by floral resource-provisioning flowers (Tuell *et al.* 2008).

M. SLA→Floral resource availability: Sites supporting communities of species with greater SLA values will support a lower abundance (cover) of floral resources. Species with lower SLA values have more conservative resource strategies and will put fewer resources into flowering (Grime, 1977).

N. Soil moisture→Aboveground biomass: Sites with wetter will support greater aboveground biomass, independent of plant community composition effects. Availability of soil nutrients will allow individual plants to grow larger (Borer *et al.* 2014) .

O. Fire frequency→Aboveground biomass: Sites burned more frequently will support more aboveground biomass, independent of plant community composition effects. Fire stimulates productivity in prairies by removing litter and promoting new rapid growth (Knapp & Seastedt 1986).

P. Vegetative height→Aboveground biomass: Sites supporting communities of species with greater vegetative height will produce more biomass (Butterfield & Suding 2013) .

Q. Soil moisture→Decomposition rate: Sites with wetter soils will support higher decomposition rates, independent of plant community composition effects. Soil moisture availability is related to decomposition rate (Singh & Gupta 1977).

R. Fire frequency→Decomposition rate: Sites burned more frequently will support lower decomposition rates, independent of plant community composition effects. Fire decreases soil moisture by removing litter (Briggs & Knapp 1995); soil moisture availability increases decomposition rates (Singh & Gupta, 1977).

S. Site age→Decomposition rate: Older sites - those sown longer in the past - will support higher decomposition rates, independent of plant community composition effects. Important decomposers, such as invertebrates, increase in abundance over successional time (Majer, Brennan, & Bisevac 2002).

T. Vegetative height→Decomposition rate: Sites supporting communities of species with greater vegetative height will support greater decomposition rates. Taller plants produce more shading and increase soil moisture (Gross *et al.* 2008). Higher soil moisture is related to higher decomposition rates (Singh & Gupta 1977).

U. Fire frequency→Arthropod predation: Sites burned more frequently will support lower rates of arthropod predation, independent of plant community composition effects. Fire can eliminate arthropod predators (Anderson, Leahy, & Dhillion 1989) and arthropod consumers take time to recolonize burned sites (Knight & Holt 2005).

V. Vegetative height→Arthropod predation: Sites supporting communities of species with greater vegetative height will support greater rates of arthropod predation. Arthropod diversity and abundance is greater at more productive sites with more plant biomass (Siemann 1998) .

W. Site age→Arthropod predation: Older sites- those sown longer in the past - will support greater arthropod predation, independent of plant community composition effects. Un-degraded reference sites support a greater diversity of arthropod predators than restorations or degraded sites (Majer, Brennan, & Bisevac 2002), suggesting that arthropod predator communities reassemble over time following disturbance.

X. Landscape context→Arthropod predation: Sites surrounded by forest and grasslands will support greater arthropod predation rates, independent of local plant community composition effects. Natural vegetation supports a greater abundance of arthropod predators, relative to agricultural and urban areas, which can colonize adjacent sites (Gardiner *et al.* 2009).

Y. Fire frequency→Seed predation: Sites burned more frequently will support greater rates of seed predation, independent of plant community composition effects. Frequent fire eliminates litter and increases predator movement and seed visibility (Reed, Kaufman, & Kaufman 2004). However, we also consider the alternative hypothesis that seed predation will be reduced under frequent fire because consumers recolonize burned sites slowly (Knight & Holt 2005).

Z. Vegetative height→Seed predation: Sites supporting communities of species with greater vegetative height will support greater rates of seed predation. Communities with taller, denser vegetation support more seed predators and higher rates of seed predation, than communities with short vegetation (Mittelbach & Gross 1984).

AA. Site age→Seed predation: Older sites will support greater seed predation, independent of plant community composition effects. Older sites will have more time to accumulate seed predator communities. For example, sites with a longer time since restoration support more diverse and abundant ant communities (Menke *et al.* 2015).

BB. Landscape context→Seed predation: Sites surrounded by forest and grassland will support greater rates of seed predation, independent of local plant community composition effects. These habitat types support a greater abundance of seed predators, relative to agricultural and urban areas, which can colonize adjacent sites (Farwig *et al.* 2009).

CC. Soil moisture→Belowground biomass: Sites with wetter soils will support greater root biomass, independent of plant community composition effects. Fine-root production is greater on productive sites than on unproductive sites (Nadelhoffer, Aber, & Melillo 1985).

DD. Site age→Belowground biomass: Older sites will support greater belowground biomass, independent of plant community composition effects. Older sites will have had more time to accumulate root biomass (Cairns *et al.* 1997).

EE. Vegetative height→Belowground biomass: Sites supporting communities of species with greater vegetative height will support more belowground biomass. Larger plants produce more roots (Craine *et al.* 2002).

FF. SLA→Belowground biomass: Sites supporting communities of species with lower SLA values will support more belowground biomass. Species with low SLA values invest more resources into belowground tissue production both strategies related to surviving low nutrient environments (Craine *et al.* 2002).

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CHAPTER FIVE

PLANT PHYLOGENETIC DIVERSITY AND LANDSCAPE CONTEXT ARE POSITIVELY RELATED TO ECOSYSTEM MULTIFUNCTIONALITY

Abstract

There is strong evidence for a positive relationship between biodiversity and ecosystem functioning at local spatial scales. Yet, how different aspects of biodiversity relate to suites of ecosystem functions (multifunctionality) across heterogeneous landscapes, and how the magnitude of biodiversity and environmental effects on functioning compare, remains poorly understood. We compared the relationships between plant phylogenetic, functional, and taxonomic diversity and ecosystem multifunctionality across 29 restored grasslands. Phylogenetic diversity was positively associated with multifunctionality, more strongly than other diversity measures; however, landscape composition explained five times more variation in multifunctionality than did phylogenetic diversity. Specifically, restorations surround by forests and grasslands supported higher multifunctionality than restorations within human-modified landscapes, dominated by agriculture. Specific ecosystem functions were typically more strongly correlated with environmental variables than with the metrics of diversity we examined. Our findings illustrate that both plant biodiversity and underlying environmental conditions underpin ecosystem multifunctionality in restored grasslands, Furthermore, how biodiversity is measured determines the strength and direction of the relationship with different ecosystem functions. Finally, we show that environmental variation unrelated to local biodiversity may structure functioning more than previously recognized. Landscape context, in particular, should be considered when investigating diversity-ecosystem function relationships at large spatial scales and when planning and evaluating restoration projects.

Introduction

Understanding the determinants of ecosystem function is a central goal of ecology and of strong pragmatic importance, given widespread human-caused changes in the diversity and functioning of ecosystems (Cardinale *et al.* 2012; Haddad *et al.* 2015) . In part motivated by these anthropogenic impacts, substantial attention has been paid to the relationship between biodiversity and ecosystem function (Tilman, Isbell, & Cowles 2014) . Widespread evidence exists for a positive relationship between diversity, typically measured as plant species richness, and ecosystem functioning, most often measured as plant productivity. Much of this understanding has been generated through small-scale experimental manipulations of plant species richness. However, the nature of biodiversity-ecosystem function relationships in real world systems, characterized by high environmental heterogeneity that in turn shapes patterns of biodiversity, remains unknown (Srivastava & Vellend 2005; van der Plas *et al.* 2016; Duffy, Godwin, & Cardinale 2017; Hautier *et al.* 2017) . Four key research objectives are necessary to push this area of research forward: considering 1) multifunctionality, 2) multiple aspects of biodiversity, 3) diversity function relationships within natural systems, and 4) how ecosystem functions tradeoff (Isbell *et al.* 2017) .

First, we must consider how diversity and environmental conditions jointly and independently affect multiple aspects of ecosystem function. Whereas diversity-ecosystem function studies have primarily focused on productivity as a measure of ecosystem function(Tilman, Isbell, & Cowles 2014) , a few studies have studies begun to consider ecosystem multifunctionality by evaluating the drivers of multiple different ecosystem functions concurrently(*et al.* 2010; Gamfeldt *et al.* 2013; van der Plas *et al.* 2016; Hautier *et al.* 2017) . Biodiversity should increase multifunctionality through the same mechanisms that it increases individual functions. A diversity of traits should increase any given ecosystem function (complementarity) and a diversity of species should increase the chance of the best trait for a particular function being present (selection effect) (Tilman, Isbell, & Cowles 2014) . Yet, diversity alone does not determine individual functions or multifunctionality. For example, while decomposition ratemay be correlated with plant tissue quality, underlying soil moisture conditions can have direct influences on decomposition, independent of diversity effects. We still lack an understanding of how diversity and environmental conditions together drive ecosystem multifunctionality.

Second, we must understand how multiple aspects of biodiversity (taxonomic, functional, and phylogenetic) all of which may influence ecosystem functioning, yet rarely are effects of different aspects of diversity on function compared. The vast majority of diversity-function studies have focused on species richness. Positive relationships between richness and productivity (Tilman, Isbell, & Cowles 2014) are thought to be due in part to complementarity among species with different niches, allowing for more complete resource use (Cardinale *et al.* 2012) . While easy to measure, taxonomic metrics of diversity, may be incomplete proxies of utilized niche space compared to functional trait or phylogenetic diversity metrics. Taxonomic species richness, which provides no direct information about traits, may positively correlate with ecosystem functioning only because increasing the number of species will probabilistically increase the diversity of traits. Functional traits can relate to how species use resources and, therefore, functional diversity may be a particularly good predictor of ecosystem functioning (Díaz & Cabido 2001). Yet, because it is infeasible to measure all functional traits related to every function of interest, phylogenetic diversity may be a useful predictor of ecosystem functioning because closely related taxa have similar functional traits (Cadotte *et al.* 2009) . However, a phylogenetic signal may not always be present for functional traits related to each ecosystem function if traits related to functions are not phylogetically conserved (Davies *et al.* 2016). Thus, it remains unclear whether metrics of taxonomic diversity provide sufficient information to predict particular functions or multifunctionality, or whether measures that contain more mechanistic information, such as functional or phylogenetic diversity, can be better predictors.

Third, we must understand the importance of biodiversity for ecosystem functioning within natural ecosystems spanning broad environmental gradients. This requires understanding the role of biodiversity across the range of diversity present in nature, relative to environmental conditions, and controlling for environmental gradients when evaluating how biodiversity structures functions. Environmental conditions and variation in context such as nutrients, water availability, land-use history, and landscape context have been shown to be important drivers of ecosystem function (Farwig *et al.* 2009; Werling *et al.* 2014; Hautier *et al.* 2014; Allan *et al.* 2015). At large spatial scales, environmental variation among sites could overwhelm or enhance effects of diversity on ecosystem function. While some studies have shown that biodiversity has a stronger effect than environmental conditions on ecosystem function (Tilman, Reich, & Isbell 2012; Hooper *et al.* 2012; Craven *et al.* 2016) studies testing diversity-function theory at spatial scales larger than a field or plots are lacking. Two recent studies (van der Plas *et al*. (2016) and Hautier *et al*. (2017)) found that across large spatial scales (forests across Europe and grasslands across the world) environmental variation had a comparable to sometimes greater effect on multifunctionality than biodiversity. Yet, it remains unclear how variation in biodiversity and environmental conditions structure ecosystem function.

Finally, if our goal is to study multiple ecosystem functions simultaneously we need to understand how these functions increase together or tradeoff with each other. Diversity may tend to increase multiple functions simultaneously(Pasari *et al.* 2013) while environmental conditions may cause one ecosystem function to trade off with one another, reducing levels of multifunctionality (Gamfeldt *et al.* 2013) . Moreover, levels of multifunctionality may be driven by all functions increasing simultaneously or by only a few functions that respond strongly to diversity or environmental conditions (Byrnes *et al.* 2014) . Because of this it is also important to understand how individual functions respond to biodiversity and environmental conditions as well as how different ecosystem functions contribute to multifunctionality.

Here we evaluate how environmental conditions and plant diversity relate to individual functions and contribute to ecosystem multifunctionality. We study these relationships across a set of restored tallgrass prairies in southwestern Michigan, in which sites span a wide range of environmental conditions and vary in species richness from 2 to 31 species per m^2 (Grman, Bassett, & Brudvig 2013; Grman *et al.* 2015; Zirbel *et al.* 2017). Here we address four main questions:

1. Is taxonomic, functional, or phylogenetic diversity a better predictor of ecosystem multi-functionality?
2. What are the relative effects of biodiversity and site-to-site variation in environmental conditions on multifunctionality?
3. Do the relative effects of diversity and environmental conditions vary among ecosystem functions?
4. Do tradeoffs exist among ecosystem functions and, if so, how do these influence multifunctionality?

Methods

Study sites and community composition

We addressed these questions in a set of 29 restored tallgrass prairies in southwest Michigan. Sites were restored on abandoned agricultural land via seed sowing (Grman, Bassett, & Brudvig 2014). At each site, we established a 46m transect, randomly oriented in the middle of each site and sampled from ten 1x1m plots along each transect (n=290 total plots). We measured percent cover of all vascular plant species within each 1x1m plot at each site in August of 2013.

Ecosystem functions

We measured seven ecosystem functions in each plot at each site: aboveground biomass production, belowground biomass production, decomposition rate, floral resource availability, floral species richness, seed predation, and arthropod predation. We measured aboveground biomass production by clipping all plant material at the end of the 2013 growing season. We sorted samples to remove litter and oven dried at 65°C for at least 48 hours before weighing. To measure belowground biomass, we removed fours core (~7.6 cm wide by 20cm) adjacent to each plot. We then filled these holes with sand. At the end of the growing season we took a single 3 cm^2 by 20 cm deep core from the center of each sand-filled hole. We passed sand cores through a 2 mm sieve to collect all roots which were then washed and dried at 65°C for 48 hours before weighing. We also determined roots per gram of sand from these samples. To estimate decomposition rate, we placed 15.5 x 15.5 cm mesh bag (mesh size 2 mm^2) filled with 3.80±0.01 g of cellulosic fiber paper at the soil surface, beneath the litter layer, adjacent to each plot. We deployed bags in May of 2013 and collected in September of 2013, (108-123 days) and dried at 65°C for 48 hours before weighing. We calculated decomposition rate by subtracting final mass from starting mass and dividing by the time they remained in the field. We measured floral resource availability by estimating the percent cover of flowers likely pollinated by animals within each 1x1 m plot in June, July, and September 2013. We calculated pollinator resource availability by averaging across all three sampling periods. We measured floral richness by counting the number of unique flowering species in each plot at the same time floral resource availability was measured. We calculated floral richness by averaging the number of flowering species per plot across the three sampling points. To estimate seed predation we placed 20 seeds of each of four prairie species common across our sites (*Sorghastrum nutans, Desmodium canadense, Monarda fistulosa, and Rudbeckia hirta*) on a layer of sand in 12 x 12 x 5.5 cm plastic containers with two 6.5 x 4.5 cm openings cut from adjacent sides of each container. This allowed arthropod and mammalian seed predators to enter the traps and reduced seed loss from rain. This design excluded birds that may also function as seed predators in this system(Howe & Brown 1999) . We placed one container adjacent to each plot and collected after 13 days. We calculated seed predation rate as the total number of seeds removed from each trap. To estimate arthropod predation, we placed four wax worms (*Galleria mellonella*) on a petri dish and then covered worms with a small amount of sand to reduce desiccation but allow visibility (Meehan *et al.* 2012) . We placed the petri dishes at ground level adjacent to each plot and covered them with a wire cage, with 1.27 cm wide holes, to prevent predation from birds and mammals, owing to concerns of uniformly high predation. After 24 hours we counted the number of wax worms removed from each plate by arthropod predators.

Functional traits

We compiled a database of functional traits for species observed during our plant composition surveys using standard methods (Pérez-Harguindeguy *et al.* 2013) . We measured three traits from plants growing in our sites (vegetative height, specific leaf area (SLA), and seed mass) and seven categorical traits taken from the literature (dispersal mode, life history, clonality, photosynthetic pathway, root morphology, nitrogen fixing, and pollination mode). We selected these traits because of their presumed relationships to important ecosystem functions (Díaz & Cabido 2001) . Diversity in some traits may increase function through the selection effect. For example, sites supporting communities of species with greater vegetative height may produce more aboveground biomass (Butterfield & Suding 2013) . A larger proportion of clonally reproducing species may also lead to greater aboveground biomass (Dickson *et al.* 2014) . Diversity in other traits may increase function through complementarity. For example, a variety of root morphologies should increase belowground biomass production because increasing plant functional group diversity has been shown to increase belowground production(Reich, Tilman, & Naeem 2004) . It is likely that communities that have a range of seed masses will support a greater diversity of granivores at a site leading to increased seed predation rates. This is because different sized seed predators prey upon different sized seeds (Stiles 2000). A higher proportion of animal dispersed seeds at a site can maintain a greater diversity of seed predators increasing seed predation rates. Species that produce flowers attractive to pollinators will likely support a greater abundance (cover) of floral resources. Life history should also affect pollinator resources because species with different life histories often produce different amounts of flowers at different times during the growing season(Grime 1977) . Photosynthetic pathway will likely influence decomposition because C3 plants tend to decompose more rapidly than C4(Ross *et al.* 2002) . Finally, the ability to fix nitrogen will likely also influence litter quality and therefore decomposition rate because litter with higher N concentration will decompose faster (Cornwell *et al.* 2008) .

We collected traits from healthy, flowering adults in full sun (Pérez-Harguindeguy *et al.* 2013) located at least 10 m away from a site edge. We measured vegetative height as the distance between the ground and highest photosynthetic structure on 20 individuals. We measured SLA by collecting 2 leaves from each of 10 individuals. We kept leaves turgid and stored for <10 hours until area was determined with a leaf area scanner. We then dried leaves at 65°C for 48 hours before weighing. We calculated SLA as leaf area divided by dry mass. We determined seed mass from samples of 50 seeds from at least 5 individuals for each species dried at 80°C for 48 hours before weighing. For some species (17% of our sample) we were not able to collect seed samples from the field so used seed mass data from the KEW seed information database (Royal Botanic Gardens Kew, 2016). We collected categorical traits from online trait databases and floras (Flora of North America Editorial Committee, eds. 1993, Iverson et al. 1999, Royal Botanic Gardens Kew 2016, National Plant Data Team 2017). We determined pollination mode by classifying whether or not a species produces showy flowers likely to be attractive to insect pollinators. We classified dispersal mode following categories in Pérez-Harguindeguy *et al.* (2013). We classified life history as annual, biennial, or perennial (ILPN). We classified whether a species had the ability to reproduce vegetatively (clonal spread) or whether reproduction must occur by seed. We classified root morphology as fibrous (small to no differentiation in root size classes), primary (clear differentiation in root size classes, including taproots), or rhizomatous (underground stems producing adventitious roots) (ILPIN). We classified photosynthetic pathway using either C3 or C4 photosynthesis. Finally, we described whether or not a species was able to fix nitrogen through symbiotic relationship with bacteria. In sum, across field collect traits, we acquired vegetative height, and SLA trait data for species representing 90% of abundance in our surveys. We collected 78% of seed mass data in the field and 17% from Kew. We acquired categorical traits for species representing cumulative 99.8% of abundance in our surveys.

Phylogeny

We created a phylogeny of all 170 species found during our survey using phylomatic (Webb, Ackerly, & Kembel 2008) . We used a dated molecular tree of >32,000 species to construct our tree (Zanne *et al.* 2014) . This technique provides high resolution for relationships among families and most genera, and for where data were available, also at the species level. When resolution for our taxa was not present in the Zanne *et al*. (2014) phylogeny, Phylomatic incorporated our species as polytomies at the lowest level that data were available. Lack of resolution at terminal branches has little effect on calculations of phylogenetic diversity and tends to make estimates more conservative(Swenson 2009) . We used TimeTree(Kumar *et al.* 2017) to find branch lengths for 2 species not present in the Zanne *et al.* tree and added them to our phylogeny using the pez package (Pearse *et al.* 2015).

Environmental conditions

Sites within this study varied in environmental conditions in ways that affect different ecosystem functions (Zirbel *et al.* 2017) . The time since restoration ranged from 5-10 years at the time of sampling. Because restoration sites often support a greater diversity of arthropod predators than degraded sites (Majer, Brennan, & Bisevac 2002), arthropod predator communities likely reassemble over time following disturbance, we expected older sites to support greater arthropod predation. Sites were burned 0-4 times between the year of sowing and when sampling occurred to slow woody encroachment and clear litter that hinders seedling establishment. Because floral resources often decreases with time since fire(Vogel, Koford, & Debinski 2010) , increased fire frequency may increase floral cover. We calculated fire frequency by dividing the number of prescribed fires at each site by the age of the site. Sites also varied in their soil conditions. To assess differences in soil we took 20cm by $3cm^2$ soil cores at the corner of each plot. Cores were aggregated at the plot level. We measured soil water holding capacity at the plot level by calculating the proportion of oven dried weight to saturated wet weight (Brudvig & Damschen 2011) . We then combined soil samples within sites and analyzed these for soil organic matter, soil texture (sand, silt, and clay content), Mehlich-III phosphorus, Bray-II phosphorus, and pH (Brookside Laboratories, New Knoxville, OH, USA). We anticipate that wetter and more nutrient rich soils will support higher decomposition rates. Soil moisture availability is regularly related to decomposition rate(Singh & Gupta 1977) .We also quantified the landscape surrounding each restoration using(Grman, Bassett, & Brudvig 2014) to determine the area of grassland, forest, wetland, agriculture, or development within 500m of the center of each site. Sites surrounded by forest and grassland are expected to support greater rates of seed predation, independent of local plant community composition effects. These habitat types can support a greater abundance of seed and arthropod predators, relative to agricultural and urban areas, which can colonize adjacent sites(Farwig *et al.* 2009; Meehan *et al.* 2012).

Analysis

We conducted analyses in R v.3.3.0 (R Development Core Team 2013). We used three metrics of diversity: Simpsons (taxonomic), Rao's Q (functional), and the standardized effect size of Faith's PD (phylogenetic). We calculated diversity metrics at the plot level. We calculated Simpson's diversity for each plot (Oksanen et al. 2016). To calculate functional diversity we used Rao's Q from the FD package in R (Laliberté & Legendre 2010) . We used the PhyloMeasures package in R to calculate the standardized effect of phylogenetic diversity which is a measure of phylogenetic diversity that is independent of species richness (Tsirogiannis and Sandel, 2015). Because of correlations among soil variables and among landscape context variables we used two principle components analyses (PCA) to create one variable describing soil conditions and one describing landscape context. The soil PCA included soil organic matter, soil texture (sand, silt, and clay content), Mehlich-III phosphorus, Bray-II phosphorus, pH, and water holding capacity. The first PC axis described 56% of variation in soil variables and was positively related to silt, clay, soil organic matter, pH, and water holding capacity and negatively related to sand and both measures of phosphorus. The landscape context PCA included the total amount of land covered by agriculture, forest, wetland, grassland, or development. The first PC axis described 59% of variation in landscape variables and was positively related to forest, grassland, and wetland cover and negatively related to agriculture and development. To calculate ecosystem multifunctionality for each plot, we scaled each function to its maximum and took the average across all functions in each plot(Byrnes *et al.* 2014b)

To answer questions 1, whether, taxonomic, functional, or phylogenetic diversity is a better predictor of multifunctionality, and 2, the relative importance of diversity and environmental conditions on multifunctionality, we constructed linear mixed effect models with plot level ecosystem multifunctionality as the response variable. We created three models, one for each diversity metric (Simpson's diversity, Rao's Q, standardized effect of PD). Each model also included site age, fire frequency, soil PC axis, and landscape context PC axis. Multifunctionality and diversity data are at the plot level while environmental conditions are at the site level. Site was included as a random effect in each model to control for non-independence of sampling plots. All model predictors had a VIF < 2 indicating that multicollinearity between predictors was not a concern (Borcard et al. 2011). We then compared these models using AICc to determine the best fitting model. We used a 2 ΔAICc cutoff to determine whether a model was a significantly better fit to the data (Burnham and Anderson 2002). To answer question 3, the relative importance of diversity and environmental conditions on individual functions, we used the same approach, but with separate models for each of the seven ecosystem functions as response variables. This resulted in a comparison between the three diversity models for each of the seven ecosystem functions. For each model, we report the full model R^2 as well as the standardized regression coefficients and partial R^2 for each predictor (Nakagawa & Schielzeth 2013) . To answer question 4, how tradeoffs among ecosystem functions influence multifunctionality, we used linear mixed effects models with site as a random effect to calculate the correlation coefficient for each set of ecosystem functions. For each pair of ecosystem functions we report the significance and strength of the correlation between them.

Results

Ecosystem multifunctionality

The phylogenetic diversity model best explained ecosystem multifunctionality compared to the taxonomic (ΔAICc= 4.75) and functional (ΔAICc= 7.10) diversity models (Table 5.1), and phylogenetic diversity explained more variation in multifunctionality than either functional or taxonomic diversity (Table 5.2). Within this model, phylogenetic diversity and landscape context were both significant predictors of ecosystem multifunctionality, with landscape context explaining five times more variation in multifunctionality than phylogenetic diversity (partial-R^2= 0.20 vs 0.04, Figure 5.1a). More phylogenetically diverse sites (β =0.16), and sites surrounded by forest and grasslands rather than agriculture and development (β =0.42), had higher levels of ecosystem multifunctionality (Figure 5.2).

Individual functions

Aboveground biomass production was best predicted by both the functional and taxonomic diversity models (ΔAICc= 1.45, Table 5.1), in which diversity, soil moisture, site age, and landscape context all significantly predicted aboveground biomass. Functionally diverse sites (β=-0.15) that were older (β=-0.21 to -0.23) and had sandier soils (β=0.22 to 0.26) produced more biomass. Biomass production was higher in sites surrounded by forest and grasslands rather than by agriculture and development (β =0.22, Figure 5.1b).

Belowground biomass production was best predicted by the taxonomic diversity model compared to the functional (ΔAICc= 5.09) and the phylogenetic (ΔAICc= 6.52) diversity models (Table

5.1). Taxonomic diversity and site age were both significant predictors. Young (β =-0.25) taxonomically diverse (β =-0.18, Figure 5.1d) sites had the highest belowground biomass.

Decomposition rate was best predicted by both the phylogenetic and taxonomic diversity models (ΔAICc= 0.29, Table 5.1) with diversity, soil moisture, and site age all being significant predictors. Phylogenetically diverse sites (β =0.19) that were older (β= 0.25 to 0.29) and had high soil moisture (β= 0.25 to 0.27) had higher decomposition rates. However, decomposition rate was lower on taxonomically diverse sites (β= -0.20, Figure 5.1c).

Seed predation rate was best predicted by the phylogenetic diversity model compared to the taxonomic (ΔAICc= 2.95) and the functional (ΔAICc= 3.10) diversity models (Table 5.1) with phylogenetic diversity and landscape context being marginally significant predictors (p=0.07, p=0.06). Phylogenetically diverse sites (β= 0.11) surrounded by forest and grassland rather than agriculture and development (β= 0.23, Figure 5.1e) had higher seed predation rates.

Arthropod predation rate was equally predicted by all three models (ΔAICc= 0.43) with landscape context being a significant predictor while phylogenetic diversity and site age were only marginally significant (p=0.10, p=0.10). Phylogenetically diverse sites (β= 0.10) that were older (β= 0.15 to 0.16) and surrounded by forest and grassland rather than agriculture and development (β= 0.21, Figure 5.1f) had higher arthropod predation rates.

Pollinator resource availability was best predicted by the taxonomic and functional diversity models (ΔAICc= 1.50) with functional and taxonomic diversity both being significant predictors. Fire frequency and landscape context were both marginally significant predictors (p=0.08, p=0.08). Functionally (β= 0.16) and taxonomically (β= 0.15) diverse sites, not burned frequently (β= -0.21), and that were surrounded by forest and grassland rather than agriculture and development (β=0.21 to 0.22, Figure 5.1g) had higher pollinator resource availability.

Floral richness was best predicted by the functional diversity model compared to the taxonomic (ΔAICc= 3.62) and phylogenetic (ΔAICc= 5.2) diversity models (Table 5.1) with functional diversity being a significant predictor. Functionally diverse sites (β= 0.12, Figure .51h) had the highest floral richness.

Tradeoffs between ecosystem functions

Between our seven ecosystem functions only 4 of 21 pairs showed significant correlations (Figure 5.3). Of these four, three were positive and one was negative. We found positive correlations between aboveground biomass production and decomposition rate (r=0.12), seed predation rate and pollinator resource availability (r=0.14), and pollinator resources availability and floral richness (r=0.34). We found a negative correlation between floral richness and decomposition rate (r=-0.13).

Discussion

We evaluated relationships between plant diversity and ecosystem multifunctionality across large, heterogeneous landscapes. We found that phylogenetic diversity and landscape context best predicted ecosystem multifunctionality, while the predictors of individual ecosystem functions varied. Although one or more diversity metrics were correlated with individual ecosystem functions, we found that environmental conditions usually had stronger relationships with both ecosystem multifunctionality and individual functions than did diversity. Finally, we found that most of the ecosystem functions we measured did not tradeoff with one another and were either uncorrelated or positively related.

Our finding that phylogenetic diversity is correlated with ecosystem multifunctionality extends past work showing a positive relationship between phylogenetic diversity and productivity (Cadotte *et al.* 2009) , Flynn et al. 20011). In particular, we found that three of seven functions correlated positively with phylogenetic diversity while the other four had no relationship, likely because phylogenetically diverse plant assemblages encompassed a diversity of traits that were important for these functions. The fact that phylogenetic diversity was a better predictor of multifunctionality and of some individual functions than was functional diversity suggests that there were unmeasured phylogenetically conserved traits within our community, which were important for the functions we measured. For example, inclusions of traits such as specific root length and leaf nitrogen content might have improved the predictive capacity of functional diversity for functions such as belowground productivity and decomposition. At least until understanding of trait-function relationships improves, phylogenetic diversity may continue to serve as a proxy of trait diversity when considering multiple ecosystem functions.

We found that sites surrounded by grasslands and forest supported higher levels of multifunctionality than sites surrounded by agriculture and development and that this effect was driven by several individual functions (seed predation, arthropod predation, floral resource production, and aboveground biomass production). Landscape context also explained five times more variation in multifunctionality than did the diversity metrics. We suggest that landscape effects on predation rates likely arose from greater influx of mobile consumers from natural habitat features, aligning with other studies that have also found an effect of landscape context on ecosystem functions related to higher trophic levels such as pest suppression, pollination, and seed predation(Farwig *et al.* 2009; Werling *et al.* 2014; Williams *et al.* 2015) . Landscape effects on floral resources and biomass production are more difficult to explain and we consider several hypotheses. First, landscape context could have mediated the influx of non-sown plants which, in turn, may have increased floral resources or biomass; however, we do not find support for this as landscape context did not influence the richness or cover of non-sown species (p>0.05). Second, herbivores from the surrounding landscape may influence floral resources (through herbivory that prevents flowering) and productivity (Anderson *et al.* 2004; Royo *et al.* 2010; Borer *et al.* 2014). Third, management decisions or environmental conditions could unintentionally correlate with landscape context. We didn't find any evidence of this as landscape context was not correlated with any of the measured environmental conditions. Sites within more natural landscapes did have more species sown into them (p=0.03), but neither seeding richness nor seeding density correlated with measured floral richness or cover (p>0.05), suggesting that correlations between landscape context and seeding management do not explain the observed landscape effect. It is difficult to know, however, if an unmeasured environmental variable correlated with landscape context, so this hypothesis remains a possibility. Our results along with this body of work suggests that considering landscape context will be important for understanding how ecosystems produce multiple functions related to higher trophic levels simultaneously.

Although the predictors of individual ecosystem functions varied widely, overall we found that environmental conditions typically explained more variation in ecosystem functions than any metric of diversity. This suggests that when diversity-function relationships are measured on large spatial scales the effect of local plant diversity on ecosystem function might be overshadowed by strong environmental heterogeneity. Tilman et al. (2012) found greater or comparable effects of diversity on productivity relative to other experimental manipulated environmental conditions (Nitrogen addition, herbivory, drought, and fire) across experiments at Cedar Creek. While the BIODEPTH experiment (study of 8 European grasslands) did not explicitly include environmental variables, these sites are located across many countries and so likely encompass considerable environmental variation. In this study, species richness explained 18% of the variation in productivity while location explained 28% (Hector *et al.* 1999) . We found comparable effects of environmental conditions and diversity on aboveground biomass production across the 29 grasslands we sampled in SW Michigan, but not for other functions which were primarily explained by environmental conditions (Figure 5.1). Thus the ecosystem function of interest as well as the spatial scale in relation to diversity and environmental gradients will be important for determining the relative importance of diversity and environmental conditions on ecosystem functions.

Although tradeoffs among ecosystem functions within a site can determine levels of multifunctionality (Byrnes et al. 2014a), we did not find evidence for this. Rather, we found that across our sites we see very weak correlations between functions at the plot level (Figure 5.3). We find that all ecosystem functions at our sites tend to increase with multifunctionality (Figure 5.1). This suggests that most functions are not trading off with one another but are independently affected by diversity, environmental, and landscape variables. In this case the processes that increase many individual functions –increased phylogenetic diversity and more natural landscapes- will increase multifunctionality.

Understanding how relationships taken from biodiversity-ecosystem function experiments scale up to the real world will require an approach that considers a broad range of functions and multiple aspects of diversity, considered at compatible scales. Our results show that while we generally find a positive diversity function relationship, environmental factors tend to explain more variation in multifunctionality and individual functions than does plant diversity. Specifically, the landscape in which a site is situated can be very important for promoting multiple ecosystem functions at a site. We also show the need to consider metrics of diversity beyond species richness, as richness should only ever be correlated with ecosystem function because it probabilistically increases functional trait diversity. However, across the individual functions we found support for all three diversity metrics we considered. This is likely because we have incomplete knowledge of the functional traits that drive ecosystem function at our sites. This suggests that it will be important to consider how different aspects of diversity might influence individual functions. As others have suggested (Byrnes *et al.* 2014a) , we show that it is important to consider the ways individual functions relate to biodiversity and environmental conditions when considering metrics of ecosystem multifunctionality. Positive, negative, and a lack of correlation between individual functions and diversity are all possible at high levels of multifunctionality, and taking this into consideration will be important for both understanding ecosystem multifunctionality and attaining ecosystem function goals in an applied setting. All of this suggests that while it is important to maintain diversity to promote the functioning of ecosystems, considering environmental conditions and landscape context will also be critical.

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APPENDIX

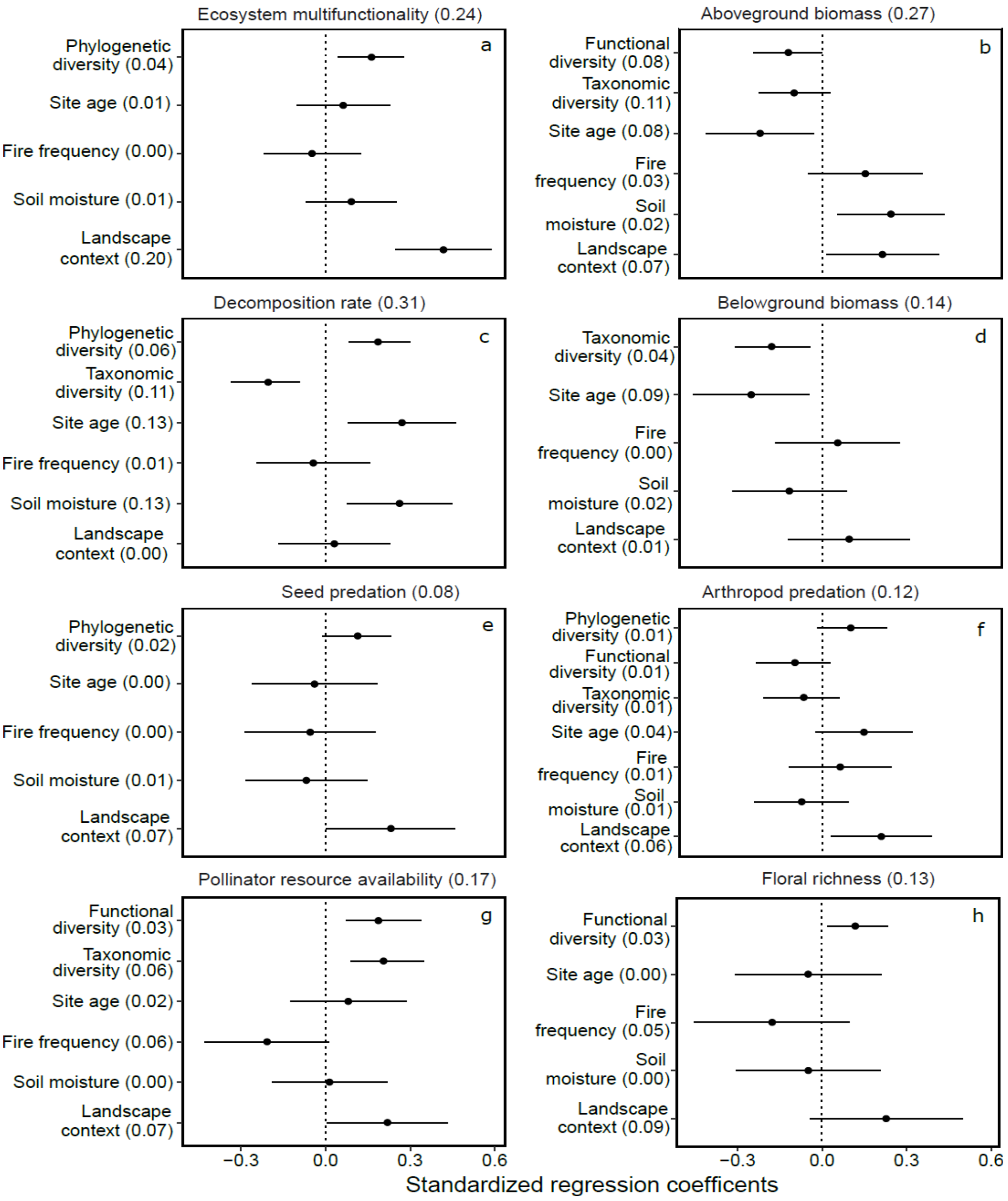

Figure 5.1. Standardized regression coefficients (β) for the significant predictors of (a) multifunctionality and (b-h) individual function models. Full model R^2 are reported for each function for the best model or models based on AICc (Table S1). Partial-R^2 for each predictor given in parentheses. Error bars are 95% confidence intervals.

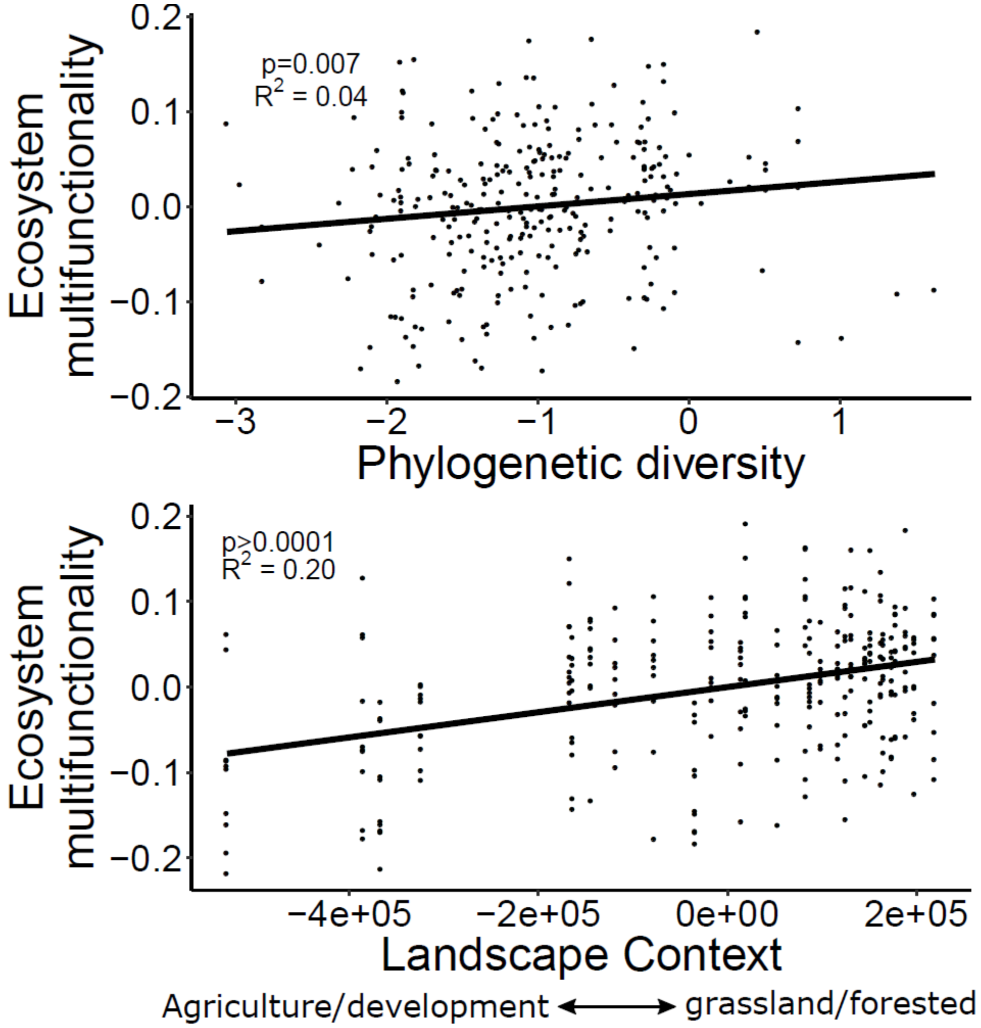

Figure 5.2. Multifunctionality increased with (a) plant phylogenetic diversity and (b) landscape context (sites surrounded by agriculture and development vs forest and grassland) in restored tallgrass prairies. Each point represents a plot.

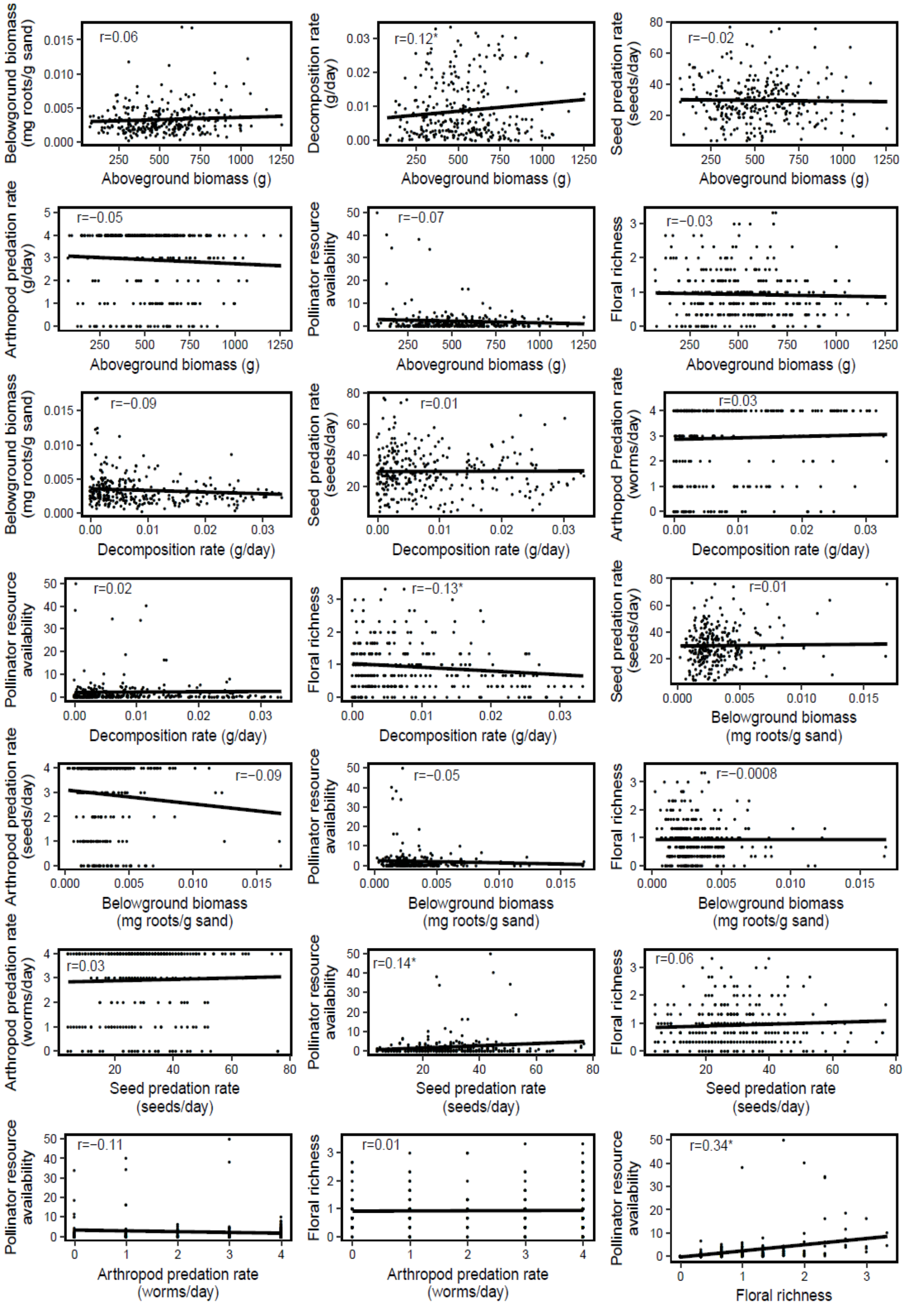

Figure 5.3. Plot level correlations between ecosystem functions. Pearson correlation coefficients are reported for each pair of ecosystem functions and * indicates that the correlation is significant at $p<0.05$.

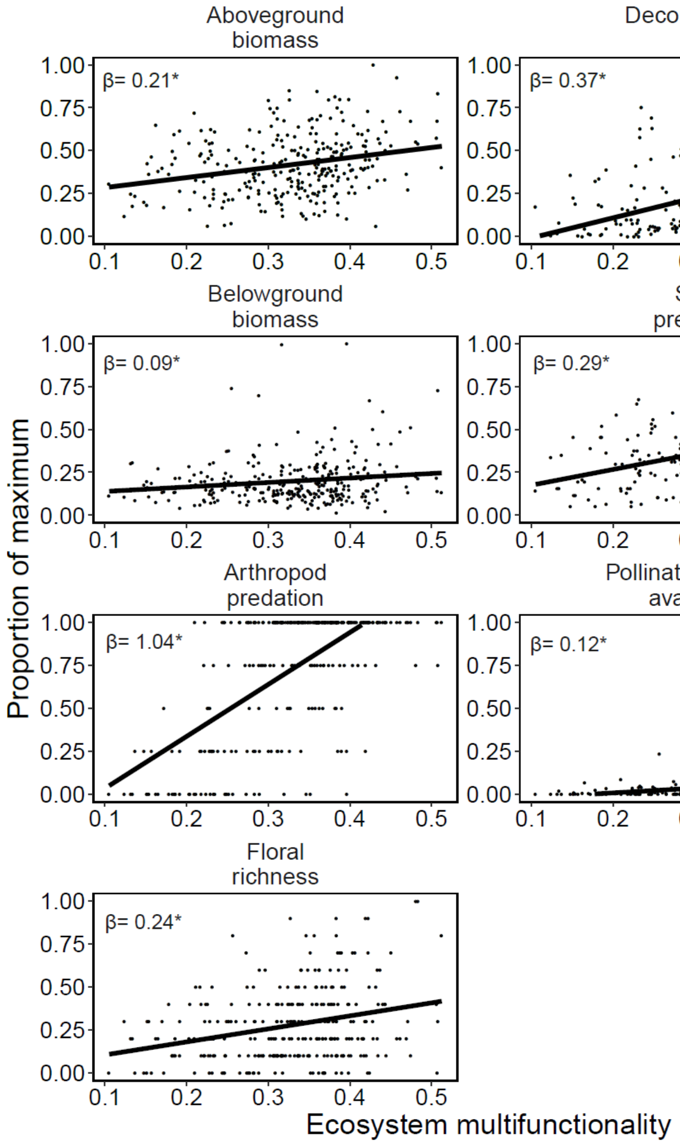

Figure 5.4. Ecosystem function (proportion of its maximum) positively correlates with ecosystem multifunctionality. Significant relationships at $p<0.05$ are indicated with a *. Each figure also includes standardized coefficients (β) for each model. To calculate standardized coefficients and p-values we constructed linear mixed effect models with plot level ecosystem function as the response variable and ecosystem multifunctionality as the predictor variable. Site was included as a random effect in each model to control for non-independence of sampling plots. We used a separate model for each of the seven ecosystem functions.

AICc table

Ecosystem function	Diversity metric	df	AICc	ΔAICc
Multifunctionality	Phylogenetic	8	764.8212	0
	Functional	8	771.9214	7.1002
	Taxonomic	8	769.5692	4.748
Aboveground Biomass	Phylogenetic	8	735.5598	2.6606
	Functional	8	732.8992	0
	Taxonomic	8	734.3358	1.4366
Decomposition rate	Phylogenetic	8	711.5674	0
	Functional	8	721.544	9.9766
	Taxonomic	8	711.86	0.2926
Belowground Biomass	Phylogenetic	8	780.884	6.516
	Functional	8	779.4541	5.0861
	Taxonomic	8	774.368	0
Seed predation rate	Phylogenetic	8	769.1356	0
	Functional	8	772.2325	3.0969
	Taxonomic	8	772.0805	2.9449
Arthropod predation Rate	Phylogenetic	8	796.1822	0
	Functional	8	796.6122	0.43
	Taxonomic	8	797.7687	1.5865
Pollinator resource Availability	Phylogenetic	8	745.6151	9.679
	Functional	8	737.4346	1.4985
	Taxonomic	8	735.9361	0
Floral richness	Phylogenetic	8	679.9336	5.2017
	Functional	8	674.7319	0
	Taxonomic	8	678.3523	3.6204

Table 5.1. df, AICc, and ΔAICc values for each of the models used in this study.

All effects table

Ecosystem		Phylogenetic		Functional		Taxonomic	
Function (R^2)	Predictor	effect	partial R^2	effect	partial R^2	effect	partial R^2
Multifunctionality	Diversity	**0.16**	**0.04**	-0.01	0.00	-0.10	0.01
0.24	Site age	0.06	0.01	0.12	0.02	0.10	0.01
0.21	Fire frequency	-0.05	0.00	-0.05	0.00	-0.03	0.00
0.22	Soil moisture	0.09	0.01	0.08	0.01	0.08	0.01
	Landscape context	**0.42**	**0.20**	**0.40**	**0.18**	**0.41**	**0.19**
Aboveground	Diversity	0.06	0.01	**-0.15**	**0.03**	-0.10	0.01
biomass 0.25	Site age	**-0.24**	**0.08**	**-0.21**	**0.07**	**-0.23**	**0.08**
0.27	Fire frequency	0.13	0.03	0.17	0.04	0.15	0.03
0.26	Soil moisture	**0.27**	**0.11**	**0.22**	**0.07**	**0.26**	**0.10**
	Landscape context	*0.21*	*0.06*	**0.22**	**0.07**	**0.22**	**0.06**
Decomposition rate	Diversity	**0.19**	**0.06**	-0.08	0.01	**-0.20**	**0.07**
0.29	Site age	**0.25**	**0.10**	**0.32**	**0.15**	**0.29**	**0.13**
0.26	Fire frequency	-0.06	0.01	-0.05	0.00	-0.03	0.00
0.30	Soil moisture	**0.27**	**0.12**	**0.24**	**0.09**	**0.25**	**0.11**
	Landscape context	0.03	0.00	0.02	0.00	0.03	0.00
Belowground	Diversity	0.03	0.00	-0.10	0.01	**-0.18**	**0.04**
biomass 0.10	Site age	**-0.24**	**0.07**	**-0.22**	**0.07**	**-0.25**	**0.09**
0.11	Fire frequency	0.02	0.00	0.04	0.00	0.06	0.00
0.14	Soil moisture	-0.11	0.02	-0.14	0.03	-0.12	0.02
	Landscape context	0.08	0.01	0.09	0.01	0.10	0.01
Seed predation	Diversity	*0.11*	*0.02*	0.02	0.00	-0.03	0.00
0.08	Site age	-0.04	0.00	0.00	0.00	-0.01	0.00
0.07	Fire frequency	-0.05	0.00	-0.07	0.00	-0.05	0.00
0.07	Soil moisture	-0.07	0.01	-0.07	0.01	-0.08	0.01
	Landscape context	*0.23*	*0.06*	*0.22*	*0.06*	*0.22*	*0.06*
Arthropod predation	Diversity	*0.10*	*0.01*	-0.04	0.00	-0.07	0.01
0.11	Site age	0.13	0.02	*0.16*	*0.04*	*0.15*	*0.03*
0.10	Fire frequency	0.06	0.00	0.06	0.00	0.07	0.01
0.11	Soil moisture	-0.06	0.00	-0.08	0.01	-0.07	0.01
	Landscape context	**0.21**	**0.05**	**0.21**	**0.05**	**0.21**	**0.05**

Table 5.2. Model R^2, partial R^2, and standardized regression coefficients for each of the three diversity models for multifunctionality and each of the individual functions. Bolded values are significant at $p<0.05$. Italicized values are significant at $p<0.10$.

Table 5.2 (cont'd)

Pollinator resource availability	Diversity	-0.05	0.00	**0.13**	**0.02**	**0.21**	**0.06**
0.11	Site age	0.09	0.01	0.06	0.01	0.10	0.02
0.12	Fire frequency	-0.17	0.04	-0.21	0.06	*-0.21*	*0.06*
0.16	Soil moisture	-0.02	0.00	0.02	0.00	-0.01	0.00
	Landscape context	*0.23*	*0.07*	*0.22*	*0.07*	*0.21*	*0.07*
Floral richness	Diversity	-0.05	0.00	**0.12**	**0.03**	0.09	0.02
0.11	Site age	-0.02	0.00	-0.05	0.00	-0.03	0.00
0.13	Fire frequency	-0.15	0.04	-0.18	0.05	-0.16	0.05
0.12	Soil moisture	0.01	0.00	0.05	0.00	0.02	0.00
	Landscape context	0.24	0.10	0.23	0.09	0.23	0.09

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CHAPTER SIX

CONCLUDING REMARKS & LOOKING FORWARD

Concluding remarks

Trait-based approaches hold promise for understanding both the assembly and functioning of restored ecosystems, yet - in spite of repeated calls - these ideas remain poorly tested (Temperton et al. 2004; Funk *et al.* 2008; Montoya, Rogers, & Memmott 2012; Perring *et al.* 2015). We know very little about how actions taken during restoration to shape community composition favor species with particular traits that, in turn, determine function, as the effects of restoration on species composition/diversity and function have been typically studied separately (Montoya, Rogers, & Memmott 2012). Furthermore, Restored ecosystems offer unique opportunities to study community assembly and diversity-function relationships under realistic field conditions (Bradshaw 1987; Grman, Bassett, & Brudvig 2013; Zirbel *et al.* 2017).

My dissertation confronts these knowledge gaps by coupling community assembly and biodiversity-ecosystem function theory with functional traits and restoration to address the core question:

How do plant functional traits structure the community assembly and ecosystem functioning of ecosystems undergoing restoration?

To answer this question my dissertation focused on two main areas of research: **1)** Testing theory in trait-based community assembly and **2)** Building a link between community assembly and biodiversity ecosystem function theory using functional traits.

My first two chapters take a trait-based approach to studying processes such as invasion and species establishment that underlie community assembly using experimentally manipulated prairie restorations. I found that the extent to which a species' traits are adapted to the local environment, but not how much their traits overlap with species already residing at a site, influence a species' ability to invade a novel community. Likewise, trait-environment interactions play an important role in the invasion process, further supporting the idea that having traits that are adapted to a particular environment is important for invasion success. Furthermore, considering traits independent of their environmental context is inadequate for understanding community assembly processes and trait-environment interactions determine seedling establishment rates in recent prairie restorations.

My last two chapters attempt to use functional traits to link community assembly and ecosystem. I found that both functional traits and environmental conditions play an important role in shaping ecosystem functioning during restoration, and the importance of both traits and environment on functioning depends on the function of interest. Because of this, variation in environmental conditions will be necessary to promote multiple ecosystem functions across restored landscapes. These results highlight the utility of functional traits for connecting community assembly and ecosystem functioning during restoration. I also found that phylogenetic diversity and the makeup of the landscape surrounding a restoration determine ecosystem multifunctionality, though the effect of landscape is much stronger than the effect of diversity. I also found no tradeoffs between ecosystem functions that contribute to multifunctionality across sites; instead, functions are independently affected by diversity, environmental, and landscape variables. In this case, the processes that increase many individual functions—increased phylogenetic diversity and more natural landscapes—will increase multifunctionality.

All of this work demonstrates that trait-based approaches to restoration can help improve our understanding of community assembly and ecosystem functioning at the ecosystem scale, explain variation in restoration outcomes, and show how restored systems can offer a unique test of ecological theory at the scale of ecosystems.

Looking forward

Future work should continue to push forward trait-based restoration ecology research and use restored systems to test ecological theory. Based on what I have learned from my dissertation there are four areas of research that may help to further improve our ability to explain variability in restoration outcomes and create a better understanding of how communities assembly and produce ecosystem functions. These are: **1)** Focusing on individual level trait variation, **2)** considering the importance of trait co-variation for community assembly, **3)** develop a conceptual framework to explain trade-offs among ecosystem functions, and **4)** develop forecasting models for restoration ecology.

Intraspecific trait variation

We now know that as much as 25% of all trait variation occurs within species (Siefert *et al.* 2015). Intraspecific trait variation is an important aspect of trait-based assembly. Variation in an individual's traits may allow them to optimize trait-environment relationships and increase establishment success. For the sake of simplicity an average trait value of a species is often used for each species in a community and potentially important individual variation is often ignored (Bolnick *et al.* 2011). Very few studies today have attempted to quantify the importance of intraspecific trait variation in community assembly. However, those that have quantified its importance have seen large effects of intraspecific variation (Jung *et al.* 2010; Siefert 2012). Future trait-based community assembly work should move towards considering intraspecific trait variation whenever possible as it likely has important consequences for our understanding of how communities assemble and function.

Trait co-variation

In the last ten years, the field of trait-based ecology has grown tremendously, and some of this work has led to important advances in the field. However, a large portion of trait-based ecology has been overly simplistic (e.g. correlating mean trait values to species abundance) and lacking a strong conceptual framework related to how traits of individuals should interact with their environment to determine their fitness, which will ultimately have consequences for population dynamics and the assembly of communities (Laughlin *et al.* 2018). One particular line of research that has been understudied in functional trait research is the consequences of trait covariation.

The focus of trait-based ecology research has been considering how individual traits respond to environmental conditions. This approach is unfortunately fails to take into account the fact that many traits occur within a single individual and these different traits may be influenced by a variety of environmental conditions. Tradeoffs in resource allocation and evolutionary constraint cause traits within individuals to covary with one another. Because of this it is impossible for individuals to possess all values of a set of traits. Different traits on an individual may be responding differently to ecological selection at the same time. An individual cannot respond to two different selective pressures independently if the two traits under selection are tightly correlated. Our models of population growth and community assembly should explicitly consider this trait covariation. This could lead to a better understanding of how species use multiple different strategies to survive in a world with many co-occurring selective pressures.

How do tradeoffs drive multifunctionality?

Ecosystems produce multiple functions simultaneously. If our goal is to study multiple ecosystem functions simultaneously we need to understand how these functions increase together or tradeoff with each other. There has been very little work to conceptualize the drivers of multiple ecosystem functions. Ecosystem can either promote multifunctionality or constrain it through many different processes that occur within a site. These fall into three major categories (1) Ecosystem functions directly influence one another, (2) ecosystem functions are driven by the same processes (e.g. an environmental conditions that drive multiple functions directly cause correlations between functions), or (3) traits that drive different functions occur within the same individual. Moreover, levels of multifunctionality may be driven by all functions increasing simultaneously or by only a few functions that respond strongly to diversity or environmental conditions (Byrnes *et al.* 2014). Because of this it is also important to understand how individual functions respond to biodiversity and environmental conditions as well as how different ecosystem functions contribute to multifunctionality. There is still a great deal of debate in the literature as to what is the best way to quantify ecosystem multifunctionality (Byrnes *et al.* 2014). To do this it will be necessary to develop conceptual models to illustrate how functions may or may not tradeoff with one another.

Prediction in ecology

Ecology has great potential to be a predictive science and these predictions have significant implications for environmental and social policy (Clark 2003). Policy makers, managers, and voters often make decisions based on what they believe will happen in the future. These decisions are made every day, and will be made with or without input from ecologists. In the face of unprecedented global change and uncertainty, we need to position ourselves to aid in this decision making. Pushing ecology to focus on forecasting is one such way forward. The combination of a large temporal and spatial extent of ecological data and increased computational abilities lends itself well to forecasting future changes in ecological communities (Dietze 2017). If we hope to understand how ecological communities might respond to climate change and other human perturbations we will need to make robust forecasts that we validate and improve upon (Tredennick *et al.* 2016). Being able to predict which systems will respond negatively and which will be more resistant has important implications for which systems we chose to protect and how we go about managing endangered natural systems. Future work in both ecology and restoration ecology will need to move towards becoming a more predictive science if we hope to have real impact on the management of imperiled ecosystems.

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