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Title: In tallgrass prairie restorations, relatedness influences neighborhood-scale plant invasion while resource availability influences site-scale invasion

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Abstract

Attempting to control invasive plant species in tallgrass prairie restorations is time-consuming and costly, making improved approaches for predicting and reducing invasion imperative. Both biotic and abiotic factors mediate plant invasions, and can potentially be used by restoration managers to reduce invasion rates. Biotic factors such as plant species richness and phylogenetic diversity of the native community may impact invasion. Relatedness of invading species to those in recipient communities has also been shown to influence invasion success. However, the direction of this influence is variable, reflecting Darwin’s Naturalization Conundrum. Abiotic factors such as fire regime and soil factors may impact invasion by selecting against invasive species or indicating suitable habitats for them. We surveyed 17 tallgrass prairie restorations in Illinois, USA, to investigate the effects of biotic and abiotic factors on invasion by non-native plant species at two different scales. We predicted we would find support for Darwin's Naturalization Hypothesis at the plot (neighborhood) scale with invasion by distantly related species, and find support for the Pre-adaptation Hypothesis at the site scale. We hypothesized that biotic factors would exert more influence at the neighborhood scale, while abiotic factors would be more influential at a coarser site scale. Contrary to our expectations, at the neighborhood scale we found that closely related invasive species are more likely to invade, supporting the Pre-adaptation Hypothesis. We found that native species richness and age of restoration were negatively correlated with invasion. At the site scale, soil organic matter [SOM] concentrations and heterogeneity in SOM were positively associated with the number of invasive species while pH heterogeneity was negatively associated. Restoration practitioners may be able to reduce plant invasions by increasing native species richness, and non-native species most closely related to the resident community should potentially be prioritized as those most likely to be highly invasive.

Keywords: grassland; invasion; phylogenetic diversity; relatedness

Introduction

Ecological restoration is an important means of conserving plant communities and associated ecosystem services (McDonald, Gann, Jonson & Dixon 2016). But key gaps remain in managers' ability to restore ecosystems that are structurally and functionally similar to reference ecosystems (Brye & Kucharik 2003; Zedler & Lindig-Cisneros 2000). Invasive plant species persistently frustrate restoration managers and subvert restoration goals. This is certainly true for tallgrass prairie restoration in the Midwestern United States, where management of invasive plant species is costly and time consuming (Rowe 2010). It would be valuable if restorations could be designed and managed in ways that would confer greater resistance to invasion (Hipp, Larkin, Barak, Bowles, Cadotte et al. 2015). Doing so requires improved understanding of the factors—both biotic and abiotic—that influence the likelihood of invasion.

Biotic factors, both the identity of an invading plant species and its relatedness to the recipient community, can predict invader colonization and establishment. Darwin’s (1859) Naturalization Hypothesis posits that invaders closely related to species in a community may be at a disadvantage due to increased competition with functionally similar species, also known as limiting similarity. Conversely, Darwin recognized that the presence of closely related native species could indicate high habitat suitability for an invader with shared evolutionary history and traits, which is referred to as the Pre-adaptation Hypothesis (Ricciardi & Mottiar 2006). Together, these competing hypotheses comprise Darwin’s Naturalization Conundrum (Diez, Sullivan, Hulme, Edwards & Duncan 2008). Recent studies have found support for both the Naturalization (Strauss, Webb & Salamin 2006) and Pre-adaptation hypotheses (Cadotte, Hamilton & Murray 2009b; Daehler 2001; Fleming, Dibble, Madsen & Wersal 2015; Li, Guo, Cadotte, Chen, Kuang et al. 2015; Ricotta, Godefroid & Rocchini 2010). In addition, there is evidence for scale-dependence in these phenomena, with naturalization favored at neighborhood scales where competition dominates; and pre-adaptation associated with broader site scales, beyond the spatial scale at which plants directly interact and where environmental filtering can exert a strong influence on community assembly (Carboni, Münkemüller, Lavergne, Choler, Borgy et al. 2015; Cavender-Bares, Kozak, Fine & Kembel 2009; Diez et al. 2008; Ma, Li, Pu, Tan, Liu et al. 2016).

In addition to invader identity, diversity of the recipient community has been found to influence invasibility. Elton's hypothesis (Elton 1958; Levine & D'Antonio 1999) predicts that communities with higher species richness should exhibit greater resistance to invasion due to higher competition, lower resource availability, and greater niche occupancy, making colonization by new species less likely. Evidence from some experimental studies indicates that communities with high plant species richness are more resistant to invasion (Knops, Tilman, Haddad, Naeem, Mitchell et al. 1999; Naeem, Knops, Tilman, Howe, Kennedy et al. 2000). This pattern also exhibits scale-dependence (Levine 2000; Levine et al. 1999; Stohlgren, Binkley, Chong, Kalkhan, Schell et al. 1999): at the neighborhood scale, competition may exclude invading species from species-rich communities, but at larger scales, the same factors that foster native species richness, such as resource availability and site heterogeneity, also foster invasive species richness. This is referred to as the biotic acceptance hypothesis (Fridley, Stachowicz, Naeem, Sax, Seabloom et al. 2007; Stohlgren, Jarnevich, Chong & Evangelista 2006), wherein sites that are suitable for native species are suitable for invasive species as well (Stohlgren, Barnett & Kartesz 2003).

Moving beyond species richness, diversity can also be quantified as the amount of evolutionary history represented by the species in a community, i.e., phylogenetic diversity (PD; Faith 1992). Phylogenetic diversity captures information about trait evolution by incorporating the influence of evolutionary time. This is because closely related species are more likely to have similar traits due to trait conservatism (Blomberg, Garland & Ives 2003; Felsenstein 1985). Phylogenetic diversity has been shown to positively predict primary productivity (Cadotte 2013;

Cadotte, Cardinale & Oakley 2008; Cadotte, Cavender-Bares, Tilman & Oakley 2009a), stability (Cadotte, Dinnage & Tilman 2012), and diversity at higher trophic levels (Dinnage, Cadotte, Haddad, Crutsinger & Tilman 2012). Higher PD may also confer greater resistance to invasion. For example, Gerhold et al. (2011) found that communities with lower PD had more non-native species. In contrast, Bennett et al. (2014) found that community resistance to invasion was linked to nutrient availability, not PD. Effects of PD on invasion resistance are likely to diminish at larger spatial scales, as species interactions that operate at fine scales give way to environmental, historical, and biogeographic factors (Cavender-Bares et al. 2009).

In addition to biotic factors, community dynamics and invasion are mediated by abiotic conditions. For example, variation in soil physical and chemical properties influences resource availability and produces site heterogeneity, and sites with higher soil fertility have been found to have more non-native species (Fridley et al. 2007; Stohlgren et al. 1999). Another abiotic factor that may influence invasibility—and one that is more tractable to restoration managers—is fire regime. Fire is a historically important disturbance that promotes diversity and species persistence and influences community phylogenetic structure in remnant prairies (Bowles & Jones 2013; Larkin, Hipp, Kattge, Prescott, Tonietto et al. 2015; Leach & Givnish 1996). Fire also shapes community composition in restored prairies (Towne & Ken 2003; Towne & Owensby 1984). Prescribed burning is widely used in prairie restoration and management to control invasive species (Rowe 2010) and prevent encroachment by woody species (Towne et al. 1984). Frequently burned restorations may resist invasion due to higher species richness (Leach et al. 1996), exclusion of invasive species not adapted to frequent fire, and/or positive responses of native species that become dominant and out-compete invasive species (Smith & Knapp 1999). Recovery of native prairie species following fire is almost immediate, with a flush of growth in the season following a burn (Towne et al. 1984). The age of a restoration may also play a role in invasion, as older restorations often have higher species diversity (McLachlan & Knispel 2005), established perennial populations (Camill, McKone, Sturges, Severud, Ellis et al. 2004) and additional time for invasive species management including burning. Older restorations also have different soil factors than younger restorations, with decreases in soil carbon and nitrogen pools as restorations age (Potter, Torbert, Johnson & Tischler 1999; Tiessen, Stewart & Bettany 1982).

We investigated how biotic (species richness, community phylogenetic diversity, and phylogenetic relatedness of invaders to resident assemblages) and abiotic (soil properties, restoration age, and fire frequency) factors influenced plant invasions in tallgrass prairie restorations at two different spatial scales. We performed vegetation and environmental sampling at the 'neighborhood' or plot scale at which plants directly interact and at the scale of an entire restoration site ('site' scale). Our hypotheses are summarized in Table 1. At the neighborhood scale, we predicted that biotic factors would impact invasion. We hypothesized that, as predicted by Darwin's Naturalization Hypothesis, species would be less likely to invade plots with close native relatives due to limiting similarity. We also hypothesized that higher species richness and phylogenetic diversity would confer invasion resistance, reducing the probability of a plot being invaded. At the site scale, we predicted that invader richness would be positively correlated with species richness, as predicted by the biotic acceptance hypothesis. We hypothesized that at the site scale species would be more likely to invade sites with related individuals as predicted by Darwin's Pre-adaptation Hypothesis. We also hypothesized that abiotic soil factors such as soil resource availability and heterogeneity would positively affect invasion at the site scale. For both scales, we predicted that invasion would be negatively correlated with prescribed burning and with restoration age.

Materials and methods

Study sites and vegetation data

We surveyed 17 restored prairie sites at six preserves across the Chicagoland region (Illinois, USA; Appendix B) from June to August 2015 as described in Barak et al. (2017). Restored sites ranged from <1 to >250 hectares and were 3 to 17 years old at the time of sampling. Restorations were all performed by a single company, Pizzo and Associates, Ltd (Leland, IL, USA). We distinguished multiple restorations sites within the same preserves based on differences in restoration ages and original seeding mixes. At each site we sampled a total of 20 $0.25m^2$ circular plots along two 50m transects, recording presence of all species; these plot-level data comprise our neighborhood-scale dataset. We also took two soil samples from each plot, described below. We identified species using Swink and Wilhem (1994), Black and Judziewicz (2009), and Cochrane, Elliot and Lipke (2008). In September 2015 we performed walking surveys approximately one hour long at each site to identify additional species not previously observed in plots; aggregated plot and walking survey observations constitute the site-level dataset. Plot- and site-level richness measures are the absolute number of species for each plot and site.

Ecologically invasive species are considered noxious weeds or have been shown to have detrimental ecological impacts. Given our interest in ecologically invasive non-native species that managers routinely and deliberately control, we divided observed species into native species, non-native species, and ecologically invasive non-native species using national and regional lists (Black et al. 2009; Swink et al. 1994; USDA National Resources Conservation Service 2017).

We used the subset of ecologically invasive species for all plot- and site-level measures of invasion.

Fire and soil data

We obtained prescribed fire records for each site from land managers. We calculated the number of years since a site had last been burned, which ranged from 0 (for sites that were burned the year of sampling) to the age of the restoration (for sites that had never been burned).

Soil samples were collected from all plots in all sites, excluding two plots from a single site where samples were lost, which were removed from subsequent analyses (338 total plots). We measured gravimetric soil moisture (GSM), loss on ignition (a proxy for soil organic matter [SOM]; Nelson & Sommers 1982), electrical conductivity (EC), and pH using methods described in Barak et al. (2017). We applied natural-log transformation to GSM, SOM, and EC to better approximate normality. We then checked for collinearity among soil variables and removed GSM and EC due to high collinearity with SOM and pH, respectively ($R^2 = 0.61$ and 0.47). At the site scale, we calculated means and variation (coefficients of variation; CV) for all soil variables. Due to a bimodal distribution of mean pH values at the site level (discussed in Results below), we also included soil type as a binary variable, contrasting native but disturbed soils found in abandoned farm fields (non-engineered) with novel soils created by adding dredged sediments and imported topsoil (engineered).

Analyses

All analyses were performed in R 3.2.3 (R Core Team 2015) in R Studio 1.0.136 (RStudio Team 2016). We quantified native species richness as the number of native species observed in individual plots or in entire sites. To calculate phylogenetic diversity, we used a phylogeny from Barak et al. (2017), which was based on a phylogenetic tree from Zanne et al.

(2014). We removed taxa from the tree not found in our dataset, and did not include species in our dataset that were not identified to species. We used this tree (Appendix A) to calculate two metrics of native species phylogenetic diversity, mean pairwise phylogenetic distance (MPD) and mean nearest taxon distance (MNTD), using the R package *Picante* v. 1.6-2 (Kembel, Cowan, Helmus, Cornwell, Morlon et al. 2010) for each plot and site. MPD measures mean pairwise phylogenetic distance between all species in a community, while MNTD is the average of the distance between each species and its closest relative in a community, and both are widely used in community ecology (Tucker, Cadotte, Carvalho, Davies, Ferrier et al. 2017). Generally MPD reflects deeper (older) clade-level relationships between species, while MNTD reflects shallower (more recent) relationships and clustering at the tips of the tree (Webb, Ackerly, McPeek & Donoghue 2002). We calculated standardized effect sizes of MPD and MNTD using *Picante* with 10,000 tip-shuffling randomizations using the “frequency” null model (comparable to Net Relatedness Index*-1 and Nearest Taxon Index*-1, respectively; Webb 2000). Here, we use MPD and MNTD instead of their respective standardized effect sizes because of high collinearity between raw and standardized values ($R^2 = 0.99$ for both) and easier interpretability of raw values. We removed two plots from our analyses because they had <2 native species, precluding calculation of MPD or MNTD, leaving 336 plots. For each plot- or site-level occurrence of each invasive species, we calculated net phylogenetic relatedness with co-occurring native species based on MPD (“MPD.i”, comparable to MPD.t in Bennett, Lamb, Hall, Cardinal-McTeague & Cahill 2013) and MNTD (“MNTD.i”) for each plot and site. MPD.i was calculated by measuring the distance between each invasive species and all native species in a plot. MNTD.i was calculated using the phylogenetically nearest native species co-occurring with the invasive species in a plot. These measures indicate how closely related each invasive species is to the recipient native plant assemblages.

We used linear models to analyze the effects of plant-community and soil measures on invasion. For plot-level analyses, we used generalized linear mixed models (GLMM) to predict probability of invasion as a binary response of presence/absence of invasive species in a plot using the R package *lme4* v. 1.1-12 (Bates, Mächler, Bolker & Walker 2015), employing the Laplace approximation. Our fixed effects were native species richness, MPD, MNTD, MNTD.i, MPD.i, SOM, pH , restoration age, soil type (engineered or non-engineered), and years since last burn (site-level measures). All predictor variables were standardized to mean = 0 and standard deviation = 1 prior to analysis to facilitate comparison of effect sizes among variables. For each model, we included site as a random effect to account for non-independence of multiple plots nested within the same site. To estimate the standardized effect of each variable on plot-level probability of invasion we created a global model with all variables and visualized the predicted values using the R package *sjplot* v. 2.1.1 (Lüdecke 2016). This global model is likely over-parameterized given the structure of our data and number of variables, but shows the general effect of each variable. Assessing the significance of fixed effects in GLMMs is difficult (Bolker, Brooks, Clark, Geange, Poulsen et al. 2009), so we used a forward addition stepwise regression approach to refine models and test significance (Legendre & Legendre 1998). To create a final model, we first tested the null hypothesis of an intercept-only model versus models with single fixed effects, then advanced models that outperformed the null model to test against models with two fixed effects. This forward addition procedure helps ensure that models are not over-parameterized (Legendre et al. 1998; but see Guillaume, Pierre & Daniel 2008). We tested the significance of each fixed effect using likelihood ratio tests (LRT) and, because applying LRT to

GLMMs can be problematic (Bolker et al. 2009), also used parametric bootstrapping with 500 simulations as implemented in the *pbkrtest* package v. 0.4-6 (Halekoh & Højsgaard 2014). In general, these two methods agreed, though parametric bootstrapping was more conservative.

For site-level data, we used linear models to predict invasive species richness. Our fixed effects were native species richness, MPD, MNTD, MPD.i, MNTD.i, site-mean soil SOM and pH, SOM and pH CVs as measures of within-site heterogeneity, restoration age, soil type, and years since last burn. We again standardized all predictor variables to mean = 0 and S.D. = 1. We created a global model to visualize standardized effect sizes for each variable and used LRT to calculate significant effects relative to a null, intercept-only model using the forward addition stepwise regression as described above.

Results

Plots contained a total of 210 species that could be assigned to native or non-native status and had, on average, 8.1 ± 0.8(SE) native species, 2.6 ± 0.1 non-native species of which 0.6 ± 0.005 were ecologically invasive species. At the site scale (plots plus meander surveys), there were 255 species and an average of 67.7 ± 2.7 native species, 12.1± 0.8 non-native species of which 5.8 ± 0.4 were ecologically invasive species per site. A total of 21 ecologically invasive plant species were observed, the most common of which were *Bromus inermis* Leyss. (Poaceae; 7.9% of plots), *Convolvulus arvensis* L. (Convolvulaceae; 6.2% of plots), *Daucus carota* L. (Apiaceae; 20.3% of plots), *Leucanthemum vulgare* Lam. (Asteraceae; 5.9% of plots), and *Trifolium pretense* L. (Fabaceae; 8.8% of plots), all of which are native to Europe and Asia (Table 2).

Soil pH was grouped into two groups, with lower values concentrated in urban sites and higher values in suburban sites that had previously been under agricultural production. In particular, sites within the city of Chicago had higher (average pH = 8 vs. 6.6) and less variable soil pH than all other sites (*t*-tests, df = 14; mean pH: $t = 6.2$, $p < 0.01$; pH coefficient of variation: $t = -23.02$, $p < 0.01$). The soils at these sites were created from dredged lake sediment and topsoil (B. Tsang, City of Chicago Park District, pers. comm.). This leads to the creation of the 'soil type' variable contrasting engineered versus non-engineered soils. Mean LOI and LOI CV did not significantly differ between urban and suburban sites (*t*-tests, df = 14, mean LOI: $t = 0.1$, $p > 0.8$; LOI CV: $t = 1.2$, $p > 0.2$).

Plot-scale models

Our global model with all variables showed that plots were less likely to be invaded if they had more native species, higher SOM, an absence of close relatives of the invader (high MNTD.i), and occurred in older restorations (Fig. 1). Plots were more likely to be invaded if they had higher pH/engineered soils, the native community was less closely related to the invader (MPD.i), and they occurred in a site that had not been burned recently. Our final model included a mix of biotic and abiotic factors: native richness, MNTD.i, and age of restoration (Table 4). This indicates that plots were less likely to be invaded if they had more native species, lacked close relatives of the invader, and occurred in older restorations.

Site-scale models

At the site scale, we found that generally native richness, MNTD, MNTD.i, MPD.i, mean pH, and pH variation were negatively correlated with invasive species richness (Fig. 2). MPD, mean SOM, SOM variation, and age of restoration were positively correlated with invader richness. This indicates that sites had fewer invasive species with more distant nearest relatives within the resident community, lower relatedness to invaders, higher pH, and less recent fire. Conversely, sites had more invasive species with higher native species richness and overall phylogenetic diversity and higher and more variable levels of SOM. We found two models through our stepwise regression process, both of which contained only abiotic factors. One model, which was significantly better than the null, included pH variation (Table 3); that is, sites with high variation in pH had fewer invasive species. Based on our observations of the distribution of pH across sites, we explored additional models. We found that a model with SOM variation was marginally better than the null ($p = 0.08$). When we used this model with stepwise forward regression, we found that mean SOM and SOM variation were significantly better than the null and the model with just pH variation. We discuss both the model with pH variation and the model with mean SOM and SOM variation below.

Discussion

At the plot scale, we found that a mixture of biotic and abiotic factors impacted invasion. Species richness, relatedness between invader and recipient assemblages, and restoration age influenced invasion probability, with higher native species richness and greater phylogenetic distance between invaders and resident species associated with lower probability of invasion (Table 1). This suggests that biotic resistance may be operating at neighborhood scales and supports the Pre-adaptation Hypothesis of Darwin’s naturalization conundrum (Darwin 1959; Diez et al. 2008). In contrast, at the site scale, we found that abiotic factors impacted invasion (Table 1). Sites with higher SOM and more variable pH and SOM had higher invasive species richness. This is in agreement with previous studies that have found that, at larger spatial scales, invasions are positively correlated with greater resource availability and site heterogeneity (Fridley et al. 2007; Stohlgren et al. 2003).

Biotic resistance and pre-adaptation at the neighborhood scale

At the neighborhood scale, plots with high native species richness were less likely to be invaded. This is consistent with small-scale and experimental studies demonstrating diversity-dependent biotic resistance to invasion (Gerhold et al. 2011; Knops et al. 1999; Naeem et al. 2000), i.e., more-diverse plant neighborhoods are more resistant to invasion. This is theoretically due to niche filling in species-rich communities, with greater niche occupancy and fewer available resources with greater numbers of species (Levine et al. 1999). Higher species richness also increases the probability that one or more native species could exclude an invasive species due to limiting similarity, independent of phylogenetic relationships. Negative relationships between native and invasive species richness are not always observed at the neighborhood scale, likely due to the wide range of processes that affect local coexistence, including variation in immigration and disturbance rates (Fridley et al. 2007). Although we used neighborhood-scale probability of invasion, not invasive species richness, our data shows the expected strong negative relationship between native species richness and the probability of invasion.

Relatedness between invading and resident native species was another important predictor of invasion. Plots with close native relatives of invasive species were more likely to be invaded. This supports the Pre-adaptation Hypothesis of Darwin’s Naturalization Conundrum, contrary to our original hypothesis that we would find support for the Naturalization Hypothesis. This is consistent with close relatives exhibiting similar responses to environmental filters due to phylogenetic niche conservatism (Cavender-Bares et al. 2009; Wiens & Graham 2005). That is, closer relatives are likely to be more similar in their traits and thus able to exploit similar niches. Previous studies have found support for the pre-adaptation hypothesis, albeit often at larger spatial scales (Cadotte et al. 2009b; Carboni et al. 2015; Diez et al. 2008; Ricotta et al. 2010). Li et al. (2015) found evidence for the pre-adaptation hypothesis in a fine-scale investigation of invader establishment; they proposed that relatives share similar microbiomes and that native species may engineer soil microhabitats in ways that favor related invasive species. In a meta-analysis, Ma et al. (2016) found support for pre-adaptation at the local scale when considering invasion impact (magnitude of effects of non-native species) and support for naturalization when considering invasion success (species' ability to establish and spread). Perhaps the most important point when comparing our results to previous work is that measures of invasion and definitions of neighborhood and site scales vary across studies, and investigators do not examine a uniform set of abiotic and biotic factors that could potentially impact invasion (Thuiller, Gallien, Boulangeat, De Bello, Münkemüller et al. 2010). We suggest that future research include multiple scales, especially those of interest to restoration managers, along with quantifying species richness and soil factors. Careful studies of how species' traits impact their interaction and potential for invasion would also be useful to tease apart niche complementarity, limiting similarity, and pre-adaptation (Zeldin 2017; Zirbel, Bassett, Grman & Brudvig 2017).

Similarly, restoration age had a negative relationship with probability of invasion. As native species establish, they may limit the ability of species to invade through niche filling. Ruderal native and non-native species often disappear as restorations age, and clonal or rhizomotous species become more established (McLachlan et al. 2005). In particular, establishment through time of native prairie grasses may competitively exclude non-native species (Smith et al. 1999) along with native forbs (Baer, Kitchen, Blair & Rice 2002). Although not included in our final model, years since last burn had a substantial effect, with more recently burned plots less likely to be invaded. This reinforces the importance of prescribed fire in prairie restoration (Rowe 2010).

Overall phylogenetic diversity of recipient assemblages (MPD and MNTD) was not included in our final model (Fig. 1). This was counter to our expectation that plots with high phylogenetic diversity would be less likely to be invaded due to greater biotic resistance. There was a slight positive relationship between MNTD and probability of invasion, and a slight negative relationship between MPD and probability invasion. The few previous studies that have explicitly tested invasion and phylogenetic diversity have also found mixed results, with a negative relationship between PD and invasion (Gerhold et al. 2011) or no relationship (Bennett et al. 2014). We do note that restored prairies have significantly lower native PD than remnant prairies (Barak et al. 2017), and that PD levels may thus not have been high enough to deter invasion.

Site-scale patterns

At the site scale, different factors explained invasion compared to the neighborhood scale (Table 1). Instead of biotic factors like diversity, abiotic soil variables predicted invasive species richness. Our model predicted higher invasion in sites with higher soil pH heterogeneity, which may reflect the characteristics of urban sites restored on engineered soils. The urban sites did have higher invasive richness on average than suburban sites, though this was difference was not statistically significant. We found an additional model with a positive relationship between average SOM and SOM variation and site-level invader richness. This aligns with previous research on invasion dynamics at larger scales, wherein “the rich get richer,” i.e., sites with higher resource availability support more native and invasive species (Stohlgren et al. 2003), and heterogeneity provides more niches for native and invasive species alike (Fridley et al. 2007; Stohlgren et al. 1999). Indeed, Bennett et al. (2014) found that soil properties were more predictive of invasion than phylogenetic measures, with plots with higher nutrient availability more likely to be invaded by *Bromus inermis*, a common invasive species in our plots and sites.

In contrast to the plot-level results, we did not find that species richness, restoration age, or resident-invader relatedness affected site-level invasive species richness. We interpret this to mean that species interactions like competition and facilitation operating at finer spatial scales were not influential relative to resource availability and environmental heterogeneity at the site scale. Similarly, our measures of PD and years since last burn did not have an impact at the site scale.

Implications for management

Establishing high-diversity plant communities is a common goal of prairie restoration for biodiversity conservation, aesthetics, and support for wildlife and food webs. Our results indicate that high neighborhood-scale plant diversity can also confer greater resistance to invasion, which demonstrates the importance of restoring communities that not only have high overall diversity but are also diverse on finer spatial scales (Barak et al. 2017; Martin, Moloney & Wilsey 2005). Beyond species richness, we did not find a strong relationship between PD of the resident community, and invasion, although PD confers other ecosystem benefits in restorations (Cadotte 2013; Cadotte et al. 2012; Dinnage 2013). However, information about phylogenetic relatedness to the invader provided additional power for predicting invasion. If forced to triage management of non-native species, managers might choose to concentrate on invasive species closely related to common native species in their restoration, which may be more likely to establish and persist (Cadotte et al. 2009b; Li et al. 2015).

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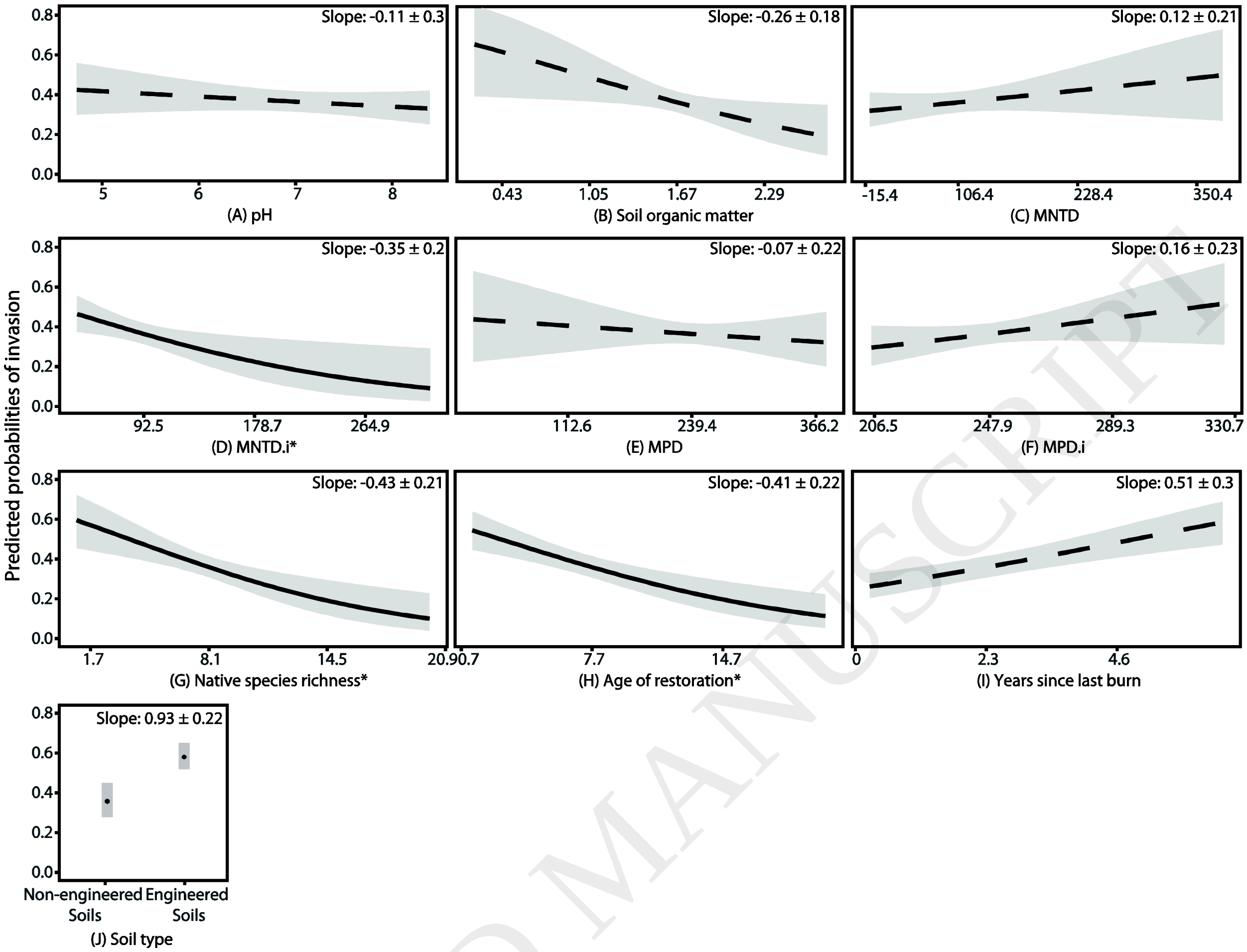
Figure Captions

Fig. 1. Generalized linear mixed model results for plot-level invasion probability. Variables with * were included in the final model. Gray boundaries are 95% confidence intervals and significant variables have a solid line. Values were standardized for analyses. MPD – mean pairwise distance, MNTD – mean nearest taxon distance, MPD.i – mean pairwise distance between invasive species and plot-level native assemblage, MNTD.i – mean nearest taxon distance between invasive species and plot-level native assemblage. Slope is ± standard error.

Fig. 2. Linear model for the number of ecologically invasive species per site. Variables with * were included in the final model, while † indicates inclusion in our alternative model. Gray boundaries are 95% confidence intervals and significant variables have a solid line. Values were standardized for analyses. MPD – mean pairwise distance, MNTD – mean nearest taxon distance, MPD.i – mean pairwise distance between invasive species and site-level native assemblage, MNTD.i – mean nearest taxon distance between invasive species pool and site-level native assemblage. Slope is ± standard error.


Predicted probabilities of invasion
0.0
0.2
0.4
0.6
0.8
Slope: -0.11 ± 0.3
5
6
7
8
(A) pH
Slope: -0.26 ± 0.18
0.43
1.05
1.67
2.29
(B) Soil organic matter
Slope: 0.12 ± 0.21
-15.4
106.4
228.4
350.4
(C) MNTD
Slope: -0.35 ± 0.2
92.5
178.7
264.9
(D) MNTD.i*
Slope: -0.07 ± 0.22
112.6
239.4
366.2
(E) MPD
Slope: 0.16 ± 0.23
206.5
247.9
289.3
330.7
(F) MPD.i
Slope: -0.43 ± 0.21
1.7
8.1
14.5
20.9
(G) Native species richness*
Slope: -0.41 ± 0.22
0.7
7.7
14.7
(H) Age of restoration*
Slope: 0.51 ± 0.3
0
2.3
4.6
(I) Years since last burn
Slope: 0.93 ± 0.22
Non-engineered Soils
Engineered Soils
(J) Soil type

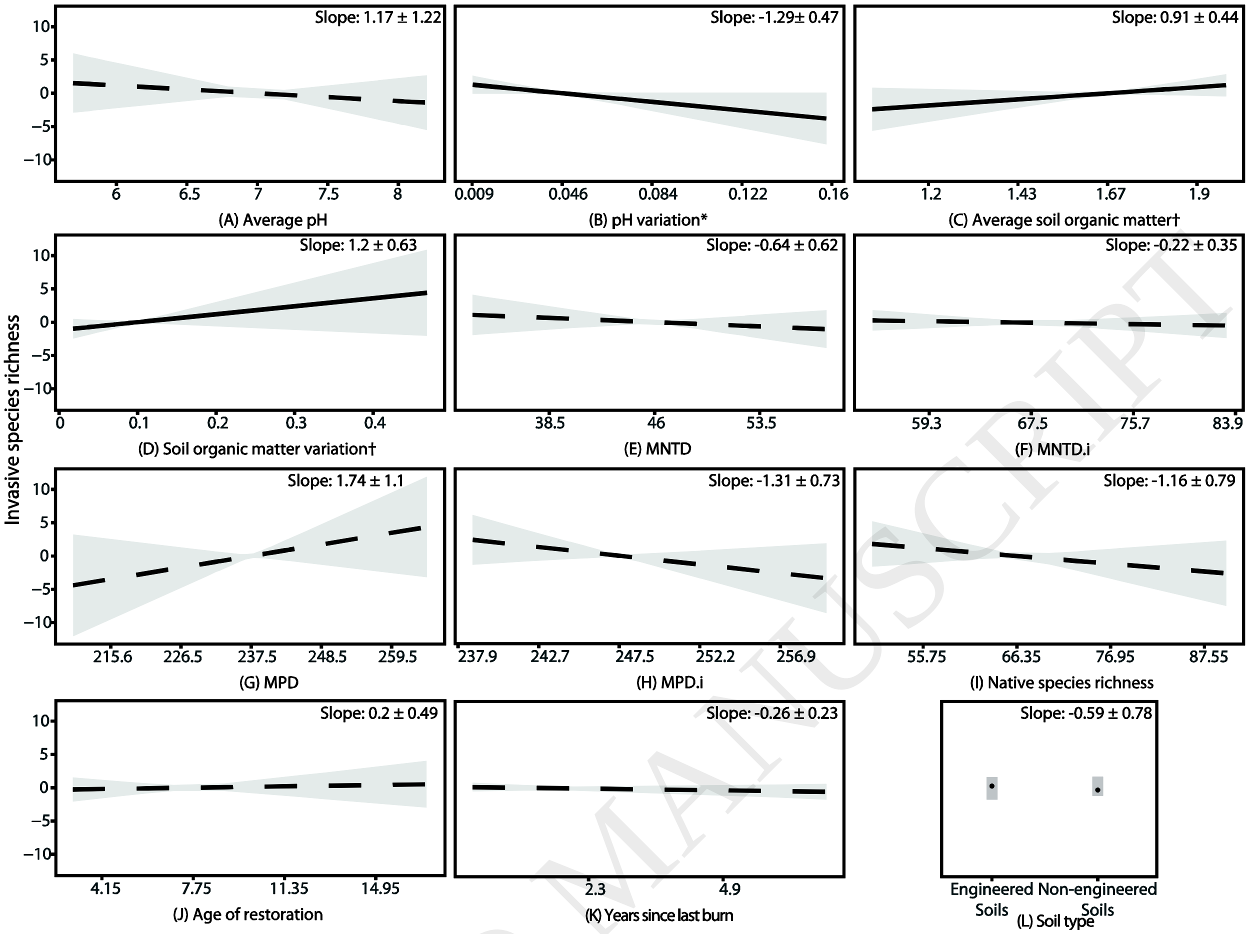

Invasive species richness
10
5
0
−5
−10
Slope: 1.17 ± 1.22
6
6.5
7
7.5
8
(A) Average pH
Slope: -1.29± 0.47
0.009
0.046
0.084
0.122
0.16
(B) pH variation*
Slope: 0.91 ± 0.44
1.2
1.43
1.67
1.9
(C) Average soil organic matter†
Slope: 1.2 ± 0.63
0
0.1
0.2
0.3
0.4
(D) Soil organic matter variation†
Slope: -0.64 ± 0.62
38.5
46
53.5
(E) MNTD
Slope: -0.22 ± 0.35
59.3
67.5
75.7
83.9
(F) MNTD.i
Slope: 1.74 ± 1.1
215.6
226.5
237.5
248.5
259.5
(G) MPD
Slope: -1.31 ± 0.73
237.9
242.7
247.5
252.2
256.9
(H) MPD.i
Slope: -1.16 ± 0.79
55.75
66.35
76.95
87.55
(I) Native species richness
Slope: 0.2 ± 0.49
4.15
7.75
11.35
14.95
(J) Age of restoration
Slope: -0.26 ± 0.23
2.3
4.9
(K) Years since last burn
Slope: -0.59 ± 0.78
Engineered Soils
Non-engineered Soils
(L) Soil type

Table captions

Table 1. Summary of hypotheses in this study including the predicted relationship between variables and invasion and the support found for each.

Scale	Type of factor	Hypothesis	Measure	Predicted relationship	Supported	Results
Plot	Biotic	Darwin's Naturalization Hypothesis	Phylogenetic distance between invasive species and the native community (MPD.i and MNTD.i)	positive	Opposite; Pre-adaptation Hypothesis, closely related invasive species more likely to invade	Fig. 1D and 1F
		Elton's Hypothesis - biotic resistance	Species richness	negative	Yes; species-rich restorations have fewer invasive species	Fig. 1G
			Phylogenetic diversity (MPD and MNTD)	negative	No	Fig. 1C and 1E
	Abiotic	Fire removes invaders	Years since last burn	positive	No	Fig. 1H
		Older restorations have fewer invasive species	Restoration age	negative	Yes; older prairies have fewer invasive species	Fig. 1I

Site	Biotic	Darwin's Pre-adaptation Hypothesis	Phylogenetic distance between invasive species and the native community (MPD.i and MNTD.i)	negative	No	Fig. 2F and 2H
		Biotic acceptance hypothesis	Species richness	positive	No	Fig. 2I
			Phylogenetic diversity (MPD and MNTD)	positive	No	Fig. 2E and 2G
	Abiotic	Fire removes invaders	Years since last burn	positive	No	Fig. 2K
		Older restorations have fewer invasive species	Restoration age	negative	No	Fig. 2J
		Soil organic matter availability and environmental heterogeneity	Soil variables	positive	Yes; higher soil organic matter and soil heterogeneity had more invasive species	Fig. 2C and 2D

Table 2. Ecologically invasive species found in this study and their frequency. Species present at sites but not found in plots were identified during meander surveys. There are 17 sites and 336 plots.

Family	**Species**	**Invasion freq. (sites)**	**Invasion freq. (plots)**
Asteraceae	*Arctium minus* Bernh.	6	0
	Cichorium intybus L.	24	0
	Cirsium arvense (L.) Scop.	35	5.1
	Cirsium vulgare (Savi) Ten.	41	1.1
	Leucanthemum vulgare Lam.	35	5.9
Apiaceae	*Daucus carota* L.	100	20.3
Convolvulaceae	*Convolvulus arvensis* L.	47	6.2
Cyperaceae	*Cyperus esculentus* L.	24	0
Dipsacaceae	*Dipsacus laciniatus* L.	12	0
Fabaceae	*Lotus corniculatus* L.	24	2.8
	Melilotus alba (L.) Lam.	24	1.4
	Securigera varia (L.) Lassen	12	3.4
	Trifolium pratense L.	47	8.8
Hypericaceae	*Hypericum perforatum* L.	18	0
Lamiaceae	*Glechoma hederacea* L.	18	2.3
Lythraceae	*Lythrum salicaria* L.	12	0
Poaceae	*Bromus inermis* Leyss.	53	7.9
	Phalaris arundinacea L.	24	0.8
Rhamnaceae	*Rhamnus cathartica* L.	6	0

Table 3. Linear models used to predict invasion in plots and number of ecologically invasive species in sites in restored prairies.

SOM – soil organic matter, MNTD.i – mean nearest taxon distance between invasive species pool and plot community.

Dataset	**Model type**	**Response**	**Final model**	**Versus next best model $\chi2$ likelihood ratio test**	**Versus next best model Parametric bootstrap test[2]**	**Versus null model $\chi2$ likelihood ratio test**	**Versus null model Parametric bootstrap test**	**Fixed Effect**	**Slope estimate / standardized effect size**	**Slope standard error**
Plot	GLMM	Invaded - yes/no	Native Species Richness + MNTD.i + Restoration Age	*p* (1, 5.4) = 0.02	*p* = 0.03	*p* (3, 17.3) < 0.001	*p* = 0.002	Native Species Richness	-0.55	0.21
								MNTD.i	-0.33	0.22
								Restoration Age	-0.58	0.21
Site[1]	Linear model	Number of invasive species	pH coefficient of variation	-	-	*p* (1, 7.9) = 0.01	-	pH coefficient of variation	-0.59	0.2
	Linear model	Number of invasive species	SOM coefficient of variation + Average SOM	*p* (1, 5.82) = 0.04	-	*p* (2, 8.9) = 0.003	-	LOI coefficient of variation	0.83	0.18
								Average LOI	0.72	0.23

1: Includes two models

2: with 500 simulations for GLMM