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# Intraspecific trait variation and community assembly in old-field grasslands

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## Abstract

Trait-based approaches are increasingly used in plant community ecology, but previous research has largely ignored functional trait variation within species. Here I investigated the role of intraspecific trait variation in community assembly and responses to spatial and temporal environmental variation in old-field plant communities in the eastern United States. In the first study I analyzed spatial patterns of functional divergence in old fields in central New York on spatial scales from 1-1500 m. Results showed that spatial divergence in functional traits at the community and intraspecific levels corresponded with spatial heterogeneity in edaphic variables, consistent with predicted patterns resulting from trait-based environmental filtering. In the second study I tested for evidence of environmental filtering and niche differentiation based on trait dispersion patterns, with or without accounting for intraspecific trait variation. The tests provided evidence of strong trait-based environmental filtering and weak niche differentiation, and these patterns were strengthened by the inclusion of intraspecific trait variation, demonstrating its importance for community assembly. In the third study I examined the contributions of intraspecific variation and species turnover to community trait responses to environmental gradients across a 1200-km latitudinal extent in the eastern United States. Community trait shifts in response to broad-scale climatic variation were driven primarily by species turnover, but intraspecific variation contributed strongly to trait shifts along edaphic gradients and at fine spatial scales. Finally I investigated the role of intraspecific variation in community trait responses to experimental nutrient enrichment in old-field communities and the influence of community functional diversity and dispersal in mediating these responses. After three years, community functional responses were driven almost entirely by intraspecific trait shifts, which were strongest in communities with high initial intraspecific variation for some traits. Taken together, my results suggest that intraspecific trait variation plays a strong role in the assembly of old-field plant communities and shed light on the circumstances in which intraspecific variation is likely to be important for plant community ecology in general.

# Intraspecific trait variation and community assembly in old-field grasslands

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# Chapter 1

## Introduction

The structure and diversity of ecological communities vary in space and time, and ecologists are increasingly using trait-based approaches to describe and understand that variation (McGill et al. 2006). Functional traits are morphological, physiological, and phenological characteristics of individual organisms that influence fitness and responses to and effects on the environment (Diaz and Cabido 2001, Violle et al. 2007). From a trait-based perspective, a community may be characterized by the distribution of functional traits of the individuals it comprises (Ackerly 2003). Because of the direct links between traits and the functioning of organisms, trait distributions offer powerful insights into how communities are assembled and how they influence ecosystem processes (Cornwell and Ackerly 2009, Diaz and Cabido 2001). Since the core traits that determine community assembly and ecosystem processes may be shared among communities across the globe (Diaz et al. 2004), the knowledge gained through trait-based approaches may be highly generalizable (McGill et al. 2006), overcoming a major stumbling block for community ecology.

Trait-based approaches in plant community ecology have gained momentum over the last 15 years, and much progress has been made in areas such as developing lists of key functional traits that define independent aspects of plant strategies (Weiher et al. 1999), measuring those traits for large numbers of species and compiling global trait databases (Kattge et al. 2011), documenting shifts in functional trait distributions across environmental gradients in space and time (Fonseca et al. 2000, Wright et al. 2004), describing the relationship between community trait distributions and ecosystem processes (Garnier et al. 2004, Lavorel and Garnier 2002), and inferring the processes that drive trait-based community assembly (Stubbs and Wilson 2004, Kraft et al. 2008). Despite this progress, there are still important gaps in knowledge that must be addressed to form a more complete view of communities and the processes shaping them. My research focused on two themes that are important for understanding the spatial and temporal variation of plant communities but currently poorly integrated into the trait-based research program: intraspecific trait variation and spatial patterns of functional traits.

Most studies measuring community trait distributions do so using species mean trait values, ignoring trait variation within species. This approach reflects the assumption that intraspecific trait variation is negligible compared to variation among species (Garnier et al. 2001, Baraloto et al. 2010). However, there is increasing evidence that intraspecific variation represents a large proportion of total trait variation in many cases (e.g., Jung et al. 2010, Messier et al. 2010) and that intraspecific variation has important consequences for a wide variety of ecological processes and properties, such as competition (Fridley et al. 2007), coexistence (Clark et al. 2010), productivity (Kotowska et al. 2010), and resistance to disturbance and invasion (Hughes and Stachowicz 2004). Studies only measuring traits at the species level may miss much of the spatial and temporal variation in community trait distributions and therefore much of the action of community assembly and ecosystem functioning. My research addressed fundamental questions related to the role of intraspecific trait variation in plant communities: 1) What is the relative magnitude of intraspecific vs. interspecific trait variation? 2) How does accounting for intraspecific trait variation influence the detection of community assembly processes? 3) How do intraspecific shifts in trait values contribute to changes in community trait distributions in space and time?

Another component missing from most trait-based studies in plant ecology is an explicit consideration of space. It is widely recognized that ecological patterns and processes are spatially structured and scale dependent (Wiens 1989), and understanding how diversity is organized in space is a major focus in community ecology. Spatial patterns of species diversity, such as the species-area relationship and distance decay of community similarity, have received considerable attention for decades and have provided insights into the processes driving community assembly (Preston 1962, Connor and McCoy 1979, Rosenzweig 1995). Spatial patterns of functional trait variation, in contrast, are largely unknown, leaving fundamental questions unanswered: 1) How is variation in functional trait values at the community and species levels distributed in space? 2) What spatial patterns of functional traits are generated by different community assembly mechanisms? 3) How does the relative amount of interspecific vs. intraspecific trait variation vary with spatial scale?

## Research overview

My research combined observational and experimental approaches in old-field plant communities in the eastern United States to address the questions abovementioned questions. Old-field communities are a useful study system for this research because they have been the focus of previous research linking functional traits to community assembly, ecosystem functioning, and responses to environmental variation (Garnier et al. 2007); they contain species known to exhibit large and ecologically-meaningful intraspecific trait variation (Roscher et al. 2011, Gubsch et al. 2011); and they are experimentally tractable.

My first study (chapter 2) examined spatial patterns of functional traits in old-field plant communities in Green Lakes State Park in central New York. In this study, I developed novel hypotheses linking community assembly mechanisms (niche differentiation, environmental filtering, and dispersal limitation) with patterns of spatial divergence in functional trait values among communities and individuals. I evaluated these hypotheses by analyzing spatial patterns of key functional traits (vegetative height, SLA: specific leaf area, and LDMC: leaf dry matter content) and environmental variables (soil depth and moisture) in old fields on spatial scales of 1-1500 m using semivariograms. All traits displayed nonrandom spatial patterns consistent with the environmental filtering hypothesis. The strength and scale of spatial divergence varied among traits, with vegetative height showing strong spatial dependence driven by spatial heterogeneity in soil depth, whereas most divergence in SLA and LDMC occurred on very fine scales (< 1 m). Spatial patterns of functional divergence also differed among the four dominant species in the study site (*Solidago altissima*, *Bromus inermis*, *Poa pratensis*, and *Galium mollugo*), indicating differences in intraspecific responses to environmental heterogeneity.

My second study focused on the role of intraspecific trait variation in old-field community assembly. Two primary processes—environmental filtering and niche differentiation—are proposed to drive community assembly by causing differential success of individuals based on their trait values, generating nonrandom trait dispersion patterns at the community level (Weiher et al. 1998, Stubbs and Wilson 2004, Kraft et al. 2008). Previous studies testing for these patterns have used species mean trait values, thereby not accounting for intraspecific trait variation. Using a null model approach, I tested for patterns of environmental filtering and niche differentiation in old-field plant communities with or without accounting for intraspecific variation among sites and individuals. The results provided evidence of environmental filtering acting on vegetative height and SLA and niche differentiation acting on SLA, and detection of these patterns was improved by accounting for intraspecific trait variation. In addition to community-level effects, there was also strong evidence of environmental filtering acting within individual species. Together, these results show that intraspecific trait responses to environmental filters play a key role in community assembly.

My first two studies and other recent work demonstrate that intraspecific variation contributes strongly to community functional responses to environmental variation at local spatial scales (e.g., Jung et al. 2010, Auger and Shipley 2012, Kichenin et al. 2013), but the degree to which intraspecific variation matters at broader scales encompassing strong climatic gradients is largely unknown. My third study (chapter 4) investigated the relative contributions of species turnover and intraspecific variation to community trait-environment relationships across a 1200-km latitudinal extent in the eastern United States. In particular, I asked whether the relative importance of intraspecific variation depended on the breadth and type (climatic vs. edaphic) of environmental gradient being examined. I found that the contribution of intraspecific variation to community trait responses was greatest at fine spatial scales and along edaphic gradients, whereas species turnover dominated at broad scales and along climatic gradients. These findings provide new insights into the role of intraspecific variation in community responses to the environment and suggest guidelines for when it is important to consider intraspecific variation in plant community studies, a fundamental question for trait-based ecology (Albert et al. 2011).

My final study (chapter 5) examined community trait responses to environmental change through time and how community functional diversity mediates those responses. I hypothesized that the ability of a community to shift its trait values to fit a new set of environmental conditions would be positively related to the initial amount of trait variation (functional diversity) within the community and the rate of dispersal of individuals with appropriate trait values from the local species pool (Ackerly 2003). I tested these hypotheses by conducting a three-year nutrient and seed addition experiment in the previously established old-field plots in Green Lakes State Park. Community mean height and leaf area increased significantly in response to fertilization through intraspecific trait shifts, with the strongest shifts occurring in communities that had high initial intraspecific trait variation. In contrast, trait shifts due to species turnover were generally negligible. The strength of trait responses to fertilization varied among species, and this variation could be partly explained by species' functional characteristics. For example, small, understory species had stronger shifts in SLA and LDMC but weaker shifts in leaf area compared to taller species. Seed addition had little effect on community functional responses, possibly due to limited recruitment opportunities. Overall, these results highlight the importance of intraspecific variation for short-term responses of communities to environmental change and demonstrate that community functional diversity may mediate these responses.

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# Chapter 2

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## Spatial patterns of functional divergence in old-field plant communities

Andrew Siefert

## Abstract

Spatial patterns of functional traits have received little attention in community ecology but have the potential to provide insights into the processes that structure communities. In this study, I used semivariograms to describe spatial patterns of functional traits and evaluate processes (niche differentiation, environmental filtering, and dispersal limitation) driving functional divergence in old-field plant communities. I collected spatially explicit data on key plant functional traits (vegetative height, specific leaf area [SLA], and leaf dry matter content [LDMC]) and environmental variables (soil depth and soil moisture) across a range of spatial scales (<1-1500 m) in old fields in central New York. All traits displayed nonrandom spatial patterns consistent with the environmental filtering hypothesis, but patterns differed among traits. Height had strong spatial dependence at scales congruent with spatial heterogeneity of soil depth, indicating that soil depth acted as a spatial template for divergence in height. SLA and LDMC had much weaker spatial dependence, with > 90% of total divergence occurring within 1-$m^2$ plots, demonstrating that high levels of functional divergence may occur at very fine spatial scales. Spatial patterns of intraspecific functional divergence differed among four common species (*Solidago altissima*, *Bromus inermis*, *Poa pratensis*, and *Galium mollugo*), indicating that species differed in their trait responses to environmental variation. This study provides novel descriptions of spatial patterns of functional traits in plant communities and demonstrates how these patterns can help understand the processes driving functional divergence across spatial scales.

## Introduction

A central theme in community ecology is using patterns to understand the processes that structure communities. Because the traits that organisms possess are directly linked to their performance and responses to the environment (Diaz and Cabido 2001, Violle et al. 2007) patterns of functional diversity, the value and range of functional traits of organisms present in a community, have been used to infer community assembly processes (Cornwell et al. 2006, Kraft and Ackerly 2010, Weiher et al. 1998). Functional divergence, the degree to which organisms are spread out in trait space, is a key component of functional diversity (Mason et al. 2003), and the processes that drive functional divergence in plant communities have been the source of much debate (Grime 2006, Wilson 2007). Though they have received little attention, spatial patterns of functional traits may provide novel insights into the processes that drive functional divergence and the spatial scales at which they operate.

Several ecological processes have been proposed to influence functional divergence in plant communities, and these processes lead to different hypotheses about spatial patterns of functional divergence. If functional trait variation is neutral with respect to plant fitness and individuals disperse randomly, functional trait values will be randomly distributed in space, and the amount of divergence in functional trait values between individual plants or between communities will not depend on the spatial distance separating them. In other words, there will be no relationship between functional divergence and spatial distance (Fig. 1a). This situation serves as a null hypothesis for evaluating the roles of nonrandom processes in generating spatial patterns of functional divergence. Resource competition may favor niche partitioning among competing individuals, leading to increased functional divergence at the small distances over which plant competition occurs (Weiher and Keddy 1995) (niche differentiation hypothesis; Fig.

1b). Conversely, environmental filtering may limit the range of viable trait values in a given site, leading to decreased functional divergence within environmental patches and increased divergence between patches with different optimal trait values (Weiher et al. 1998). If environmental filtering is important, spatial patterns of functional divergence will depend on the strength and spatial scale of environmental heterogeneity (environmental filtering hypothesis). For example, a continuous environmental gradient would produce a monotonically increasing relationship between functional divergence and spatial distance (Fig. 1c), whereas a patchy environment would generate a positive but saturating relationship, with functional divergence leveling off at a distance corresponding to the average size of environmental patches (Fig 1d). Similar patterns could also be generated by dispersal limitation, which causes spatial clustering of genetically (and possibly functionally) similar individuals (Levine and Murrell 2003), potentially leading to decreased functional divergence at scales smaller than mean dispersal distance (dispersal limitation hypothesis).

Though these hypothetical relationships between functional divergence and spatial scale follow from well-known processes, very little is known about spatial patterns of functional divergence or the processes driving them.  Previous studies partitioning functional trait variance in plant communities at multiple spatial scales have found that most regional trait variance occurs within local communities, indicating high functional divergence at small spatial scales (Wright et al. 2004, de Bello et al. 2009, Messier et al. 2010, Freschet et al. 2011). Recent studies comparing observed trait distributions to those produced by null models have found that functional divergence due to niche differentiation is most evident at fine spatial scales (Stubbs and Wilson 2004), whereas functional convergence due to environmental filtering is strongest at fine to intermediate scales (Kraft and Ackerly 2010). Though these analyses provide some information about spatial patterns of functional divergence and the processes driving them across spatial scales, there is a need for spatially explicit analyses that provide a continuous rather than discrete view of the relationship between functional divergence and spatial scale.

In this study, I measured spatial patterns of functional divergence in old-field plant communities and used those patterns to evaluate processes driving functional divergence. I collected spatially explicit data on key plant functional traits (vegetative height, specific leaf area, leaf dry matter content) and environmental variables that represent potentially important environmental filters (soil depth and soil moisture) using a clustered sampling design that allowed analysis of spatial patterns across a continuous range of scales (1-1500 m). I used semivariograms to describe spatial patterns of environmental variables and functional traits and tested for spatial nonrandomness using null models. I also analyzed spatial patterns of functional divergence within four common species (*Solidago altissima*, *Bromus inermis, Poa pratensis*, and *Galium mollugo*) to determine whether patterns of intraspecific functional divergence (due to genetic variation and phenotypic plasticity) varied among species and how patterns at the species level compared to those at the community level. I hypothesized that functional divergence at the community and species levels would exhibit spatial nonrandomness driven by spatial variation of soil depth and soil moisture, supporting the environmental filtering hypothesis.

## Methods

### *Study site*

I collected functional trait and environmental data in old-field plant communities at Green Lakes State Parks, Fayetteville, NY (43° 2’ N, 75° 59’ W), in July-September, 2010. The 150-ha study site lies on a shale plateau overlain by silt-loam soils with depth to bedrock ranging from 0 to >

100 cm. The vegetation consists of a matrix of fields and forests in various stages of secondary succession. I selected six early-successional fields (5-10 ha each) that had been abandoned for at least 14 years and were dominated by goldenrods (*Solidago* spp.), other forbs (e.g., *Galium mollugo*, *Picris hieracioides*), and grasses (e.g., *Bromus inermis*, *Poa pratensis*). Within each field, I randomly selected and geolocated two 5 m x 5 m sampling areas, one in deep soil (> 60 cm) and one in shallow soil (< 30 cm), ensuring that samples captured variation in soil depth, which I hypothesized would be an important environmental filter for plant functional traits. I established 1-$m^2$ sampling plots at the four corners of each sampling area to create a total of 48 sampling plots. By including a wide range of distances between plots, including within-field (4-200 m) and between-field (200-1500 m) comparisons, this sampling design facilitated analysis of spatial patterns across multiple scales (Fortin et al. 1989). Because sampling areas within fields were intentionally placed in locations that varied in soil depth, variability in soil depth between sampling areas within fields was probably exaggerated relative to a random sampling design.

### *Environmental variables*

In each plot, I measured environmental variables related to plant resource availability following standard protocols (Robertson 1999). Soil depth was determined by driving a probe into the ground until bedrock was reached at five locations per plot and taking the average of the values. For analysis of soil chemical and physical properties, I collected a soil core (0-15 cm depth) at the center of each plot. Gravimetric water content was measured as percent fresh mass of soil cores lost after oven drying for 72 hours at 105°C. Soil organic matter content was measured as percent dry mass lost after ignition at 500°C. Total carbon and total nitrogen were determined by dry combustion using a CN autoanalyzer. Relative nitrogen availability was determined using ion exchange resin bags (Binkley and Matson 1983). At one corner of each plot, a nylon stocking containing mixed-bed ion exchange resin (8 g wet mass) was buried to a depth of 10 cm and incubated for 45 days. Resin bags were then retrieved and extracted in KCl, and $NH_4^+$ and $NO_3^-$ concentrations of extracts were measured using an autoanalyzer.

Preliminary analysis revealed collinearity between many of the environmental variables. PCA showed that soil depth and gravimetric water content had the highest loadings on the first and second principle components, respectively, which together accounted for >99% of total variance in the environmental data. I chose to use soil depth and gravimetric water content rather than principle component scores in subsequent analyses because this allowed better interpretability of results, with little loss of information.

*Plant functional traits*

To characterize the distribution of functional traits in sampling plots, I measured functional traits of 48-51 total individuals per plot, with the number of individuals sampled per species being proportional to species relative abundances, as determined by visual estimation of percent cover using the CVS cover class scheme (Peet et al. 1998). Individuals within species were selected haphazardly, avoiding only obviously damaged and very young plants. This sampling design accounted for relative abundances of species and incorporated interspecific and intraspecific trait variation within and among plots. In total, traits were measured on 2337 individuals representing 55 species.

I measured three traits that represent important components of plant functional strategies: vegetative height, specific leaf area (SLA), and leaf dry matter content (LDMC). Vegetative height, the distance between ground level and the tallest vegetative structure in the general canopy of the plant, is strongly associated with competitive ability (Gaudet and Keddy 1988) and reflects the tradeoff between light acquisition and stem construction costs (Westoby et al. 2002).

SLA, the ratio of leaf fresh surface area to dry mass, is a key component of the leaf economics spectrum (Wright et al. 2004), and reflects the tradeoff between rapid resource uptake and resource conservation (Reich et al. 2003). LDMC, the ratio of leaf dry mass to fresh mass, is also related to the leaf economics spectrum and correlates positively with leaf lifespan, water use efficiency, and herbivore resistance (Cornelissen et al. 2003). SLA and LDMC were measured following the full rehydration protocol recommended by Garnier et al. (2001)

*Data analysis*

I described spatial patterns of environmental variables and functional traits using semivariograms. Semivariance, $\gamma(h)$, is a measure of the dissimilarity of a variable between sample pairs separated by a given distance, or spatial lag (h), and is calculated using the function:

$$\gamma(h) = \frac{1}{2n(h)} \sum_{i=1}^{n(h)} [z(x_i) - z(x_i + h)]^2 ,$$

where $z(x_i)$ is the value of variable z at sampling location $x_i$ and n(h) is the number of pairs of sampling points located at distance h from each other (Fortin and Dale 2005). In the context of functional traits, semivariance provides a spatially-explicit measure of functional divergence, the amount of spread in trait space (Mason et al. 2005), between samples. Semivariograms, which plot semivariance against lag distance, are used to describe spatial dependence of a variable, which occurs when values at points separated by a specific distance are more or less similar than expected at random. For spatially dependent variables, semivariance typically increases with increasing distance before reaching an asymptotic value, called the sill, which represents the total sample variance. In the context of functional traits, the sill corresponds to the overall functional divergence in the study area. The distance at which the sill is reached is called the spatial range, and it describes the scale of spatial dependence or patchiness of the variable (Schwarz et al. 2008). The semivariance at the shortest lag distance, called the nugget, accounts for random (non-spatially dependent) and fine-scale variability. The normalized sill is the ratio of the partial sill (difference between sill and nugget) to the sill, and provides a standardized measure of the overall strength of spatial dependence (Schwarz et al. 2008).

Estimates of spatial dependence depend critically on sampling grain, the size of the sampling unit used in analyzing the data (Palmer and White 1994, He et al. 2006). To explore the effect of grain size on spatial patterns of functional divergence, I calculated semivariograms using two grain sizes: 1-$m^2$ plots and individual plants. At the 1-$m^2$ grain size, semivariance was calculated using plot mean trait values; semivariance values therefore reflected the amount of functional divergence between plots. At the individual grain size, semivariance was calculated using trait values of individual plants; semivariance values therefore reflected functional divergence between individuals, including both between- and within-plot divergence. Because I did not measure distances between individual plants, plants within a given plot were considered co-located (lag distance = 0). All within-plot trait divergence was therefore included in the nugget.

In addition to overall community-level patterns, I described spatial patterns of intraspecific functional divergence by calculating separate semivariograms for each of the four most frequently occurring species in the study area (each found in at least 56% of plots): *Solidago altissima*, *Bromus inermis*, *Galium mollugo*, and *Poa pratensis*. *Solidago altissima*, a forb, and *Bromus inermis*, a grass, are highly competitive species that form dense, monospecific patches (Goldberg 1987, Nerberg and Dale 1997). *Galium mollugo*, a forb, and *Poa pratensis*, a grass, are smaller, subordinate species that were found throughout the study area but typically at low density. Semivariograms for individual species were only calculated using individual trait values, since using plot means would have resulted in sample sizes below the recommendation for robust semivariograms (Fortin and Dale 2005).

Semivariograms may be sensitive to outliers and skewed data (Krige and Magri 1982), so I checked the data prior to computing semivariograms. Most variables were approximately normally distributed and free of outliers, but plot mean and individual SLA values had log-normal distributions. I computed semivariograms using log-transformed values, but they were very similar to semivariograms computed with untransformed values. For ease of interpretation, I therefore present only results of analyses using the untransformed data.

I estimated spatial parameters (nugget, range, and sill) by fitting spherical, exponential, and Gaussian models to all empirical semivariograms. Spherical models provided the best or nearly best fit for every variable based on information criteria ($\Delta$AIC < 2). Parameter estimates from different model types may not be directly comparable, so to facilitate comparison between variables, I present parameter estimates from spherical models only. All empirical semivariograms and models were calculated using the geoR package (Ribeiro and Diggle 2001) in R (R Core Development Team 2012).

I tested for spatial dependence of environmental variables and functional traits at multiple distances using a randomization procedure. Observed values were randomly assigned to sampling locations to create 10,000 randomized datasets, and semivariance was calculated for each trait at multiple distance classes (0-10 m, 10-200 m, 200-400 m, 400-600 m, 600-800 m, 800-1200 m) to create 95% confidence envelopes. A trait was considered significantly spatially dependent at a particular distance if the observed semivariance value fell outside the envelope; small observed semivariance values indicate positive autocorrelation (less divergence than expected at random), and large values indicate negative autocorrelation (more divergence than expected at random).

## Results

Across plots, mean height increased with increasing soil depth ($r = 0.59$, $p < 0.001$) and soil water content ($r = 0.44$, $p = 0.002$; Table 1). SLA also increased with increasing soil water content ($r = 0.31$, $p = 0.03$), but LDMC was not correlated with any environmental variable ($p > 0.4$; Table 1). Height was independent of the other traits ($p > 0.1$), but SLA and LDMC were negatively correlated ($r = -0.49$, $p < 0.001$; Table 1).

Soil depth and soil water content both showed strong spatial dependence (normalized sill > 67%; Table 2), with positive autocorrelation between nearby plots (Fig. 2a-b). Rather than showing the typical asymptotic sill, semivariance of soil depth peaked at about 100 m (Fig. 2a), reflecting the arrangement of sampling plots to capture within-field variation in soil depth. The range of spatial dependence for soil depth was relatively small (83 m), indicating fine-scale, within-field patchiness, whereas soil water content had a much larger range (778 m; Table 2), indicating a broad, between-field gradient.

At the 1-$m^2$ plot grain size, all functional traits showed spatial dependence, with positive autocorrelation (less divergence than expected by chance) between plots separated by < 10 m (Fig. 3a-c). The overall strength of spatial dependence was about 25% greater for height than for SLA or LDMC (Table 2). Similar to patterns found for environmental variables (Fig. 2a-b), divergence of all traits peaked at intermediate distances (Fig. 3a-c). The range of spatial dependence was relatively small for all traits (74-95 m; Table 2), indicating that most functional divergence in the site could be found within fields. However, visual inspection of semivariograms showed that divergence of SLA and LDMC peaked at distances > 200 m, indicating the presence of some additional between-field divergence (Fig. 3b-c).

At the individual grain size, the spatial dependence of functional traits was relatively weak (Table 2; Fig. 4a-c). All traits were positively autocorrelated (less divergence than expected by chance) at distances < 5 m, but functional divergence between individuals within 1-$m^2$ plots still accounted for 55% of total divergence in height and > 90% of total divergence in SLA and LDMC (Table 2), indicating high functional divergence at very fine scales. The range of spatial dependence for all traits was < 30 m, also indicating functional divergence was mostly found at fine scales (Table 2).

Spatial patterns of intraspecific functional divergence varied among species. At all distances, intraspecific divergence in height was 200-400% stronger in competitive dominants (*S. altissima, B. inermis*) than in subordinates (*G. mollugo, P. pratensis*) (Fig. 5a). Height showed strong spatial dependence in all species (normalized sill = 40-70%), and the range of spatial dependence was > 200 m for all species except *B. inermis* (Table 2), indicating broad-scale, between-field intraspecific divergence in height. Unlike height, intraspecific divergence in SLA and LDMC was greater in subordinate than in dominant species at all distances (Fig. 5b-c). Spatial dependence of SLA was on average 400% stronger in subordinate than in dominant species, whereas spatial dependence of LDMC was relatively weak (normalized sill = 8-35%) for all species except *P. pratensis* (normalized sill = 60%; Table 2). The range of spatial dependence of SLA and LDMC was small (< 30 m) for all species, indicating most intraspecific divergence in these traits occurred at relatively fine scales (Table 2).

## Discussion

Using a spatially explicit sampling design and semivariogram analysis, I found evidence of nonrandom spatial patterns of functional divergence in old-field plant communities. Specifically, divergence in three key functional traits, vegetative height, SLA, and LDMC, was less than expected at random at small distances. Though it is difficult to infer specific ecological processes from spatial patterns, these results most closely fit the environmental filtering hypothesis (Fig. 1d), suggesting environmental heterogeneity plays a key role in shaping spatial patterns of functional divergence.

Vegetative height, SLA, and LDMC all exhibited nonrandom patterns of divergence in space, but the strength and scale of spatial dependence differed among traits, suggesting different responses to environmental filters. Height exhibited the strongest spatial dependence, and the close correspondence between spatial patterns of height and soil depth (spatial ranges differed by only 4 m) and their relatively strong correlation across plots indicate that spatial divergence in height is controlled by spatial heterogeneity in soil depth. Soil depth likely influences plant height via its effects on resource availability and light competition. Increasing soil depth reduces plant stress and increases availability of belowground resources (Belcher et al. 1995), which in turn increases aboveground competition for light (Wilson and Tilman 1991). Because height plays a key role in light acquisition (Falster 2003), soil depth likely acted as an environmental filter, with tall plants favored in deep sites with strong light competition; consequently, spatial heterogeneity in soil depth acted as a template for spatial divergence in plant height, generating strong spatial patchiness of height within fields. In contrast, SLA and LDMC exhibited broad-scale, between-field divergence, possibly reflecting responses to spatial variation in soil moisture, which itself varied across a broad gradient within the study site. SLA and LDMC, which were highly correlated in this study, are components of the leaf economics spectrum, representing the tradeoff between rapid resource uptake and growth on one hand, and efficient resource use and tissue longevity on the other (Wright et al. 2004). Previous studies have found that soil moisture acts as an environmental filter on these traits, with high SLA, low LDMC leaves suited to high resource uptake and growth rates favored in moist, productive habitats (Cornwell and Ackerly 2009, Jung et al. 2010).

Despite evidence for environmental filtering acting on SLA and LDMC, divergence in these traits was still very high at fine spatial scales. This was especially evident from semivariograms of individual trait data. Whereas semivariograms of plot mean trait values showed clear patterns of increasing between-plot divergence with increasing distance up to about 300 m, divergence between individuals within 1-$m^2$ plots nearly overwhelmed this pattern, accounting for >90% of total divergence in SLA and LDMC. These results add to a growing body of evidence that high functional divergence occurs at fine spatial scales in plant communities (de Bello et al. 2009, Freschet et al. 2011, Messier et al. 2010, Wright et al. 2004). There are two likely explanations for this pattern. First, functional traits such as SLA and LDMC may be involved in complex trade-offs that result in multiple trait combinations with equivalent fitness, allowing a range of trait values to coexist within a given environment (Marks and Lechowicz 2006). Second, these traits may respond to fine-scale heterogeneity in environmental variables such as light availability. Light availability often decreases greatly from canopy to ground level within plant communities, and plants adjust their leaf traits to maximize carbon gain in the light environment they experience (Anten and Hirose 2003). Tall plants that experience high light availability tend to have relatively thick, dense (low SLA) leaves to maximize photosynthetic rate per unit light captured, whereas shaded plants have thin, low density (high

SLA) leaves to increase light capture per unit biomass (Evans and Poorter 2001). These contrasting strategies in response to fine-scale environmental heterogeneity may help maintain the fine-scale functional divergence found in many plant communities.

Though early plant functional trait research focused primarily on interspecific trait variation, this study adds to a growing body of work documenting patterns of intraspecific variation in plant communities (e.g., Hulshof and Swenson 2010, Albert et al. 2010, Gubsch et al. 2011). The amount of functional divergence within individual species in this study was similar to or even greater than community-level divergence at some scales, a result in agreement with recent studies demonstrating that intraspecific variation contributes substantially to overall trait variation in some plant communities (e.g., Jung et al. 2010, Messier et al. 2010)

As at the community level, functional divergence within individual species showed nonrandom spatial patterns fitting the environmental filtering hypothesis. Hakes and Cronin (2011) found similar patterns of spatial dependence of defense traits in *Solidago altissima* in old-field communities, which they attributed to local adaptation, via genetic structure or phenotypic plasticity, to environmental variables that were themselves spatially dependent. Spatial patterns of functional divergence were qualitatively similar in the four species analyzed in this study, but the magnitude of functional divergence and scale and strength of spatial dependence varied among species, supporting the conclusion of Albert et al. (2010) that species' trait responses to environmental variation are highly idiosyncratic. For example, the dominant species (*S. altissima* and *B. inermis*) displayed large amounts of within-field divergence in height, indicating strong genetic or plastic responses to variation in soil depth. Conversely, in the subordinate species (*G. mollugo* and *P. pratensis*), divergence in height was mostly between fields, indicating responses to broad-scale variation in soil moisture. For SLA, subordinate species had high intraspecific divergence and strong spatial dependence, whereas divergence in the dominant species was relatively weak and spatially random. The strong spatial divergence in SLA in subordinate species may be due to plant responses to spatial variation in soil resources directly or to variation in light availability, which is itself likely driven by variation in belowground resources. The contrasting spatial patterns of subordinate and dominant species fit the "niche preemption" model of Ashton et al. (2010), in which weak competitors adjust their trait values depending on the competitive environment they experience, while stronger competitors are less flexible in their functional traits. Recent studies of old-field grasses (Gubsch et al. 2011) and legumes (Roscher et al. 2011) also found that smaller, less competitive species had stronger trait responses to environmental variation. Further exploration of the spatial patterns of intraspecific functional divergence may be a useful tool for understanding intraspecific responses to environmental filters and the role of intraspecific trait variation in generating community-level patterns.

Overall, the results of this study point to the importance of environmental filtering in driving spatial patterns of functional divergence, but there are alternative interpretations of the observed patterns. Dispersal limitation could also play a role in generating spatial nonrandomness by causing aggregated distributions of species and genotypes (Levine and Murrell 2003). Many common species in the study site, such as *Solidago altissima* and *Bromus inermis*, are clonal and grow in dense patches up to at least several meters in diameter (personal observation), potentially leading to positive autocorrelation of trait values (low functional divergence) within patches Hakes and Cronin (2011). At larger scales, though, it is less likely that dispersal limitation is the primary cause of spatial dependence in functional traits. Redundancy of functional trait values among species and plasticity within species may allow communities to match their trait values to those favored by local environmental filters, even if specific species or genotypes are not able to disperse to all sites (Messier et al. 2010). Ultimately, though, observational studies alone cannot completely disentangle the roles of environmental filtering and dispersal limitation in generating spatial patterns in communities (Levine and Murrell 2003). The effects of niche differentiation on functional divergence may also be difficult to detect due to the opposing effects of environmental filtering (Schamp et al. 2008). The patterns observed in this study did not fit the predictions of the niche differentiation hypothesis, but it is possible that strong environmental filtering may have overwhelmed any increase in functional divergence at small scales due to niche differentiation. In addition, the effects of niche differentiation may have been present at distances smaller than those explicitly measured in this study (i.e., < 1 m).

This study demonstrates the potential of using spatial patterns of functional traits to shed light on the processes driving functional divergence in plant communities. The analysis of spatial patterns has a long and productive history in community ecology, but most research has focused on species diversity and composition rather than functional traits (Rosenzweig 1995). Semivariograms provide one useful tool for describing and analyzing spatial patterns of functional divergence, and the approach used in this study could be applied to any plant community at any spatial scale. Functional trait-based analogs to intensively-studied spatial patterns of species diversity, such as the species-area relationship and distance decay of community similarity, should also be developed and explored. For example, indices of functional diversity could be calculated for communities of increasing area to generate “trait-area curves”. Comparing spatial patterns of species and functional diversity may provide especially interesting insights into how communities are structured in space.

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**Table 1.** Pearson correlation matrix for environmental variables and plot mean functional trait values (n=48). Asterisks indicate significance at α=0.05.

| | SWC | H | SLA | LDMC |
|---|---|---|---|---|
| SD | 0.12 | 0.59* | 0.19 | 0.11 |
| SWC | - | 0.44* | 0.31* | -0.12 |
| H | | - | 0.23 | -0.06 |
| SLA | | | - | -0.49* |

SD = soil depth; SWC = soil water content; H = height; SLA = specific leaf area; LDMC = leaf dry matter content

**Table 2.** Semivariogram parameter estimates (spherical variogram models) for environmental variables and plant functional traits.

| Variable | Nugget | Sill | Normalized sill (%) | Range (m) |
|---|---|---|---|---|
| Soil depth | 147 | 600 | 76 | 83 |
| Soil water content | 0.00038 | 0.0012 | 67 | 778 |
| Height | | | | |
| Plot mean | 116 | 402 | 71 | 79 |
| Individual | 449 | 819 | 45 | 29 |
| *S. altissima* | 371 | 621 | 40 | 211 |
| *B. inermis* | 130 | 413 | 69 | 16 |
| *G. mollugo* | 53 | 145 | 64 | 414 |
| *P. pratensis* | 48 | 132 | 64 | 314 |
| SLA | | | | |
| Plot mean | 1.9 | 4.2 | 55 | 95 |
| Individual | 67.1 | 69.3 | 3 | 17 |
| *S. altissima* | 11.3 | 12.0 | 6 | 21 |
| *B. inermis* | 10.3 | 12.6 | 18 | 30 |
| *G. mollugo* | 77.6 | 185.6 | 58 | 28 |
| *P. pratensis* | 14.5 | 38.2 | 62 | 13 |
| LDMC | | | | |
| Plot mean | 0.0002 | 0.0005 | 57 | 74 |
| Individual | 0.0046 | 0.0049 | 6 | 32 |
| *S. altissima* | 0.0007 | 0.0009 | 21 | <1 |
| *B. inermis* | 0.0007 | 0.0010 | 37 | <1 |
| *G. mollugo* | 0.0015 | 0.0017 | 12 | <1 |
| *P. pratensis* | 0.0013 | 0.0032 | 60 | 18 |

SLA = specific leaf area; LDMC = leaf dry matter content

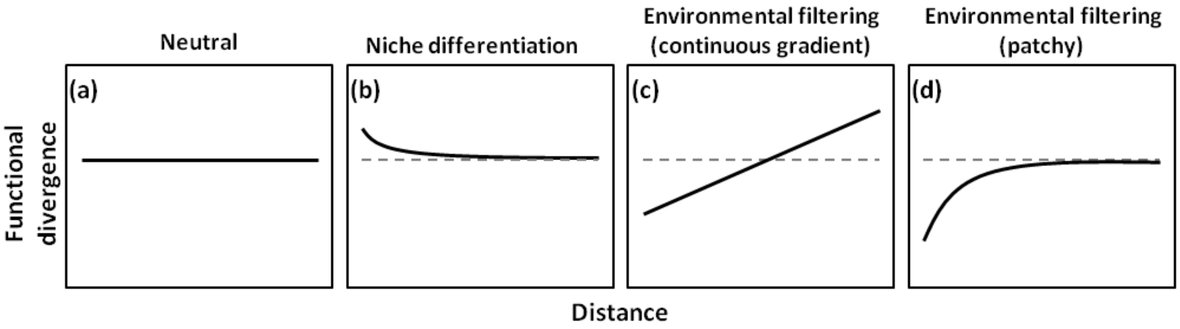

**Figure 1.** Hypotheses for spatial patterns of functional divergence. a) Neutral hypothesis- functional traits are neutral with regard to plant fitness and individuals disperse randomly; no relationship between functional divergence and distance. b) Niche differentiation hypothesis- resource competition favors niche differentiation and increases functional divergence at the small distances over which individual plants compete. c-d) Environmental filtering hypothesis- environmental factors restrict range of viable trait values, leading to decreased functional divergence within environmental patches and increased divergence between patches. Relationship between functional divergence and distance depends on spatial pattern of environmental heterogeneity.

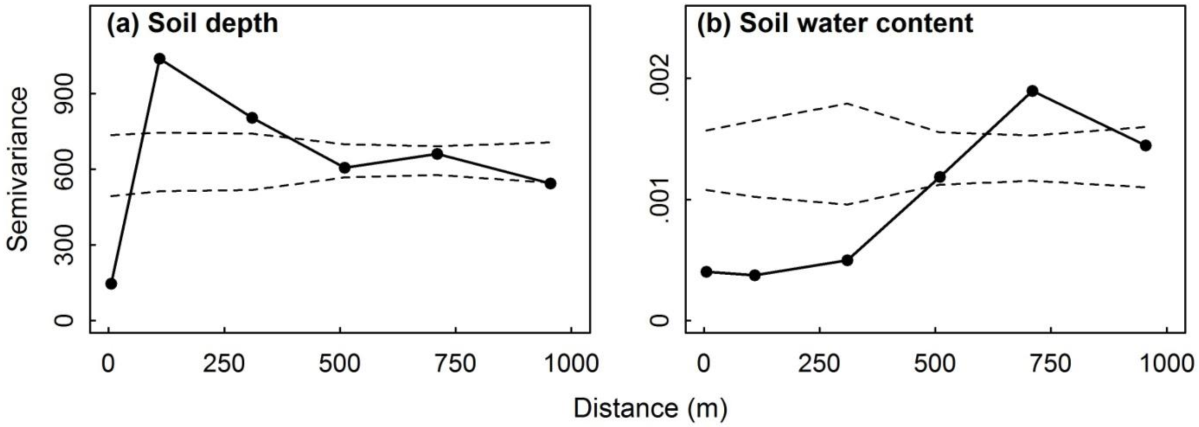

**Figure 2.** Semivariograms of environmental variables (1-m$^2$ plot grain size, n = 48 plots). Distance classes are 0-10 m; 10-200 m; 200-400 m; 400-600 m; 600-800 m; 800-1200 m. Dashed lines define 95% confidence envelope based on 10,000 randomizations of the data. Semivariance values below confidence envelope indicate positive spatial autocorrelation; values above confidence envelope indicate negative spatial autocorrelation.

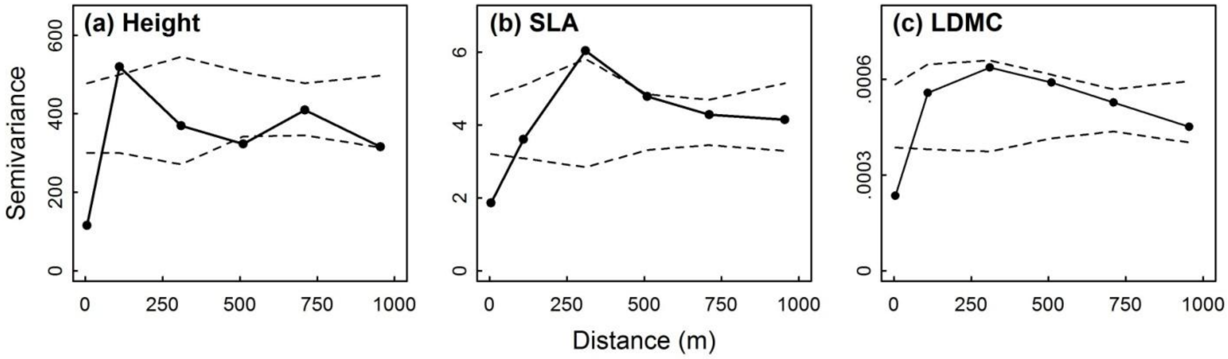

**Figure 3.** Semivariograms of plant functional traits (1-m$^2$ plot grain size, n = 48 plots). Distance classes are same as in Figure 2. Dashed lines define 95% confidence envelope based on 10,000 randomizations of the data. Semivariance values below confidence envelope indicate positive spatial autocorrelation of plot mean trait values (less divergence than expected at random); semivariance values above confidence envelope indicate negative spatial autocorrelation (more divergence than expected at random).

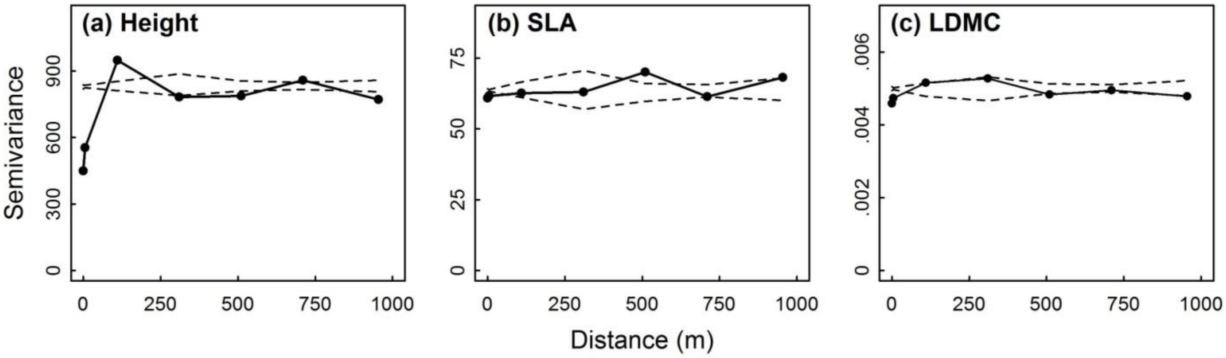

**Figure 4.** Semivariograms of plant functional traits (individual grain size, n = 2337 individuals). Distance classes are same as in Figure 2, with extra bin at distance = 0 for co-located plants (within same 1-m$^2$ plot). Dashed lines define 95% confidence envelope based on 10,000 randomizations of the data. Semivariance values below confidence envelope indicate positive spatial autocorrelation of individual trait values (less divergence than expected at random); semivariance values below confidence envelope indicate negative spatial autocorrelation (more divergence than expected at random).

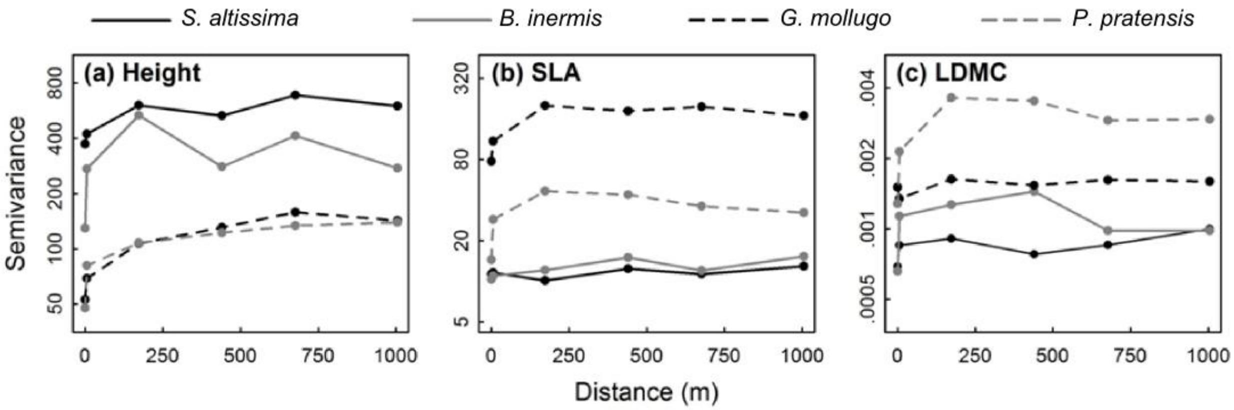

**Figure 5.** Semivariograms of plant functional traits (individual grain size) in common species: *Solidago altissima* (n = 606), *Bromus inermis* (n = 308), *Poa pratensis* (n = 239), *Galium mollugo* (n = 107). Distance classes are same as in Figure 2, with extra bin at distance = 0 for co-located plants (within same 1-m$^2$ plot). Note that semivariance is plotted on logarithmic scale so spatial patterns of all species are visible. Confidence envelopes are omitted for clarity.

# Chapter 3

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## Incorporating intraspecific variation in tests of trait-based community assembly

Andrew Siefert

### Abstract

Environmental filtering and niche differentiation are processes proposed to drive community assembly, generating nonrandom patterns in community trait distributions. Despite the substantial intraspecific trait variation present in plant communities, most previous studies of trait-based community assembly have used species mean trait values and therefore not accounted for intraspecific variation. Using a null model approach, I tested for environmental filtering and niche differentiation acting on three key functional traits—vegetative height, specific leaf area (SLA), and leaf dry matter content (LDMC)—in old-field plant communities. I also examined how accounting for intraspecific variation at the among-plot and individual levels affected the detection of nonrandom assembly patterns. Tests using fixed species mean trait values provided evidence of environmental filtering acting on height and SLA and niche differentiation acting on SLA. Including plot-level intraspecific variation increased the strength of these patterns, indicating an important role of intraspecific variation in community assembly. Tests using individual trait data indicated strong environmental filtering acting on all traits but provided no evidence of niche differentiation, although these signals may have been obscured by the effects of dispersal limitation and spatial aggregation of conspecific individuals. There was also strong evidence of nonrandom assembly of individuals within single species, with the strength of environmental filtering varying among species. This study demonstrates that while analyses using fixed species mean trait values can provide insights into community assembly processes,

accounting for intraspecific variation provides a more complete view of communities and the processes driving their assembly.

## Introduction

Plant community assembly involves a number of processes that together determine the distribution of functional trait values found in local communities. For a given site, there is a pool of individuals with varying functional attributes in the surrounding area. Some of those individuals disperse their propagules to the site and some do not, a stochastic and spatially-dependent process (Nathan and Muller-Landau 2000). Some of the individuals reaching the site survive, grow, and reproduce, while others fail. These differences in success may be random, as proposed by neutral theory (Hubbell 2001), or influenced by the functional trait values of individuals, i.e. selection (Shipley et al. 2006). Trait-based community assembly studies have focused on two selective processes: environmental filtering and niche differentiation (Stubbs and Wilson 2004, Cornwell et al. 2006). Environmental filtering may be viewed as a form of stabilizing or directional selection in which the abiotic environment selects for specific trait values, leading to trait convergence within habitats (Harper 1977, Weiher et al. 1998, Grime 2006). Niche differentiation may be viewed as a form of density-dependent selection in which competition and other biotic interactions select against trait values too similar to those of neighbors, leading to regular spacing of co-occurring individuals along trait axes (Weiher and Keddy 1995, Stubbs and Wilson 2004). In addition to causing differences in success among species and genotypes, these selective pressures may cause genotypes to express different trait values (i.e., phenotypic plasticity), also influencing the distribution of trait values within a given community. Community assembly processes such as environmental filtering and niche differentiation are rarely directly measured, but they are expected to generate predictable patterns in community trait distributions, and null model approaches can be used to detect or infer processes by comparing trait distributions of observed and randomly assembled communities (Weiher and Keddy 1995, Cornwell et al. 2006).

Although the processes involved in community assembly operate at the level of individual organisms, most previous studies have described community trait distributions using species mean trait values (e.g., Kraft et al. 2008, Schamp et al. 2008). However, traits are not fixed within species. Intraspecific variation due to genetic variation and phenotypic plasticity may contribute strongly to community-level trait variation (Hulshof and Swenson 2010, Messier et al. 2010) and community trait responses to environmental gradients (Jung et al. 2010, Lepš et al. 2011). Genetic variation and phenotypic plasticity allow species' trait values to vary among sites in response to environmental filters and interactions with neighboring species. These intraspecific shifts in trait values may reinforce interspecific patterns of trait convergence and even spacing, resulting in stronger signals of environmental filtering and niche differentiation when species are described by population- or site-specific rather than fixed mean trait values (Jung et al. 2010). Trait values also vary among individuals within populations, and this variation is known to influence plant responses to the environment (Fridley et al. 2007) and competition (Fridley and Grime 2010). Accounting for individual-level variation may therefore be necessary to detect nonrandom community assembly processes (Paine et al. 2011, Violle et al. 2012).

In this study, I used a null model approach to test for nonrandom trait-based community assembly in old-field plant communities using fixed species means, plot-specific species means, and individual trait values. I focused on three key functional traits that are known to play important roles in plant community assembly: vegetative height, specific leaf area (SLA), and leaf dry matter content (LDMC). Because specific values of these traits are expected to maximize resource capture and competitive ability under local conditions (Mason et al. 2011), I hypothesized that communities would display evidence of environmental filtering (reduced range and variance of trait values) for all three traits. SLA and LDMC also reflect trade-offs in resource acquisition and use strategies, potentially allowing plants differing in these traits to partition resources (Westoby et al. 2002, Wright et al. 2004). In contrast, competition for light is asymmetric, with taller individuals having greater access (Falster 2003). I therefore hypothesized that communities would display evidence of niche differentiation (even spacing of trait values) for SLA and LDMC but not height. Finally, I hypothesized that analyses incorporating intraspecific trait variation would reveal stronger signals of community assembly processes than analyses based on fixed species mean trait values. To further examine the role of intraspecific trait variation in community assembly, I also tested for evidence of environmental filtering and niche differentiation within the three most abundant species in the study site: *Solidago altissima*, *Bromus inermis*, and *Poa pratensis*.

## Methods

### *Study site*

I collected functional trait data in old-field plant communities in Green Lakes State Park, Fayetteville, NY (43° 2’ N, 75° 59’ W), in July-August, 2010. The site consists of 150 ha of forests and abandoned agricultural fields undergoing secondary succession. Fields used in the study had been abandoned for at least 14 years and were dominated by herbaceous plants, particularly goldenrods (*Solidago* spp.) and introduced $C_3$ grasses (e.g., *Bromus inermis* and *Poa pratensis*). Productivity and community composition were influenced by soil depth to bedrock, which varied from 0 to > 100 cm within fields (Siefert 2012). For plant trait sampling, I selected 48 1-m$^2$ sampling plots across 6 fields (8 plots per field) in a stratified, random design: within each field, 4 plots were located in areas of deep soil (> 40 cm) and 4 plots in shallow soil (< 40 cm). Distances between fields ranged from 200-1500 m, and distances between plots within fields ranged from 4-200 m.

### *Functional trait data*

In each plot, I measured functional traits of 50 individual plants in total, with the number of individuals sampled per species proportional to relative species abundances, as determined by visual estimation of percent cover following the protocol of Peet et al. (1998). Individuals within species were selected haphazardly, avoiding only obviously damaged and very young plants. This sampling approach was designed to capture the full distribution of functional trait variation, interspecific and intraspecific, within each plot. In total, I sampled 2337 individuals representing 55 species (mean species richness = 9.0 species per 1-m$^2$ plot). Using the individual trait data, I calculated "fixed species mean" trait values by averaging the trait values of all individuals of a given species sampled throughout the study site. To account for among-plot intraspecific trait variation, I also calculated "plot-specific species mean" trait values by averaging trait values of all individuals of a given species within a given plot. Community trait distributions could therefore be described using fixed species means, plot-specific species means, or individual trait values. I measured three traits that reflect key aspects of plant functional strategies (Westoby et al. 2002): vegetative height, specific leaf area (SLA), and leaf dry matter content (LDMC). Vegetative height is related to light acquisition and competitive ability (Gaudet and Keddy 1988, Falster 2003). SLA is a central component of the leaf economics spectrum, which captures the tradeoff between rapid resource acquisition and resource conservation (Reich et al. 2003, Wright et al. 2004). LDMC is also a component of the leaf economics spectrum and relates to leaf resistance to herbivory and drought (Cornelissen et al. 2003). SLA and LDMC were moderately correlated within the study site ($R^2 = 0.24$; Siefert 2012). Previous studies have shown that these traits vary across environmental gradients within and among species (Fonseca et al. 2000, Cornwell and Ackerly 2009, Jung et al. 2010, Albert et al. 2010) and display evidence of environmental filtering and niche differentiation at the community level (Kraft et al. 2008, Cornwell and Ackerly 2009)Vegetative height was measured in the field following the protocol of Cornelissen et al. (2003). Leaf traits were measured on one young but fully expanded leaf per individual following the full rehydration protocol of Garnier et al. (2001).

### *Data analysis*

For each plot/trait combination, I calculated community trait metrics to capture the independent effects of environmental filtering and niche differentiation on community trait distributions (Kraft and Ackerly 2010). The range and variance of trait values, which are expected to decrease as a result of trait convergence, were used to detect environmental filtering. Niche differentiation, which is expected to cause even spacing of trait values, was detected using kurtosis and standard deviation of neighbor distance divided by range (SDNDr). Kurtosis describes the “peakedness” of a distribution, with low kurtosis indicating even spacing of trait values (Kraft et al. 2008). SDNDr measures the standard deviation of the distances between successive species (or populations or individuals) arranged along a trait axis, with low values indicating even spacing (Kraft and Ackerly 2010). Dividing by the range ensures that the metric is only influenced by relative spacing and not the absolute magnitudes of trait values.

I tested for environmental filtering and niche differentiation using a null model approach (Gotelli and Graves 1996) that involves comparing trait metrics of observed and randomly generated communities. I conducted separate tests that accounted for 1) interspecific trait variation only, using fixed species mean trait values; 2) interspecific and among-plot intraspecific trait variation, using plot-specific species mean trait values; or 3) interspecific and among- and within-plot intraspecific trait variation, using individual trait values. In tests using fixed species mean traits, communities were assembled by randomly drawing species from the overall pool found in the study site, weighted by frequency of occurrence across the 48 sample plots. Since trait metrics are sensitive to species richness (Cornwell and Ackerly 2009), separate draws were conducted for each level of observed species richness (2-17 species). In tests using plot-specific species mean traits, communities were assembled by randomly drawing species from the overall species pool, then randomly assigning each selected species one of its plot-specific mean trait values. In tests using individual trait values, communities were assembled by randomly drawing 50 individuals from the overall pool.

In addition to these community-level tests, I also tested for environmental filtering and niche differentiation within single species by comparing trait metrics of observed and randomly generated “neighborhoods” (defined as the sampled individuals of a species within a given plot). Randomized neighborhoods were created by randomly drawing individuals from the overall pool of individuals of the given species. Separate draws were conducted for each level of observed neighborhood sample size. I conducted analyses for the three most abundant species in the site: *Solidago altissima*, a strongly competitive clonal herb; *Bromus inermis*, a strongly competitive clonal grass; and *Poa pratensis*, a widespread but competitively subordinate grass. For each species, I only considered neighborhoods with a sample size of at least 8 individuals (*n* = 15 for *S. altissima*, 11 for *B. inermis*, 12 for *P. pratensis*), since estimates of trait metrics are unreliable when sample sizes are very small.

I repeated each randomization procedure 999 times to generate null distributions of community and neighborhood trait metrics. Using these null distributions, I tested for nonrandom trait patterns at the plot level (within individual plots) and site level (across all plots in the study site). For plot-level tests, *p* values were calculated as the proportion of randomized communities/neighborhoods with trait metrics less than the observed values. Site-level tests were conducted using standardized effect sizes (SES). SES values quantify the departure of observed trait metrics from the null expectation (Gotelli and McCabe 2002):

$$\mathrm{SES} = (I_{obs} - I_{null}) / \sigma_{null},$$

where $I_{obs}$ is the observed metric, $I_{null}$ is the mean of the null distribution, and $\sigma_{null}$ is the standard deviation of the null distribution. A negative SES value indicates that the observed trait metric is less than the mean of the null distribution, and vice versa. I tested whether standardized effect sizes across all plots were significantly less than zero using Wilcoxon signed-rank tests. Tests were one-tailed, because trait metrics were predicted to decrease as a result of environmental filtering (range and variance) or niche differentiation (kurtosis and SDNDr). Because I conducted multiple tests, I assessed significance using the false discovery rate method to decrease the probability of committing type I errors (Verhoeven et al. 2005).

## Results

### *Community assembly tests*

Community assembly tests using fixed species mean trait values (i.e., not accounting for intraspecific variation) detected evidence of environmental filtering acting on height (reduced range and variance) and SLA (reduced range) at the site level (Table 1; Fig. 1). Kurtosis was significantly less than the null expectation for SLA, indicating an even spread of SLA values among species due to niche differentiation (Table 1; Fig. 1). There was also evidence of niche differentiation acting on LDMC (reduced kurtosis), though this result was not considered statistically significant (*p* = 0.05). Although nonrandom trait patterns were detected in the site-level analysis, only a small proportion of individual plots (<10%) deviated significantly from the null expectation for any particular trait/metric (Table 1).

Accounting for among-plot intraspecific variation by using plot-specific species mean trait values revealed stronger signals of environmental filtering and niche differentiation than tests using fixed species means. At the site level, mean standardized effect sizes for almost all traits/metrics became more negative (indicating greater departures of trait metrics from null expectations) when intraspecific variation was included (Table 1). Accounting for intraspecific variation also increased the percentage of plots in which the observed trait metrics deviated significantly from the null expectations (Table 1).

Tests based on individual trait values revealed strikingly different patterns. At the site level, there was evidence of strong environmental filtering acting on all traits, including significantly reduced range for LDMC, a pattern not evident from tests based on species mean trait values (Table 1; Fig. 1). In contrast, there was no evidence for niche differentiation acting on any trait at the site level in the individual-based tests (Table 1; Fig. 1). In fact, kurtosis and SDNDr of all traits were greater than the null expectation, indicating individual trait values were less evenly spaced than expected at random. Although the site-level analysis using individual trait data provided little evidence for niche differentiation, patterns varied strongly among individual plots, with some plots showing significantly reduced kurtosis and SDNDr indicative of niche differentiation (Table 1). Variation in SES values among plots was not correlated with soil depth for any trait or metric ($p > 0.1$), indicating the strength of niche differentiation did not vary across the soil depth gradient.

*Single-species assembly tests*

In the single-species tests, there was evidence of strong environmental filtering acting on height (reduced range and variance) in *Solidago altissima*, *Bromus inermis*, and *Poa pratensis* at the site level (Table 2; Fig. 2), and significant deviations from the null expectations were detected in a large proportion of individual plots (33-55%; Table 2). In *P. pratensis*, the range and variance of SLA and LDMC were less than the null expectations at the site level and in most individual plots, providing evidence of strong environmental filtering (Fig. 2; Table 2). There was also weaker evidence of environmental filtering acting on LDMC (reduced range) in *B. inermis* ($P < 0.05$ but not considered statistically significant; Table 2). The only evidence of within-species niche differentiation was a reduction of kurtosis for height in *S. altissima* (Table 2; Fig. 2).

## Discussion

In this study, I used a null model approach to test for trait-based assembly processes in old-field plant communities and examined how accounting for intraspecific trait variation influenced the sensitivity of these tests. Overall, the tests provided strong evidence of environmental filtering, based on trait convergence within communities, and weaker evidence of niche differentiation, based on even spacing of trait values. As expected, accounting for intraspecific trait variation among plots improved the detection of these patterns. Tests using plot-specific trait values revealed stronger departures of community trait metrics from null expectations at the site level and detected environmental filtering and niche differentiation in more individual plots than tests using fixed species means (Fig. 1; Table 1). These results agree with those of Jung et al. (2010), who found that incorporating among-population variation improved detection of environmental filtering and niche differentiation in flood meadow communities. Together, these findings demonstrate the important role that intraspecific trait variation plays in plant community assembly and suggest that species are not simply filtered based on their mean trait values. Rather, intraspecific trait variation due to genetic variation and phenotypic plasticity allows adaptive shifts in traits within species in response to local selection pressures. These intraspecific responses have the potential to strongly influence the functional composition and diversity of plant communities, properties that are known to regulate ecosystem processes such as primary productivity and nutrient cycling (Garnier et al. 2004). Accounting for intraspecific trait variation may therefore be critical for understanding both community assembly and ecosystem functioning.

Community assembly tests based on individual trait data produced patterns strikingly different from those of tests based on fixed and plot-specific species mean trait values. In the only other study to my knowledge that has tested for trait-based community assembly using individual trait data, Paine et al. (2011) found that accounting for individual variation strengthened signals of environmental filtering and niche differentiation in tropical rain forest communities. Similarly, in the present study, signals of environmental filtering for all traits were strongest in tests that accounted for individual variation (Fig. 1). However, in contrast to my initial hypothesis, there was no evidence of niche differentiation in tests using individual trait data. This unexpected result was likely influenced by spatial patterns of dispersal and clonal expansion of old-field plant species (Hartnett and Bazzaz 1985). The null models used in this and previous community assembly studies assume global dispersal and random spatial distribution of individuals. However, individuals of many species in the study site were highly spatially aggregated. In the most extreme case, dominant clonal species such as *Solidago altissima* and *Bromus inermis* formed dense patches of genetically identical ramets (considered individuals in this study and in other trait sampling protocols, e.g., Cornelissen et al. 2003) that dominated many 1-m$^2$ sampling plots, leading to trait distributions that were highly constrained (low range and variance) and peaked (high kurtosis and SDNDr) compared to the expectation under a random spatial distribution of individuals. Treating entire clones or genets rather than ramets as individuals may have mitigated these patterns, but determining whether ramets were genetically distinct was beyond the scope of this study. Increasing the spatial grain of the study so that individual plots encompassed multiple clones may also have produced different patterns. Regardless, the results of this study highlight the potential importance of spatial dispersal patterns in determining the structure of plant communities and suggest that nonrandom trait distributions may arise from factors other than environmental filtering or niche differentiation.

In addition to providing evidence of nonrandom assembly at the community level, analysis of individual trait data revealed nonrandom assembly within single species. In the three most abundant species in the study site, *Solidago altissima*, *Bromus inermis*, and *Poa pratensis*, the range and variation of height within plots was less than the null expectation (Fig. 2), providing evidence of within-species environmental filtering. There was also evidence of environmental filtering acting on SLA and LDMC, but the strength of filtering varied among species. The dominant competitors in the study site, *S. altissima* and *B. inermis*, displayed little evidence of environmental filtering of SLA and LDMC, whereas the competitively subordinate *P. pratensis* showed strong convergence of SLA and LDMC values. These patterns are consistent with recent studies of intraspecific trait variation in experimental grassland communities (Roscher et al. 2011, Gubsch et al. 2011). These studies found that weak competitors employed phenotypic plasticity to adjust their trait values according to local environmental conditions, whereas strong competitors maintained consistent trait values across environments. More generally, there is increasing evidence that not only are intraspecific trait responses to environmental filters common and important at the community level (Cornwell and Ackerly 2009, Jung et al. 2010), but that those responses are highly variable among species (Thuiller et al. 2010, Albert et al. 2010).

Regardless of how trait data were summarized, the old-field plant communities examined in this study consistently displayed stronger patterns of trait convergence than of even spacing, indicating a primary role of environmental filtering in driving community assembly. These results correspond with those of previous studies conducted in a wide range of plant communities (e.g., Cornwell and Ackerly 2009, Jung et al. 2010, Mason et al. 2011, Paine et al. 2011), suggesting that environmental filtering is a widespread process influencing plant community assembly. In the present study, the strength of trait convergence differed among the three traits examined, indicating that traits vary in their responses to environmental filters. The dominant environmental gradient in the study site was soil depth, which varied from less than 20 cm to greater than 100 cm among plots. Soil depth is strongly tied to water and nutrient availability (Belcher et al. 1995) and therefore likely acts as a strong environmental filter. Height showed the strongest evidence of environmental filtering, with convergence on tall stature in plots with deep, fertile soil and therefore strong competition for light, and convergence on short stature in shallow, stressful plots (Siefert 2012). SLA and LDMC, indicators of plant resource use strategy, also showed evidence of environmental filtering, with a retentive strategy (low SLA, high LDMC) favored in shallow plots with low resource availability and an acquisitive strategy (high SLA, low LDMC) favored in deeper, more fertile plots (Siefert 2012). Compared to height, the strength of convergence was weak for SLA and LDMC, indicating relatively weak environmental filtering of these traits.

SLA and, to a lesser extent, LDMC also showed some evidence of niche differentiation. The even spacing of SLA and LDMC values within plots (Fig. 1) suggests that species may adopt different strategies in order to reduce overlap of resource use. For example, plants may partition the vertical gradient in light availability, with low-SLA plants adapted to high light occupying the canopy and high-SLA plants adapted to low light occupying the understory (Anten and Hirose 2003, Mason et al. 2011). Plants are also known to partition belowground resources (Ashton et al. 2010). Although I did not measure belowground traits, SLA and LDMC may be correlated with traits that relate to belowground resource capture, such as specific root length (Freschet et al. 2010). SLA and LDMC may therefore reflect whole-plant strategies of resource acquisition and use, and the large variation and even spacing of trait values within plots suggests species coexistence may be facilitated by differentiation of resource use strategies.

The results of this study complement those of a recent study (Siefert 2012) that analyzed spatial patterns of functional traits in the same old-field plant communities. Whereas the present study focused on functional trait distributions within plots, Siefert (2012) examined patterns of functional turnover between plots separated by distances of 4-1500 m. The results showed that nearby plots were more functionally similar than expected by chance, indicating functional convergence driven by environmental filtering at spatial scales up to about 10 m. However, although the present study detected signals of niche differentiation within 1-$m^2$ plots, Siefert (2012) found no evidence of niche differentiation at broader spatial scales. Together, these results demonstrate that environmental filtering is most important for community assembly at fine to intermediate scales (1-10 m), wheareas niche differentiation is most important at very fine scales (< 1 m). A similar result was obtained by Kraft and Ackerly (2010) in tropical tree communities, although at much broader spatial scales.

### *Conclusions*

This study demonstrates that environmental filtering and niche differentiation influence the assembly of old-field plant communities, generating nonrandom distributions of trait values, and that intraspecific trait variation plays an important role in these processes. Multiple lines of evidence now support a crucial role of intraspecific variation in a variety of ecological processes (e.g., Booth and Grime 2003, Hughes and Stachowicz 2004, Jung et al. 2010, Bolnick et al. 2011), and incorporating intraspecific trait variation in future functional ecology studies should facilitate advances in knowledge of community assembly and ecosystem functioning. By examining trait-based assembly patterns at the community and intraspecific level using a consistent framework, this study also highlights important links between community ecology and evolutionary biology. Processes such as environmental filtering and niche differentiation drive trait variation among species (species sorting), among genotypes (selection), and among genetically identical individuals (phenotypic plasticity); because communities incorporate all these sources of variation, understanding community assembly requires a unified view of these processes across levels of biological organization.

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**Table 1** Results of site- and plot-level community assembly tests based on fixed species mean, plot-specific species mean, and individual trait values. Mean SES values refer to average standardized effect sizes across all plots in the study site (*n* = 48). Negative SES values for range and variance indicate environmental filtering; negative values for kurtosis and SDNDr indicate niche differentiation. Bold type indicates statistical significance based on Wilcoxon signed-rank tests. Percent significant plots refer to the percentage of individual plots in which the observed trait metric was significantly less than the null expectation. Significance was assessed using the false discovery rate method (Verhoeven et al. 2005) to control for type I errors across multiple tests.

| Trait and test | Environmental filtering | | | | Niche differentiation | | | |
|---|---|---|---|---|---|---|---|---|
| | Range | | Variance | | Kurtosis | | SDNDr | |
| | Mean SES | % sig. plots | Mean SES | % sig. plots | Mean SES | % sig. plots | Mean SES | % sig. plots |
| Height | | | | | | | | |
| Fixed species mean | **-0.61** | 8.3 | **-0.50** | 6.3 | 0.00 | 0.0 | 0.16 | 0.0 |
| Plot-specific mean | **-0.99** | 22.9 | **-0.86** | 20.8 | -0.06 | 4.2 | -0.09 | 4.2 |
| Individual | **-2.47** | 52.1 | **-2.72** | 62.5 | 0.73 | 4.2 | 0.41 | 0.0 |
| Specific leaf area | | | | | | | | |
| Fixed species mean | **-0.13** | 2.1 | 0.04 | 2.1 | **-0.26** | 8.3 | -0.15 | 6.25 |
| Plot-specific mean | -0.24 | 6.3 | -0.05 | 8.3 | **-0.38** | 18.8 | -0.20 | 6.25 |
| Individual | **-0.47** | 8.3 | -0.29 | 8.3 | 0.31 | 16.7 | 0.09 | 8.33 |
| Leaf dry matter content | | | | | | | | |
| Fixed species mean | 0.19 | 0.0 | 0.23 | 0.0 | -0.14 | 2.1 | 0.07 | 0.0 |
| Plot-specific mean | 0.07 | 0.0 | 0.13 | 0.0 | -0.11 | 2.1 | 0.11 | 0.0 |
| Individual | **-0.61** | 12.5 | -0.47 | 31.3 | 1.88 | 12.5 | 1.69 | 0.0 |

**Table 2** Results of site- and plot-level assembly tests for single species. Mean SES values refer to average standardized effect sizes across all neighborhoods of a given species in the study site (*n* = 15 for *S. altissima*, 11 for *B. inermis*, 12 for *P. pratensis*). Negative SES values for range and variance indicate environmental filtering; negative values for kurtosis and SDNDr indicate niche differentiation. Bold type indicates statistical significance based on Wilcoxon signed-rank tests. Percent significant plots refer to the percentage of individual plots in which the observed trait metric was significantly less than the null expectation. Significance was assessed using the false discovery rate method (Verhoeven et al. 2005) to control for type I errors across multiple tests.

| Trait and species | Environmental filtering | | | | Niche differentiation | | | |
|---|---|---|---|---|---|---|---|---|
| | Range | | Variance | | Kurtosis | | SDNDr | |
| | Mean SES | % sig. plots | Mean SES | % sig. plots | Mean SES | % sig. plots | Mean SES | % sig. plots |
| Height | | | | | | | | |
| *S. altissima* | **-1.53** | 33.3 | **-1.31** | 26.7 | **-0.46** | 0.0 | -0.23 | 6.7 |
| *B. inermis* | **-2.12** | 36.4 | **-2.10** | 54.6 | 0.08 | 0.0 | -0.05 | 0.0 |
| *P. pratensis* | **-1.26** | 33.3 | **-1.25** | 33.3 | 0.33 | 0.0 | 0.40 | 0.0 |
| Specific leaf area | | | | | | | | |
| *S. altissima* | -0.24 | 6.7 | -0.23 | 13.3 | 0.00 | 6.7 | -0.13 | 0.0 |
| *B. inermis* | -0.35 | 9.1 | -0.29 | 18.2 | -0.09 | 0.0 | -0.15 | 9.1 |
| *P. pratensis* | **-1.55** | 41.7 | **-1.44** | 50.0 | 0.53 | 0.0 | 0.27 | 0.0 |
| Leaf dry matter content | | | | | | | | |
| *S. altissima* | -0.27 | 20.0 | -0.31 | 26.7 | 0.29 | 0.0 | 0.07 | 0.0 |
| *B. inermis* | -0.87 | 36.4 | -0.78 | 36.4 | -0.24 | 8.3 | -0.04 | 8.3 |
| *P. pratensis* | **-2.24** | 50.0 | **-1.86** | 66.7 | 0.59 | 0.0 | 0.15 | 0.0 |

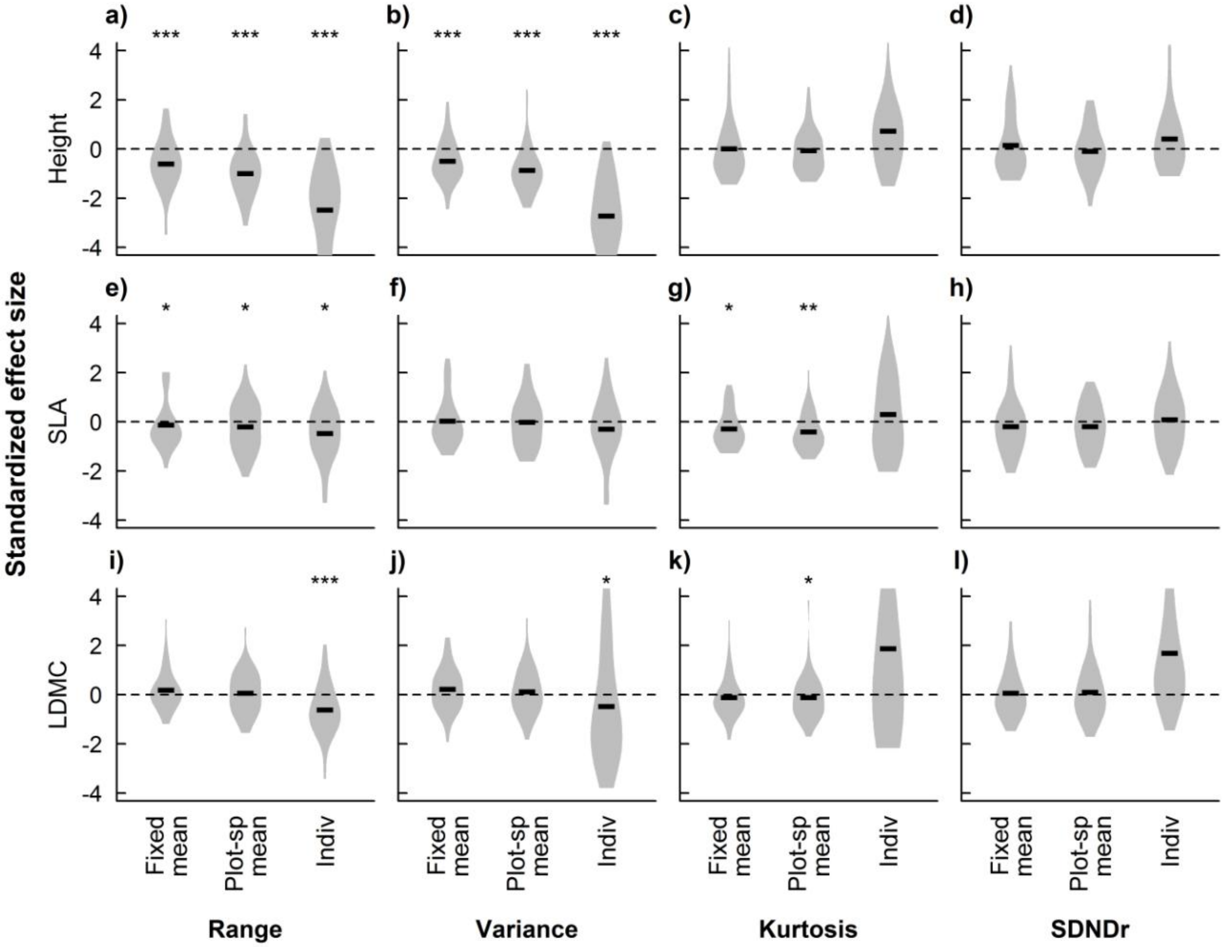

**Fig. 1** Results of community assembly tests using fixed species mean, plot-specific species mean, and individual trait values. Grey areas show the distribution of standardized effect sizes (SES; deviation of observed values from mean of the null distribution) of community trait metrics in observed plots ($n = 48$) estimated by kernel method. Horizontal bars show the mean SES across plots. Dashed lines show expected values under random community assembly (SES = 0). Negative SES values for range and variance indicate environmental filtering. Negative SES values for kurtosis and SDNDr indicate niche differentiation. Asterisks represent *p* values from Wilcoxon signed-rank tests of the hypothesis that observed trait metrics across all plots are less than the null expectation. "*": $p < 0.05$, "**": $p < 0.001$, "***": $p < 0.0001$. SLA, specific leaf area; LDMC, leaf dry matter content.

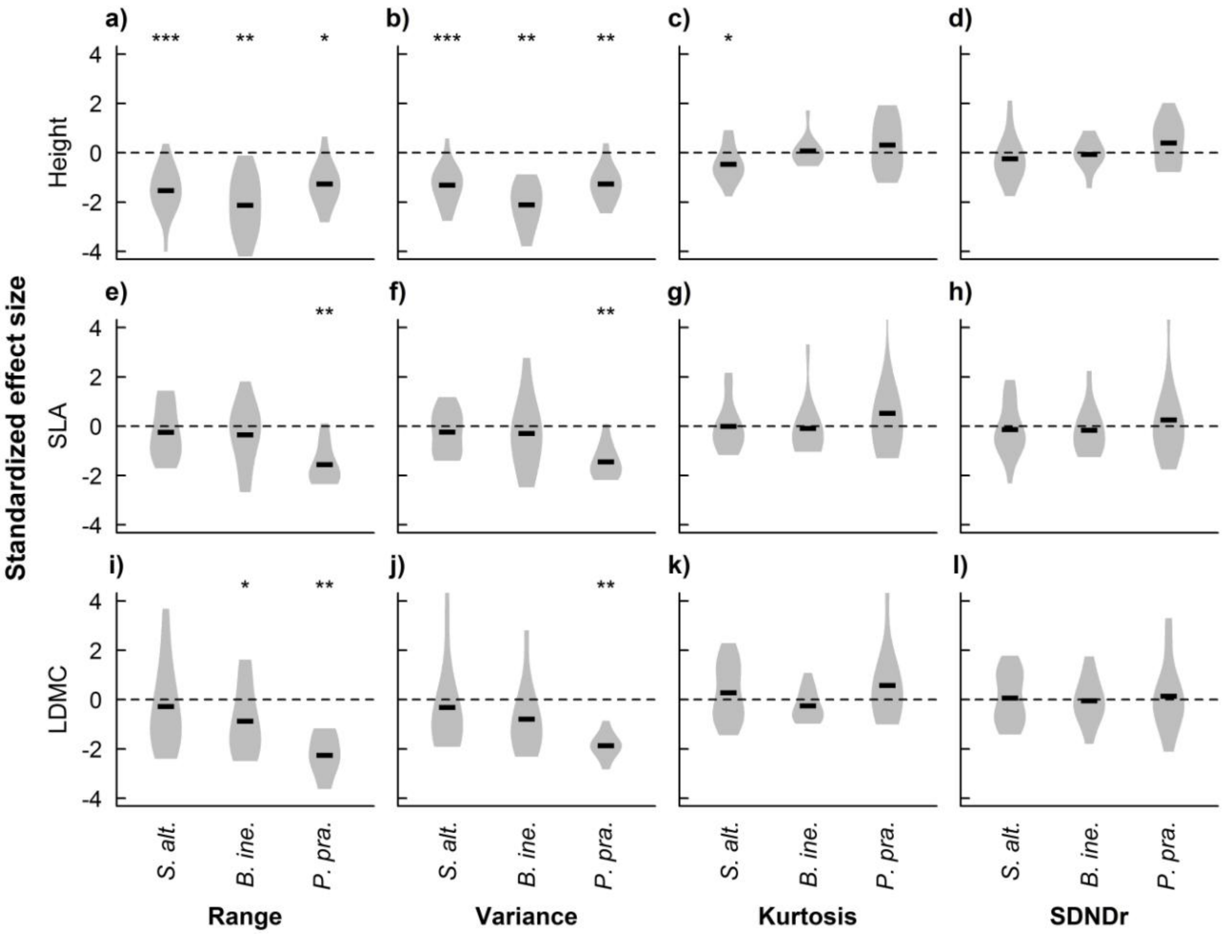

**Fig. 2** Results of single-species assembly tests. Results are shown for the three most abundant species in the study site: *Solidago altissima* (*S. alt.*), *Bromus inermis* (*B. ine*.), and *Poa pratensis* (*P. pra*.). Only plots containing at least eight individuals per species were included in the analysis. *S. altissima*, n = 15; *B. inermis*, n = 11; *P. pratensis*, n = 12. SLA, specific leaf area; LDMC, leaf dry matter content. For explanation of graphs, see Figure 1

# Chapter 4

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## Community functional responses to soil and climate at multiple spatial scales: when does intraspecific variation matter?

Andrew Siefert, Jason D. Fridley, and Mark E. Ritchie

### Abstract

Despite increasing evidence of the importance of intraspecific trait variation in plant communities, its role in community trait responses to environmental variation, particularly along broad-scale climatic gradients, is poorly understood. We analyzed functional trait variation among early-successional herbaceous plant communities (old fields) across a 1200-km latitudinal extent in eastern North America, focusing on four traits: vegetative height, leaf area, specific leaf area (SLA), and leaf dry matter content (LDMC). We determined the contributions of species turnover and intraspecific variation to between-site functional dissimilarity at multiple spatial scales and community trait responses to edaphic and climatic factors. Among-site variation in community mean trait values was generated by a combination of species turnover and intraspecific variation, with species turnover making a greater contribution for all traits. The relative importance of intraspecific variation decreased with increasing geographic and environmental distance between sites for SLA and leaf area. Community trait responses to environmental variation were primarily driven by species turnover. Intraspecific variation was most important for responses of vegetative height and responses to edaphic compared to climatic factors. Individual species displayed strong trait responses to environmental factors in many cases, but these responses were highly variable among species and did not usually scale up to the community level. These findings provide new insights into the role of intraspecific trait variation in plant communities and the factors controlling its relative importance. The contribution of

intraspecific variation to community trait responses was greatest at fine spatial scales and along edaphic gradients, while species turnover dominated at broad spatial scales and along climatic gradients.

## Introduction

Understanding and predicting how communities respond to environmental variation is a central goal of ecology, and ecologists are increasingly adopting trait-based approaches to study these responses (Lavorel and Garnier 2002, McGill et al. 2006, Suding et al. 2008). Because an organisms' functional traits directly influence its responses to and effects on the environment (Diaz and Cabido 2001), information about the traits of individuals in a community (i.e. community trait distributions) offers insights into community assembly mechanisms and can be used to predict community composition and ecosystem functioning (Chapin et al. 2000, Shipley et al. 2006, Suding et al. 2008). Understanding how community trait distributions, particularly community-weighted mean trait values (CWMs), respond to environmental variation has therefore become a major focus in community ecology (Shipley et al. 2006, Cornwell and Ackerly 2009, Ricotta and Moretti 2011).

Community trait distributions may change along environmental gradients through a combination of species turnover (changes in species presence and relative abundance) and intraspecific trait responses, including genetic adaptation and phenotypic plasticity (Ackerly 2003, Cornwell and Ackerly 2009). Most studies examining trait-environment relationships in plant communities have assigned a single, fixed trait value to each species, thereby accounting only for trait variation due to species turnover and ignoring intraspecific variation (Lepš et al. 2011). However, recent studies have shown that intraspecific variation may also play an important role in community trait responses to environmental variation. For example, Jung et al. (2014) found that intraspecific variation accounted for up to 44% of the change in CWMs of several key functional traits across an elevation gradient in flood meadow communities. Similarly, Lepš et al. (2011) found that community-level responses of multiple traits to fertilization and mowing in grassland communities were primarily driven by intraspecific responses. Results of these and other recent studies (e.g., Pérez-Ramos et al. 2012, Auger and Shipley 2012, Kichenin et al. 2013) demonstrate that accounting for intraspecific trait variation may be crucial for quantifying community trait responses to the environment, but the relative magnitude of intraspecific variation has varied strongly among and within studies. The next step beyond simply quantifying intraspecific trait variation is to understand the factors controlling its relative importance. Determining when and where intraspecific variation matters at the community level is a major concern for plant ecology, with important implications for predicting community and ecosystem responses to global change (Albert et al. 2011).

One factor that may influence the relative importance of intraspecific trait variation is the spatial scale of the studied communities. Previous studies have shown that interspecific trait variation increases with increasing spatial scale due to species turnover driven by dispersal limitation and environmental filtering along gradients of increasing breadth (Swenson et al. 2011, Siefert et al. 2013). Intraspecific variation is also expected to increase with increasing spatial scale, as more genetic and plastic variability within species is included, but it is expected saturate at large scales once the entire range and thus potential trait variation of individual species is reached (Violle and Jiang 2009, Albert et al. 2011). The relative magnitude of interspecific vs. intraspecific variation is therefore expected to increase with increasing spatial scale and breadth of environmental gradients (Albert et al. 2011). This hypothesis has not been tested to our knowledge, in part due to the lack of studies measuring intraspecific variation at broad spatial scales.

Another factor that may influence the relative importance of intraspecific trait variation is the type of environmental gradient considered. Previous studies have shown that intraspecific variation may be important for community responses to local-scale edaphic variation (Cornwell and Ackerly 2009, Jung et al. 2010), but its role in responses to broad-scale climatic variation has not been examined. Determining whether the relative importance of intraspecific variation differs between edaphic and climatic gradients is a useful step towards a more general understanding of when intraspecific variation matters at the community level. Knowledge of the role of intraspecific variation is also relevant for predicting responses of communities to climate change (Jung et al. 2014). If community trait responses to climate are driven by species turnover, climate change will result in large changes in community composition and species distributions. On the other hand, if species are able to cope with climatic variation through genetic adaptation or phenotypic plasticity, community composition may remain stable (Grime et al. 2008, Lloret et al. 2012). Assessing the degree to which intraspecific variation contributes to community trait responses to strong spatial climatic gradients will provide insights into which of these scenarios is most likely in the face of future climate change.

In this study, we examined community functional responses to environmental variation in old-field plant communities across eastern North America. The study was conducted on a broad spatial extent (1200 km in latitude), allowing us to test the relative importance of species turnover vs. intraspecific variation to community trait patterns along strong edaphic and climatic gradients at multiple spatial scales. Specifically, we addressed the following questions: 1) What is the relative contribution of species turnover vs. intraspecific variation to among-site trait variation, and how is this influenced by spatial scale? We hypothesized that the relative importance of intraspecific trait variation would decrease with increasing spatial scale and breadth of environmental gradients. 2) How do community mean trait values respond to edaphic and climatic variation, and what are the relative contributions of species turnover and intraspecific variation to these responses? We hypothesized that intraspecific variation would be more important for community responses to edaphic compared to climatic factors.

## Methods

### *Study site*

We surveyed vegetation and functional traits in 22 old fields across the eastern United States in June-August, 2012. The study area extended from central South Carolina (30°40’’N) to central New York (43°10’’N), spanning approximately 1200 km of latitude (Fig. 1). The study area encompasses strong variation in both climatic and edaphic factors (Table 1), making it a useful system for comparing the influence of these factors on community functional composition. Moving from south to north, there is a strong decrease in mean annual temperature (17.9 to 6.9 °C) and growing season length (263 to 156 annual frost-free days) and a weaker decrease in mean annual precipitation (1330 to 976 mm). In addition, with increasing latitude there is a strong increase in soil fertility and shift from coarse to fine-textured soils driven primarily by recent glaciation history (Wright and Fridley 2010).

The fields sampled had different histories of agricultural land use, but all had been abandoned for at least 5 years prior to sampling. Fields were maintained in early stages of succession by mowing in late summer or fall once every 1-2 years. Time since mowing was not significantly related to any environmental variable or response variable measured and was not included in the analyses. No burning, livestock grazing, or herbicide application had occurred in any of the fields within the past 5 years. Vegetation in the fields was almost entirely herbaceous, including a mix of grasses and forbs. Dominant species included goldenrods (e.g., *Solidago altissima*, *S. rugosa*) and grasses (e.g., *Andropogon virginicus*, *Schedonorus pratensis*, *Poa pratensis*). While there is considerable turnover in species composition across the study area, many of the dominant species are widely distributed, creating the potential for intraspecific variation to play an important role in community trait patterns.

### *Vegetation and environmental data*

In each field, we recorded the percent cover of vascular plant species in 20 1-m$^2$ quadrats arrayed along transects. The number and arrangement of transects and spacing between quadrats varied depending on the size and shape of the field. Cover values in the 20 quadrats were pooled to obtain the relative cover of each species in each field. We collected soil samples in four randomly selected quadrats in each field and pooled samples for physical and chemical analysis. Percent sand, silt, and clay were determined using the hydrometer method (Bouyoucos 1962). Percent organic matter was measured as loss on ignition at 360 °C. Soil samples were analyzed for cation exchange capacity (CEC), pH, available nitrogen (nitrate plus ammonium; KCl extraction/cadmium reduction method), available (Bray II) phosphorus (Bray and Kurtz 1945), and available (Mehlich 3 extractant) sulfur, calcium, magnesium, potassium, iron, manganese, and aluminum (Mehlich 1984). Soil analyses were performed by Brookside Laboratories, Inc., New Bremen, OH, USA. We accessed daily precipitation and temperature data (1980-2010) for each site from Daymet (http://www.daymet.org). Using these data, we derived mean annual temperature, mean temperature of the coldest month, mean temperature of the warmest month, temperature seasonality (standard deviation of monthly mean temperature), annual frost-free days, annual growing-degree days (base of 5 °C and cap of 30 °C), annual precipitation, precipitation in the driest month, precipitation in the wettest month, and precipitation seasonality (CV of monthly precipitation). Environmental data were log transformed as necessary to improve normality.

### *Trait data*

We focused on four traits that relate to different aspects of plant functional strategy: vegetative height, leaf area, specific leaf area (SLA) and leaf dry matter content (LDMC). Vegetative height is related to light acquisition and competitive ability (Gaudet and Keddy 1988, Wright et al. 2005). Leaf area relates to energy and water balance and tolerance to environmental stress (Ackerly and Reich 1999). SLA is a central component of the leaf economics spectrum, which captures the tradeoff between rapid growth and resource conservation (Wright et al. 2004). LDMC is also associated with the leaf economics spectrum as well as leaf water balance and resistance to physical stress (Wilson et al. 1999, Perez-Harguindeguy et al. 2013).

In each field, we measured functional traits of species that collectively accounted for 80-100% of the total vegetation cover. This sampling threshold has been shown to provide robust estimates of community mean trait values (Pakeman et al. 2009). In each field, we selected five mature- and healthy-looking individuals of each species from different areas of the field for trait measurements. Vegetative height was measured as the distance (cm) from the base to the highest part of the general canopy of the plant. We selected one young, fully-expanded, upper canopy leaf per individual for leaf trait measurements. Leaf area and fresh mass were measured on fully rehydrated leaves (Garnier et al. 2001), and dry mass was measured on leaves oven dried at 80 °C for 48 hours (Perez-Harguindeguy et al. 2013). SLA was calculated as leaf area divided by dry mass ($mm^2/mg$), and LDMC was calculated as leaf dry mass divided by fresh mass.

### *Data analysis*

Our first analysis partitioned the contributions of species turnover and intraspecific variation to among-site variation in functional traits following the approach of de Bello et al. (2011). For each field, we calculated three types of community-weighted mean trait values. 1) "Total CWMs", calculated as the abundance-weighted average of site-specific species mean trait values. Among-site variation in total CWMs may be generated by a combination of species turnover and intraspecific trait variation. 2) "Interspecific CWMs", calculated as the abundance-weighted average of overall species mean trait values (i.e., average across all study sites). Variation in interspecific CWMs is generated by species turnover only. 3) "Intraspecific CWMs", calculated as the abundance-weighted average of the difference between each species' site-specific and overall mean trait value. Variation in intraspecific CWMs is generated by intraspecific trait variation only. Using the total, interspecific, and intraspecific CWMs, we partitioned trait variation among sites into species turnover, intraspecific variation, and covariation components using the sum of squares decomposition approach of de Bello et al. (2011). Positive covariation indicates that species turnover and intraspecific variation reinforce each other (i.e., sites dominated by species with high trait values also have individuals with high trait values for their species), while negative covariation indicates that species turnover and intraspecific variation oppose each other (i.e., sites dominated by species with high trait values have individuals with low trait values for their species).

Our second analysis assessed community trait responses to edaphic and climatic variation and partitioned the contributions of species turnover and intraspecific variation to these responses. Due to strong correlations among variables, we attempted to reduce the dimensionality of the environmental data using principal components analysis, but the primary axes identified left much unexplained variation and were poorly related to community trait values. We therefore selected subsets of climatic (mean annual temperature and annual precipitation) and edaphic variables (sand, pH, CEC, organic matter, available nitrogen, and available phosphorus) that were expected to be important drivers of community functional structure and were not strongly correlated with each other ($r < 0.5$). We modeled relationships between community-weighted mean trait values and edaphic and climatic factors using multiple linear regressions with the full subset of edaphic or climatic variables as predictors. We then performed stepwise model selection by $\mathrm{AIC_c}$ to select the best edaphic and climatic model for each trait. To quantify the contributions of species turnover, intraspecific variation, and their covariation to overall community trait responses, we partitioned the variance explained by the edaphic and climatic models using the sum of squares decomposition described above (de Bello et al. 2011). To examine community trait responses to specific environmental factors, we conducted a similar variance partitioning analysis using single environmental variables as predictors. We also used regression analyses to quantify and compare trait responses of the five most abundant and widely distributed species in the study area: forbs *Solidago altissima* and *Solidago rugosa* and grasses *Schedonorus pratensis*, *Poa pratensis*, and *Andropogon virginicus*.

Our third analysis tested whether the between-site trait variation and the relative contribution of species turnover vs. intraspecific variation increased with increasing spatial and environmental distance. First, we calculated the geographic distance and environmental distance between each pair of sites in the study area (22 sites, resulting in 231 pairs). Geographic distance between sites was calculated as great circle distance and ranged from 6.5 to 1,151 km. Environmental distance was calculated as Euclidean distance using scaled environmental variables. Next, for each pair of plots we calculated the total dissimilarity in CWMs, dissimilarity due to species turnover, and dissimilarity due to intraspecific variation by applying the sum of squares decomposition described above (de Bello et al. 2011) to each plot pair. We quantified the relative importance of species turnover vs. intraspecific variation by taking the log of the ratio of the species turnover and intraspecific variation components. This created a symmetric measure of the relative contribution of species turnover vs. intraspecific variation to between-site trait dissimilarity, with positive values indicating a greater contribution of species turnover and negative values a greater contribution of intraspecific variation. We tested whether total between-site trait dissimilarity, dissimilarity due to species turnover, dissimilarity due to intraspecific variation, and the relative importance of turnover vs. intraspecific variation varied as a function of geographic and environmental distance using Mantel tests. Because geographic and environmental distance were strongly correlated (Mantel $r = 0.70$), we also used partial Mantel tests to test for the effect of either geographic or environmental distance while controlling for the other.

All analyses were conducted in R (R Core Development Team 2012) using the fields (Furrer et al. 2012), vegan (Oksanen et al. 2012), and ecodist (Goslee and Urban 2007) packages.

## Results

### *Partitioning among-site trait variation*

Among-site variation in community mean trait values was generated by a combination of species turnover and intraspecific variation, with species turnover making the greater contribution for each trait (Table 2). For height, SLA, and LDMC the contribution of species turnover was 2-2.5 times greater than that of intraspecific variation. For leaf area, almost all variation was due to species turnover (Table 2). There was positive covariation between species turnover and intraspecific variation for height and LDMC, indicating that the effects of species turnover and intraspecific variation reinforced each other (i.e., sites dominated by species with high values of those traits also tended to have individuals with high trait values for their species). There was little covariation between species turnover and intraspecific variation for leaf area or SLA (Table 2).

### *Community trait responses to soil and climate and relative contributions of species turnover vs. intraspecific variation*

The best linear models relating environmental variables to community mean trait values varied among traits, but for all traits edaphic factors explained more variation (16-50%) than climatic factors (<20%; Table 3). For example, CWM height was best explained by a combination of soil pH, CEC, organic matter, and available phosphorus, and the best model for CWM leaf area included soil organic matter and available phosphorus (Table 3). CWM SLA was the trait most strongly influenced by climate, showing a significant decrease with increasing mean annual temperature (Table 3).

Community trait responses to the environment were generated primarily by species turnover (Fig. 2), but the importance of intraspecific variation depended on the trait and environmental factor. Intraspecific variation contributed most strongly to community responses of height. For all traits, both the total and relative contribution of intraspecific variation to community trait responses was greater for responses to edaphic compared to climatic factors (Fig. 2). Similar results were obtained when using single environmental variables as predictors (Table 4). For example, the only cases in which intraspecific variation contributed more than species turnover were the responses of CWM height to soil cation exchange capacity and available P (Table 4). Positive covariation between species turnover and intraspecific variation contributed strongly to community responses of height and to a lesser extent SLA, indicating that changes due to species turnover and intraspecific variation reinforced each other (Fig. 2). In contrast, there was weak or even negative covariation between species turnover and intraspecific variation effects for leaf area and LDMC.

Individual species had strong trait responses to environmental variables in many cases, but these responses tended to be highly idiosyncratic, differing in strength and direction among species (Fig. 3; Table 5). There were no obvious patterns in the strength or consistency of intraspecific trait responses across species, traits, or environmental variables.

### *Effects of geographic and environmental distance on between-site trait dissimilarity and species turnover vs. intraspecific variation effects*

The influence of geographic and environmental distance on community trait dissimilarity varied among traits. Between-site dissimilarity in CWM SLA increased significantly with increasing geographic ($r = 0.23$; $P = 0.02$) and environmental distance ($r = 0.20$; $P = 0.04$; Fig. 4), indicating that nearby and environmentally similar sites had similar mean SLA. There was also a marginally significant increase in between-site dissimilarity in CWM leaf area with increasing environmental distance ($r = 0.17$; $P = 0.07$; Fig. 4). For both traits, increases in functional dissimilarity were driven by increases in species turnover, whereas intraspecific variation was insensitive to both geographic and environmental distance (Table 6). As a result, the relative importance of species turnover vs. intraspecific variation increased with increasing geographic ($r = 0.33$; $P < 0.01$) and environmental distance ($r = 0.24$; $P < 0.01$) for SLA and environmental distance for leaf area ($r = 0.12$; $P = 0.08$; Fig. 4). In contrast, between-site dissimilarity in CWMs and the relative importance of turnover vs. intraspecific variation were not related to geographic or environmental distance for height or LDMC (Fig. 4).

Due to the strong correlation between geographic and environmental distance, it was generally not possible to separate the effects of space vs. environment on community trait dissimilarity (partial Mantel tests not statistically significant; Table 6). The only exception was a positive relationship between geographic distance and the relative importance of species turnover for SLA even after removing the effect of environmental distance (partial $r = 0.24$; $P = 0.01$; Table 6).

## Discussion

Recent studies have shown that intraspecific trait variation may play a fundamental role in responses of plant communities to environmental variation (Lepš et al. 2011, Kichenin et al. 2013, Jung et al. 2014), but many questions remain about when intraspecific variation matters at the community level and the factors controlling its relative importance. By examining intraspecific trait variation in plant communities at an unprecedented spatial extent (1200 km), we were able to address unresolved questions about the relative role of intraspecific variation in community responses to the environment. We found that variation in mean trait values among herbaceous old-field communities was driven primarily by species turnover, but the relative importance of intraspecific variation depended strongly on the trait, environmental factor, and spatial scale considered. In particular, intraspecific variation was more important for responses to edaphic compared to climatic factors, and its relative importance decreased with increasing spatial scale and the related increase in breadth of environmental gradients for two of the four traits examined. These findings contribute to a more general understanding of the role intraspecific trait variation in plant communities, with implications for understanding community assembly and predicting community responses to global change.

### *Role of intraspecific variation in community trait responses to environment*

Community trait responses to environmental variation were primarily driven by species turnover, but intraspecific variation tended to play a larger role in community trait responses to edaphic compared to climatic variation. This finding may reflect differences in the spatial scale on which edaphic and climatic factors vary. Edaphic factors tend to vary on finer spatial scales than climatic factors (Lechowicz and Bell 1991), so the geographic ranges of individual species are likely to include a relatively larger proportion of the total edaphic variation than the total climatic variation found in a region. As a result of species being distributed widely along edaphic gradients but narrowly along climatic ones, there is greater potential for strong intraspecific trait responses to drive community-level trait shifts along edaphic gradients. In addition, fine-scale environmental heterogeneity is known to promote the evolution of adaptive phenotypic plasticity (Via and Lande 1985, Baythavong 2011), raising the possibility that plants have stronger plastic trait responses to fine-scale edaphic compared to broad-scale climatic factors. Future research should assess the strength of intraspecific trait responses to different environmental factors and how this relates to the spatial scale at which those factors vary.

The relative importance of intraspecific variation also varied among traits. The contribution of intraspecific variation to total among-site variation and responses to environmental factors was greatest for vegetative height. In particular, intraspecific variation played a large role in community responses to edaphic factors such as available phosphorus. This finding is in line with previous studies showing that plant height is highly responsive to soil resource availability within species and that intraspecific variation contributes strongly to community-level variation in height (Lepš et al. 2011, Gross and Börger 2013, Dantas et al. 2013). In contrast, the relative contribution of intraspecific variation was smallest for leaf area and LDMC, traits that are known to be less plastic and for which intraspecific variation tends to be much smaller than interspecific variation (Wilson et al. 1999, Roche et al. 2004).

What explains the relatively weak contribution of intraspecific variation to most community-level trait-environment relationships observed in this study? The effect of intraspecific trait responses seen at the community level is the aggregate of responses of many individual species. Although traits of individual species responded strongly to the environment in many cases, these responses were highly idiosyncratic, differing in both strength and direction. As a result, they often cancelled out and generally failed to scale up to the community level. Previous studies examining trait variation in multiple species along an environmental gradient have also found intraspecific trait responses to be highly variable (Albert et al. 2010, De Frenne and Graae 2013, Kichenin et al. 2013). This variability may have several causes. First, species may respond to environmental variation by altering their multivariate functional strategies rather than single traits in isolation (Jung et al. 2014). Functional tradeoffs can result in multiple trait combinations that are equally adaptive in a given environment (Marks and Lechowicz 2006), so responses of single traits may be variable. Second, traits respond not only to the abiotic environment, but also to biotic interactions (Callaway et al. 2003). The trait response of a particular species to an environmental change will therefore depend not only on the direct influence of the environment, but also on changes in biotic interactions mediated by traits of the target species and its neighbors (Kichenin et al. 2013). Third, some traits may have unimodal responses to environmental gradients, such that trait values are maximized at a species' environmental optimum. The observed direction of the intraspecific trait responses may therefore vary depending on the part of the gradient examined in relation to the environmental ranges and optima of the sampled species (Albert et al. 2010).

It should be noted that community trait-environment relationships observed in this study were generally weak, with much unexplained variation. This is probably due in part to a strong influence of site history on community assembly (Chase 2003). Sites with similar edaphic and climatic conditions were often dominated by functionally dissimilar species, suggesting that unknown past management regimes, along with dispersal history and stochastic effects may have played a large role in determining the functional composition of these early-successional communities. In addition, it is likely that unmeasured environmental variables such as nitrogen supply rate and midsummer water potential are the cause of some of the unexplained trait variation.

### *Influence of spatial scale on the relative importance of species turnover vs. intraspecific variation*

The broad spatial extent of our study allowed us to examine the influence of spatial scale on the relative importance of species turnover vs. intraspecific variation. Albert et al. (2011) hypothesized that the relative importance of intraspecific variation should decrease with increasing spatial scale and the accompanying increase in environmental heterogeneity. We found limited support for this hypothesis for two of the four traits examined in the study, leaf area and SLA. Trait variation due to species turnover increased with increasing geographic and environmental distance for both traits, reflecting the effects of environmental filtering, dispersal limitation, or both (Siefert et al. 2013). In contrast, intraspecific trait variation was insensitive to both geographic and environmental distance, indicating that intraspecific variation in the studied communities was for the most part spatially random or driven by unmeasured fine-scale environmental variation. This agrees with the findings of Albert et al. (2010) that most intraspecific variance in plant traits is found at fine spatial scales, i.e. within rather than between populations along an environmental gradient.

This study is the first to our knowledge to assess the contribution of intraspecific variation to community-level trait variation across a broad geographic extent encompassing strong climatic variation. The relative importance of intraspecific variation observed in this study was generally less than that observed for the same traits in previous local-scale studies of grassland communities. For example, Yuanzhi Li et al. (unpublished data) showed that intraspecific variation was the primary source of community-level changes in height, SLA, and LDMC along a soil moisture gradient in subalpine meadow communities. Similarly, Kichenin et al. (2013) found that intraspecific variation drove community shifts in SLA along an elevation gradient. At relatively small distances (<200 km), we also found that intraspecific variation contributed more than species turnover to among-site variation in SLA. For height, leaf area and LDMC, species turnover was the primary source of between-community variation even at the smallest distances resolvable in this study (6.5 km), but it is possible that a similar transition from intraspecific variation to species turnover as the main source of among-community trait variation occurred at finer spatial scales.

### *Implications*

Our results have several potentially interesting implications for plant community ecology. First, with the growing recognition that intraspecific variation may play an important role in plant communities (Violle et al. 2012) and the great effort required to measure it (Baraloto et al. 2010), there is a need for information to help researchers decide when it should be considered in plant ecology studies. To this end, Albert et al. (2011) proposed that intraspecific variation might be negligible and therefore safely ignored at very broad spatial scales encompassing strong environmental gradients. Our results provide support for this recommendation by showing for the first time that the relative importance of intraspecific variation in some traits decreases with increasing geographic and environmental distance between sites, so that species turnover dominates at very broad scales. Second, community trait-environment relationships are commonly used to infer community assembly mechanisms, particularly trait-mediated environmental filtering (Cornwell and Ackerly 2009), but most studies have only considered interspecific trait variation. Our findings suggest that different environmental filters or selection pressures operate at different levels of organization within communities. Specifically, climatic factors may filter species based on their mean trait values, resulting in species turnover along broad-scale climatic gradients, whereas intraspecific variation may be more important for responses to edaphic filters. Third, the dominance of species turnover in driving community trait responses to spatial climatic gradients suggests that species turnover will also play a large role in responses of the studied communities to future predicted climate change (Northeast Climate Impacts Assessment 2006)

To conclude, intraspecific trait variation may play an important role in community trait responses to the environment in some situations, and there is a need for empirical data to generalize when and to what extent it matters at the community level. We found that functional responses of old-field plant communities to environmental variation at broad spatial scales were primarily driven by species turnover, but several factors influenced the relative importance of intraspecific variation. Specifically, intraspecific variation was more important for responses of vegetative height compared to leaf traits, responses to edaphic compared to climatic gradients, and at fine compared to broad spatial scales. Future research should examine whether our findings extend to other plant communities.

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**Table 1.** Mean, standard deviation, and range of environmental variables included in regression analyses.

| Variable | Abbreviation | Unit | Mean | Standard deviation | Range (max-min) |
|---|---|---|---|---|---|
| Mean annual temperature | MAT | °C | 11.95 | 3.0 | 11.0 |
| Mean annual precipitation | MAP | mm | 1132 | 99.2 | 354 |
| Cation exchange capacity | CEC | mEq $kg^{-1}$ | 79.4 | 30.0 | 11.23 |
| Soil pH | pH |  | 5.6 | 0.37 | 1.5 |
| Soil available phosphorus | P | mg $kg^{-1}$ | 49.2 | 53.8 | 200.0 |
| Soil available nitrogen | N | ppm | 6.31 | 2.87 | 10.4 |
| Soil organic matter | OM | % | 4.98 | 1.73 | 7.38 |
| Sand | Sa | % | 41.75 | 18.82 | 71.91 |

**Table 2.** Percentages of total variation in community-weighted mean trait values due to species turnover, intraspecific variation and their covariation. Positive covariation indicates that sites dominated by species with high trait values also have individuals with higher than average trait values for their species.

| Trait | Species turnover | Intraspecific variation | Covariation |
|---|---|---|---|
| Height | 52% | 22% | 26% |
| Leaf area | 89% | 7% | 4% |
| SLA | 70% | 28% | 2% |
| LDMC | 52% | 27% | 21% |

**Table 3.** Relationships between community-weighted mean trait values and environmental variables measured in the study. Results are shown for the best edaphic and climatic models for each trait as determined by stepwise selection, including the predictor variables retained in each model and the direction of their effects (negative or positive) on the community trait value. Abbreviations: SLA, specific leaf area; LDMC, leaf dry matter content; predictor variables abbreviated as in Table 1.

| Trait | Model | Predictors | $R^2$ |
|---|---|---|---|
| Height | Edaphic | CEC (+), pH (-), OM (-), P (+) | 0.50 |
| | Climatic | MAP (-) | 0.17 |
| Leaf area | Edaphic | OM (-), P (-) | 0.25 |
| | Climatic | MAT (+) | 0.16 |
| SLA | Edaphic | pH (-), OM (+) | 0.26 |
| | Climatic | MAT (-) | 0.20 |
| LDMC | Edaphic | N (-), sand (+) | 0.16 |
| | Climatic | ns | - |

**Table 4.** Decomposition of variation in community-weighted mean trait values explained by single environmental variables. Total among-site variance is decomposed into species turnover, intraspecific variation, and covariation components. Values shown are percentages of total among-site variance.

| Predictor | Vegetative height | | | Leaf area | | | SLA | | | LDMC | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Turn. | Intra. | Cov. | Turn. | Intra. | Cov. | Turn. | Intra. | Cov. | Turn. | Intra. | Cov. |
| Mean annual temp. (°C) | 4.5% | 0.2% | 1.8% | 16.1% | 0.0% | -0.4% | 16.1% | 0.3% | 4.0% | 3.8% | 0.6% | -3.1% |
| Mean annual precip. (mm) | 7.3% | 2.6% | 8.8% | 1.3% | 1.0% | -2.2% | 1.1% | 0.3% | -1.1% | 1.2% | 0.0% | -0.2% |
| Soil CEC (mEq kg$^{-1}$) | 0.5% | 4.2% | 2.9% | 4.7% | 0.6% | -3.3% | 0.2% | 0.0% | 2.7% | 4.3% | 0.1% | 1.7% |
| Soil pH | 4.8% | 0.3% | -2.5% | 2.9% | 0.0% | 0.6% | 4.3% | 4.5% | 8.7% | 0.0% | 0.0% | 0.0% |
| Soil organic matter (%) | 0.0% | 0.1% | 0.0% | 9.3% | 0.1% | 1.8% | 14.8% | 0.1% | 1.8% | 7.9% | 0.1% | -2.1% |
| Soil available P (mg kg$^{-1}$) | 4.8% | 9.5% | 13.5% | 11.1% | 1.3% | -7.6% | 2.4% | 0.6% | 2.5% | 0.6% | 0.5% | -1.2% |
| Soil available N (ppm) | 2.5% | 1.1% | -3.3% | 0.0% | 0.1% | -0.1% | 0.0% | 0.7% | 0.1% | 3.1% | 1.1% | 3.6% |
| Soil sand content (%) | 2.4% | 1.0% | 3.1% | 2.1% | 0.7% | -2.4% | 4.2% | 0.9% | -3.9% | 5.3% | 0.2% | -2.0% |

**Table 5.** Slopes of intraspecific trait-environment relationships for the five most frequently occurring species in the study area. *Andropogon virginicus* (n = 8 sites), *Poa pratensis* (n = 13), *Schedonorus pratensis* (n = 15), *Solidago altissima* (n = 12), and *Solidago rugos*a (n = 8). Environmental variables were scaled to mean = 0 and sd = 1 to allow comparison of slopes among variables.

| Trait and species | Mean annual temp. (°C) | Mean annual precip. (mm) | CEC (mEq kg$^{-1}$) | pH | Organic matter (%) | Available P (mg kg$^{-1}$) | Available N (ppm) | Sand (%) |
|---|---|---|---|---|---|---|---|---|
| Vegetative height | | | | | | | | |
| *A. virginicus* | -4.84 | -1.52 | -0.92 | -0.91 | 1.00 | -2.95 | -1.91 | -3.73 |
| *P. pratensis* | 2.79 | -4.35 | 2.69 | 3.27 | -0.70 | 1.32 | 1.19 | -3.84 |
| *S. pratensis* | -0.90 | -5.78 | 3.73 | 2.48 | -4.85 | 3.36 | -0.47 | -2.23 |
| *S. altissima* | -4.17 | -10.10 | 8.88 | 2.06 | -3.66 | 17.47 | 3.58 | -13.23 |
| *S. rugosa* | -3.57 | -4.40 | 0.69 | -10.38 | -1.94 | 15.44 | 5.72 | 0.35 |
| Leaf area | | | | | | | | |
| *A. virginicus* | -1.82 | -0.34 | -0.05 | -0.45 | 0.92 | -2.50 | -1.04 | -1.38 |
| *P. pratensis* | -0.99 | 0.27 | -0.69 | -1.26 | 0.32 | 1.25 | 0.97 | 0.90 |
| *S. pratensis* | 1.62 | -5.11 | 3.59 | 0.95 | -3.42 | 2.90 | -1.85 | -3.17 |
| *S. altissima* | -1.04 | -1.47 | 0.86 | -0.50 | -0.21 | 1.27 | 0.19 | -1.05 |
| *S. rugosa* | -1.06 | -0.57 | 0.94 | -0.46 | 0.37 | 1.39 | 0.62 | -1.57 |
| Specific leaf area | | | | | | | | |
| *A. virginicus* | -1.22 | 0.55 | 0.77 | 0.41 | 1.44 | -0.98 | 1.36 | -0.06 |
| *P. pratensis* | -2.86 | 2.15 | -0.21 | -2.52 | 2.23 | 0.78 | 0.37 | 1.22 |
| *S. pratensis* | -1.70 | -0.98 | 0.32 | -1.26 | -0.17 | 3.21 | -0.67 | -0.38 |
| *S. altissima* | -0.11 | 0.58 | 0.01 | 1.32 | 0.33 | -0.17 | 0.23 | -0.56 |
| *S. rugosa* | 0.32 | 1.12 | -0.25 | 1.90 | 0.68 | -0.13 | 0.99 | 0.76 |
| Leaf dry matter content | | | | | | | | |
| *A. virginicus* | -0.015 | -0.015 | -0.002 | -0.014 | -0.006 | -0.024 | -0.030 | -0.016 |
| *P. pratensis* | 0.021 | -0.018 | 0.001 | 0.015 | -0.014 | -0.005 | -0.012 | -0.014 |
| *S. pratensis* | 0.013 | 0.010 | -0.007 | 0.001 | 0.007 | -0.025 | -0.003 | 0.003 |
| *S. altissima* | -0.009 | 0.000 | 0.006 | -0.008 | 0.000 | 0.011 | 0.001 | 0.007 |
| *S. rugosa* | -0.015 | -0.035 | 0.011 | -0.053 | -0.008 | 0.009 | -0.011 | -0.014 |

**Table 6.** Results of Mantel and partial Mantel tests for relationships between geographic and environmental distance and trait dissimilarity between study sites.

| | Geographic | | Environmental | | Geo \| Env | | Env \| Geo | |
|---|---|---|---|---|---|---|---|---|
| Response | Mantel *r* | *P* | Mantel *r* | *P* | Mantel *r* | *P* | Mantel *r* | *P* |
| Height | | | | | | | | |
| Total dissimilarity | 0.04 | 0.31 | 0.00 | 0.47 | 0.05 | 0.33 | -0.03 | 0.64 |
| Species turnover | -0.02 | 0.54 | 0.02 | 0.38 | -0.04 | 0.67 | 0.04 | 0.29 |
| Intraspecific variation | 0.02 | 0.39 | 0.04 | 0.34 | 0.00 | 0.54 | 0.03 | 0.40 |
| Turnover:Intraspecific | 0.05 | 0.28 | 0.05 | 0.29 | 0.02 | 0.38 | 0.02 | 0.39 |
| Leaf area | | | | | | | | |
| Total dissimilarity | 0.12 | 0.11 | 0.17 | 0.07 | 0.00 | 0.51 | 0.12 | 0.18 |
| Species turnover | 0.16 | 0.05 | 0.22 | 0.03 | 0.01 | 0.48 | 0.15 | 0.09 |
| Intraspecific variation | 0.09 | 0.15 | 0.05 | 0.28 | 0.08 | 0.22 | -0.02 | 0.59 |
| Turnover:Intraspecific | 0.06 | 0.24 | 0.12 | 0.08 | -0.04 | 0.67 | 0.12 | 0.12 |
| SLA | | | | | | | | |
| Total dissimilarity | 0.23 | 0.02 | 0.20 | 0.04 | 0.13 | 0.14 | 0.05 | 0.31 |
| Species turnover | 0.39 | <0.01 | 0.21 | 0.04 | 0.35 | 0.00 | -0.10 | 0.78 |
| Intraspecific variation | -0.08 | 0.76 | -0.04 | 0.61 | -0.08 | 0.75 | 0.03 | 0.40 |
| Turnover:Intraspecific | 0.33 | <0.01 | 0.24 | <0.01 | 0.24 | 0.01 | 0.01 | 0.52 |
| LDMC | | | | | | | | |
| Total dissimilarity | -0.03 | 0.63 | 0.00 | 0.48 | -0.05 | 0.69 | 0.03 | 0.34 |
| Species turnover | 0.03 | 0.36 | 0.12 | 0.13 | -0.08 | 0.74 | 0.14 | 0.10 |
| Intraspecific variation | 0.01 | 0.42 | -0.07 | 0.77 | 0.09 | 0.19 | -0.11 | 0.87 |
| Turnover:Intraspecific | 0.01 | 0.43 | 0.09 | 0.15 | -0.07 | 0.78 | 0.12 | 0.11 |

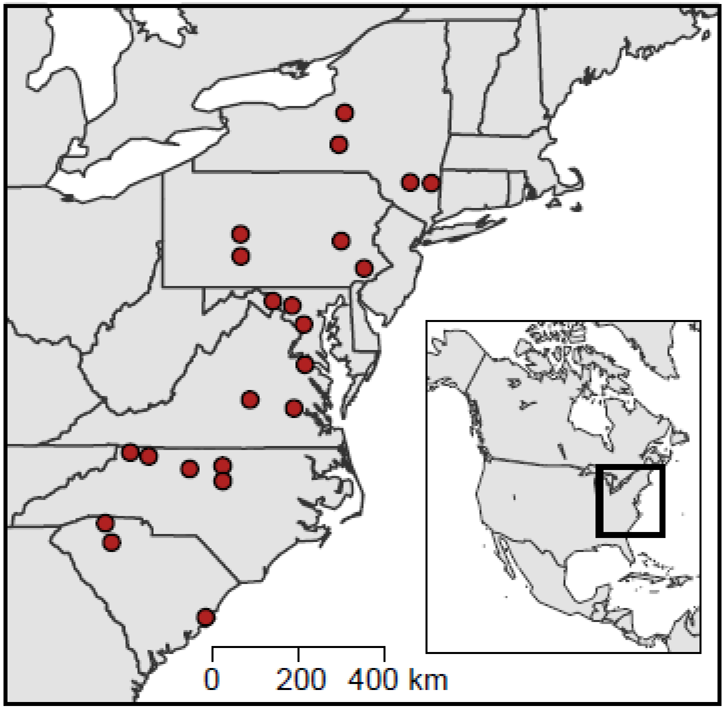

**Figure 1.** Map of study sites and location of study area within North America.

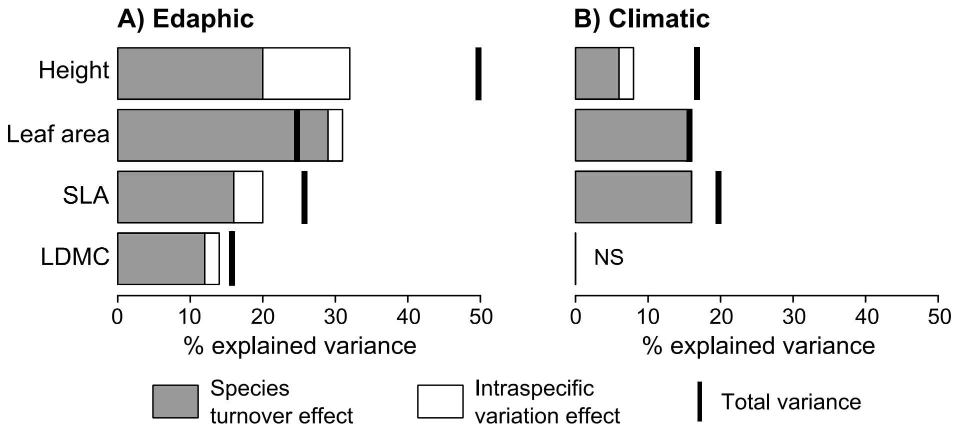

**Figure 2.** Decomposition of community trait responses to environment. Among-site variance in community-weighted mean trait values explained by (A) edaphic and (B) climatic variables is partitioned into species turnover, intraspecific variation, and covariation effects. Covariation is represented by the difference between the total variance and the sum of the species turnover and intraspecific variation effects. Total variance greater than the sum of species turnover and intraspecific variation effects indicates positive covariance. Total variance less than the sum of species turnover and intraspecific variation effects indicates negative covariance. Abbreviations: SLA, specific leaf area; LDMC, leaf dry matter content.

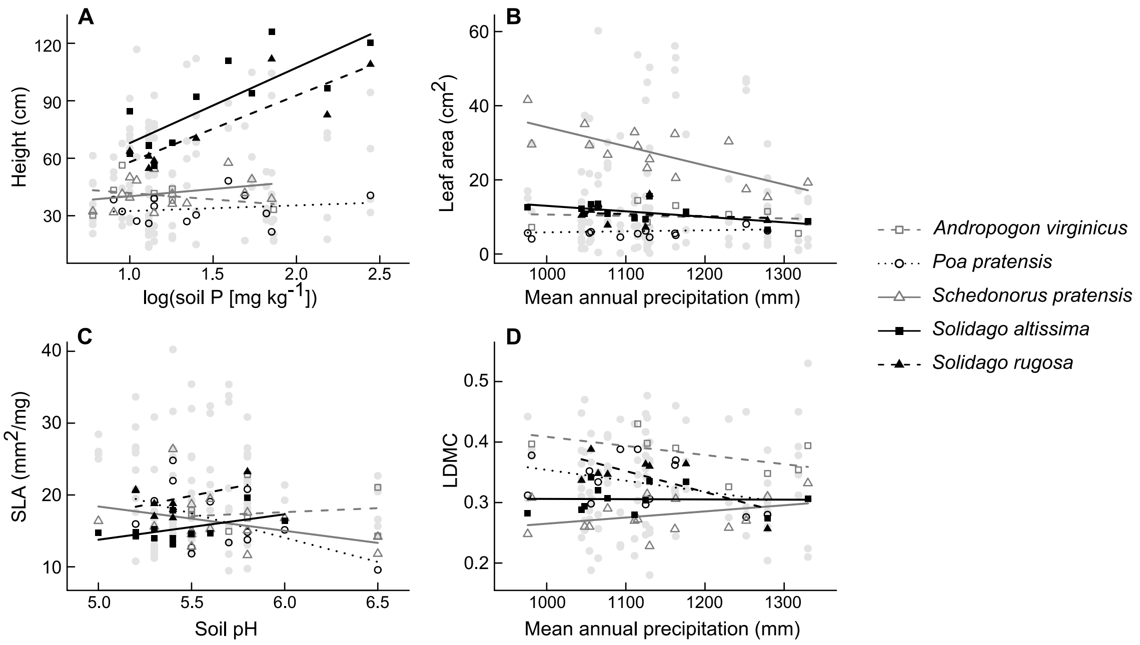

**Figure 3.** Intraspecific trait responses to environment. Examples of relationships between trait values of individual species and important environmental predictors are shown for each trait measured in the study: (A) height vs. soil P; (B) leaf area vs. mean annual precipitation; (C) specific leaf area vs. soil pH; (D) leaf dry matter content vs. mean annual precipitation. Points represent site-specific mean trait values of all species sampled in each site. Mean trait values and best fit lines from linear regressions are indicated for the five most abundant and widespread species in the study area: *Andropogon virginicus, Poa pratensis, Schedonorus pratensis, Solidago altissima*, and *Solidago rugosa*.

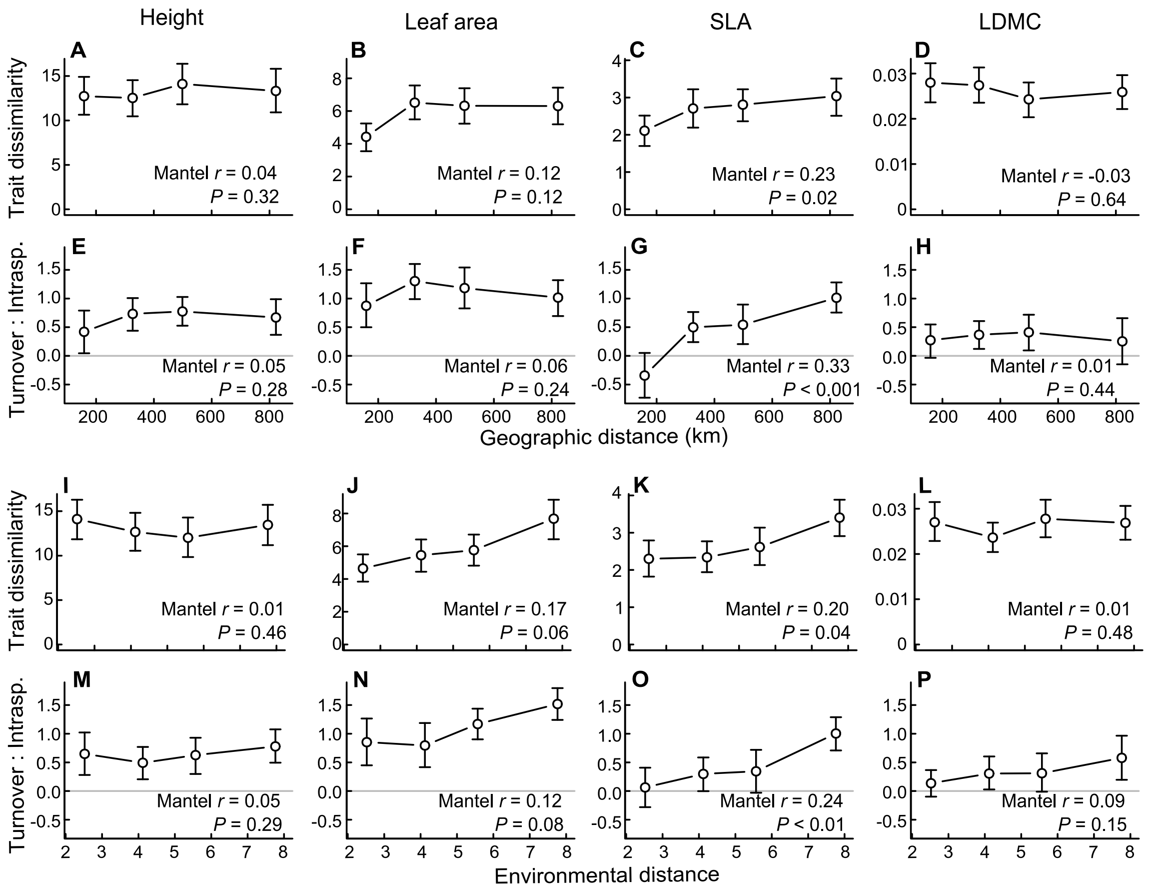

**Figure 4.** Effects of geographic and environmental distance on between-site variation in plant functional traits. Panels A-C and I-L show the trait dissimilarity (difference in community-weighted mean trait values) between sites as a function of geographic or environmental distance. Panels E-H and M-P show the relative contribution of species turnover vs. intraspecific variation (measured as log of species turnover effect divided by intraspecific variation effect) to the total trait dissimilarity between sites. Values were calculated for each pair of sites in the study area and binned by geographic or environmental distance (n = 57-58 pairs per bin) for ease of interpretation. Points represent mean values for each distance bin; error bars represent 95% bootstrap confidence intervals. Abbreviations: SLA, specific leaf area; LDMC, leaf dry matter content.

# Chapter 5

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## Intraspecific variation drives functional responses of old-field plant communities to nutrient enrichment

Andrew Siefert

### Abstract

Plant communities are expected to respond to environmental change through shifts in functional trait values, and these shifts may occur through a combination of species turnover and intraspecific variation. The strength of these shifts may depend on the availability of species and individuals with trait values adapted to new environmental conditions, represented by the functional diversity of existing community residents or dispersal from the local species pool. I conducted a three-year nutrient and seed addition experiment in old-field plant communities to examine the contributions of species turnover and intraspecific variation to community trait shifts and the influence of initial functional diversity and seed availability on the strength of these shifts, focusing on four key functional traits: vegetative height, leaf area, specific leaf area (SLA), and leaf dry matter content (LDMC). Community mean height, leaf area, and SLA increased significantly in response to fertilization, and these shifts were driven almost entirely by intraspecific variation. The strength of intraspecific shifts in height and leaf area was positively related to initial intraspecific functional diversity in these traits. Intraspecific trait responses to fertilization varied among individual species, with species of short stature displaying stronger shifts in SLA and LDMC but weaker shifts in leaf area. Trait shifts due to species turnover were generally weak and opposed intraspecific shifts for SLA and LDMC. Seed addition had little effect on community trait shifts. These results highlight the importance of intraspecific variation

for short-term community functional responses and demonstrate that the strength of these responses may be mediated by community functional diversity.

## Introduction

Trait-based approaches are increasingly used to understand and predict changes in community structure in response to environmental change (Lavorel and Garnier 2002, McGill et al. 2006, Jung et al. 2014). Local environmental conditions deterministically select or filter individuals based on their functional trait values (Keddy 1992, Weiher and Keddy 1995, Cornwell and Ackerly 2009), such that environmental changes in space and time lead to predictable shifts in community trait composition, as demonstrated by numerous studies showing correspondence between environmental conditions and community mean trait values (Fonseca et al. 2000, Ackerly et al. 2002, Garnier et al. 2004). These community-level patterns reflect processes operating at different levels of organization (Ackerly 2003): 1) phenotypic plasticity: modifications in trait values within individuals in response to the environment; 2) adaptive evolution: heritable changes in trait values within populations resulting from natural selection; 3) species sorting: changes in occurrence or relative abundance of species within communities (i.e., species turnover) resulting from differential success based on interspecific trait differences. All three processes may combine and interact to generate community-level functional responses to the environment, but most previous studies have only considered species sorting, under the assumption that interspecific trait differences are much larger than intraspecific differences arising from phenotypic plasticity or heritable genetic variation (Garnier et al. 2001a). However, recent studies have shown that intraspecific trait variation may be substantial at the community level and contribute strongly to shifts in community mean trait values in response to environmental variation (e.g., Jung et al. 2010, Messier et al. 2010, Hulshof and Swenson 2010, Lepš et al. 2011), highlighting the need to consider intraspecific trait responses when quantifying community trait responses to the environment.

Another unresolved question is how community functional structure, including the amount of interspecific and intraspecific trait variation present in the community, controls the strength of community trait responses to environmental change. In evolutionary biology, it is well known that the amount of evolutionary change in a trait is a function of the strength of selection and the amount of heritable trait variation within the population, as expressed in the Breeder's equation (Lush 1937, Falconer 1960). By extension, the amount of change in a trait within a community in response to selection may be influenced by the amount of trait variation, or functional diversity (FD), present within the community (Shipley et al. 2006). Communities with high interspecific FD, reflecting large trait differences among species, may include species with traits adapted to new environmental conditions, facilitating rapid shifts in community trait composition through species turnover. Similarly, communities with high intraspecific FD, reflecting phenotypic plasticity of resident genotypes or large genetic variation, may have a strong capacity to respond to an environmental change through intraspecific trait shifts, including plastic responses and genetic adaptation (Grime et al. 2008).

These predictions assume that communities already include species and genotypes with traits suited to the new conditions created by an environmental change. If not, the ability of a community's functional composition to track the environment will depend on dispersal of individuals with appropriate traits from the surrounding area (Ackerly 2003). Dispersal limitation may therefore limit community trait responses to environment change, particularly responses due to species sorting (Foster et al. 2011). Metacommunity theory predicts that the strength of species sorting and the correspondence between environment and species composition should be greatest in systems with high connectivity due to dispersal (Leibold et al. 2004), and this prediction has been supported by experiments manipulating seed dispersal in grassland communities (Questad and Foster 2008, Foster et al. 2011). On the other hand, dispersal limitation may have less effect on functional than taxonomic composition due to functional redundancy among species and the potential for intraspecific variation to generate functional responses in the absence of species turnover (Messier et al. 2010, Swenson et al. 2011, Siefert et al. 2013).

The strength of community trait shifts may also be influenced by interactions between species turnover and intraspecific responses. Previous studies examining trends in community mean traits along environmental gradients have found that trait shifts due to species turnover and intraspecific variation may either reinforce or oppose each other (e.g., Lepš et al. 2011, Pérez-Ramos et al. 2012, Kichenin et al. 2013). Negative interactions between species turnover and intraspecific responses may occur if changes at one level preempt changes at the other. For example, Grime et al. (2008) suggested that rapid plastic responses and expansion of genotypes of resident species prevented large shifts in species composition in response to simulated climate change in grassland communities. Conversely, rapid migration may allow species with trait pre-adapted to new environmental conditions to replace residents before they have time to adapt (Ackerly 2003). Examining the relationship between species turnover and intraspecific trait shifts in communities with varying levels of inter- and intraspecific functional diversity and dispersal limitation will shed light on these potential scenarios.

I conducted a three-year field experiment in old-field plant communities in central New York to assess community functional responses to fertilization and manipulation of seed availability. I focused on four functional traits known to be related to plant resource acquisition and use strategies: vegetative height, leaf area, specific leaf area (SLA), and leaf dry matter content (LDMC). I addressed three main questions: 1) How do community mean trait values respond to fertilization and what are the contributions of and interactions between species turnover and intraspecific trait responses? 2) How are community trait responses influenced by inter- and intraspecific functional diversity and seed availability? 3) How are trait responses of individual species influenced by their ecological and functional characteristics?

## Methods

### *Experimental design*

The study was conducted at Green Lakes State Park in central New York. The experiment was established in a 1-km$^2$ area of old fields abandoned from agricultural use in the 1960's through 1990's and presently dominated by native *Solidago* spp. and non-native grasses such as *Bromus inermis* and *Poa pratensis*. In summer 2010, I established eight 5 x 5 m square plots, each containing 1-m$^2$ quadrats located at the four corners for a total of 32 quadrats. Individual quadrats served as experimental units and plots as experimental blocks. Within each block, I randomly applied a set of 2 x 2 factorial treatments, including fertilization (no fertilizer; 16 g N m$^{-2}$ yr$^{-1}$) and seed addition (no seeds; seeds of 19 species added). I applied the treatments each year from 2011 to 2013. For the fertilization treatment, I used Osmocote slow-release fertilizer (18-6-12 N-P-K) and applied the appropriate amount to add 8 g N m$^{-2}$ in April and July of each year. This rate of nutrient addition is typical of high-nutrient treatments in previous grassland fertilization experiments (e.g., Tilman 1987, Dickson and Foster 2008). For the seed addition treatment, I added seeds of 19 species (Table 1), representing a wide range of functional strategies and trait values, that occurred within the study site. Seeds of most species were added at a rate of 1 g $yr^{-1}$ with a lower limit of 200 and upper limit of 2000 seeds per species per year, representing a tradeoff between equalizing seed mass and seed number across species (Jakobsson and Eriksson 2000). Though this rate of seed addition is higher than that of natural seed rain in grassland communities (Myers and Harms 2009), the purpose of the treatment was not to mimic natural seed rain but to overcome dispersal barriers that could limit species establishment in experimental plots. Seeds were hand broadcast into quadrats, with half the yearly amount added in November and half in April. I manually agitated the vegetation and litter layer in all quadrats to allow seeds to contact the soil.

### *Data collection*

I sampled quadrats in July-August 2010 (prior to application of experimental treatments) and 2013 (after three years of treatment application). To determine species richness and composition, I visually estimated the percent cover of each species within each quadrat (Peet et al. 1998). To quantify community trait distributions, I measured traits of 50 randomly selected individuals per quadrat, with the number of individuals sampled per species proportional to relative species abundance, thus accounting for interspecific and intraspecific trait variation (Siefert 2012). I measured four functional traits on each individual sampled: vegetative height, leaf area, specific leaf area (SLA), and leaf dry matter content (LDMC). Vegetative height relates to light acquisition and competitive ability (Gaudet and Keddy 1988). Leaf area relates to stress tolerance, with nutrient, drought, and heat stress all selecting for small leaves (Perez-Harguindeguy et al. 2013). SLA is a central component of the leaf economics spectrum, which runs from fast (high SLA) to slow (low SLA) return on investment in nutrients and dry mass in leaves (Wright et al. 2004). LDMC relates to leaf resistance to physical stress (Perez-

Harguindeguy et al. 2013) and is also part of the leaf economics spectrum. Vegetative height was measured as the distance between the ground and the top of the general canopy of the plant. One mature, healthy-looking leaf from the upper third of the canopy of each selected individual was collected for leaf trait measurements. I measured the one-sided area (in $mm^2$) and fresh mass (in mg) of each leaf after full rehydration (Garnier et al. 2001b) and dry mass (in mg) after oven drying at 80°C for 48 hr. SLA was calculated as fresh leaf area divided by dry mass, and LDMC was calculated as dry mass divided by fresh mass.

### *Data analysis*

Using data collected prior to the start of the experiment and after three years of fertilization and seed addition, I quantified changes in species richness, species composition, and community mean trait values within each quadrat. I measured the change in species richness as the difference between the number of species recorded within a given quadrat in 2010 and 2013. I measured changes in species composition in two ways. First, I quantified the magnitude of change as the Bray-Curtis dissimilarity between initial and final community composition. Second, I characterized the direction of change in multivariate space by conducting an NMDS ordination using all quadrats from 2010 and 2013 and recording the difference in quadrat scores between years for each ordination axis. I tested for effects of fertilization, seed addition, and their interactions on changes in species richness and composition (Bray-Curtis dissimilarity) using linear mixed models with “plot” as a random effect. I used non-parametric MANOVA to analyze changes in species composition, using a matrix of Euclidean distances among quadrats based on shifts in NMDS axis scores as the response. Significance was assessed using permutation tests (n = 999) with plot as a grouping factor.

I measured community-level changes in functional traits and the contributions of species turnover and intraspecific variation using a modification of the approach of Lepš et al. (2011). I measured the total change in community-mean trait values between 2010 and 2013 (ΔComm) for each quadrat as:

$$\Delta Comm_j = \sum_{i=1}^{S} p_{ij13}\bar{x}_{ij13} - \sum_{i=1}^{S} p_{ij10}\bar{x}_{ij10}\,, \qquad (1)$$

where $p_{ij13}$ and $p_{ij10}$ are the relative cover of species $i$ in quadrat $j$ in 2013 and 2010, respectively, and $\bar{x}_{ij13}$and $\bar{x}_{ij10}$are the mean trait values of species $i$ in quadrat $j$ in 2013 and 2010, respectively, and $S$ is the number of species recorded in the study. I measured the contribution of species turnover to the total change in community mean traits between years (ΔTurn) as:

$$\Delta Turn_j = \sum_{i=1}^{S} p_{ij13}\bar{x}_{ij} - \sum_{i=1}^{S} p_{ij10}\bar{x}_{ij}\,, \qquad (2)$$

where $\bar{x}_{ij}$ is the mean trait value of species $i$ in quadrat $j$ averaged across years, thus assuming no intraspecific shifts in trait values between years. I calculated the contribution of intraspecific variation to the total change in community mean traits between years (ΔIntra) as the difference between the total change in community mean traits and the change due to species turnover:

$$\Delta Intra_j = \Delta Comm_j - \Delta Turn_j\,. \qquad (3)$$

I used linear mixed models with plot as a random effect to test the effects of fertilization, seed addition, and their interactions on changes in community mean traits (ΔComm) and the contributions of species turnover (ΔTurn) and intraspecific variation (ΔIntra). To test whether community trait responses to fertilization were influenced by community functional diversity, I also included initial interspecific and intraspecific functional diversity (FD) and their interactions with fertilization as fixed effects. For each quadrat and trait, interspecific FD was calculated as the variance of species mean trait values weighted by species relative cover. Intraspecific FD was calculated as the weighted mean of within-species trait variances (Lepš et al. 2006). I tested for relationships between ΔTurn and ΔIntra across all treatments for each trait using major axis regression.

Finally, I examined intraspecific trait responses of individual species to fertilization. For each case in which a species was found in the same fertilized quadrat in both 2010 and 2013, I calculated the difference in species mean trait values between years within the quadrat, then averaged across quadrats to obtain a mean trait response to fertilization for each species. To assess whether species' trait responses to fertilization could be explained by their ecological and functional characteristics, I tested for correlations between mean trait response and initial mean trait value, trait variance, frequency (number of quadrats in which species occurred), and mean cover across species for each trait. I also hypothesized that fertilization would influence leaf traits indirectly by increasing shade, and that responses to shade would be strongest for species lower in the canopy. To test this hypothesis, I tested for correlations between mean trait responses and mean vegetative height across species.

All analyses were conducted in R (R Core Development Team 2012) using the vegan (Oksanen et al. 2012) and lmodel2 (Legendre 2013) packages.

## Results

### *Species richness and composition*

Mean species richness in 2010 at the start of the experiment was 10.4 species per quadrat. Fertilization had a significant negative effect on the change in species richness between 2010 and 2013 ($F_{1,21} = 35.1$; $P < 0.001$; Fig. 1A). Species richness decreased by 1.4 species on average in fertilized quadrats, compared to an average increase of 2.4 species in unfertilized quadrats. Seed addition had a significant positive effect on the change in species richness ($F_{1,21} = 5.6$; $P = 0.03$;

Fig. 1A), with an average increase of 1.2 species in seed addition quadrats, compared to an average loss of 0.3 species in quadrats not receiving seed addition. There was no significant interaction between fertilization and seed addition.

Fertilization had a significant effect on changes in species composition within quadrats between 2010 and 2013, as measured by shifts of quadrats in NMDS ordination space ($F_{1,31}$ = 6.82; $P$ = 0.007; Fig. 2). However, the magnitude of change in species composition, measured as the Bray-Curtis dissimilarity between 2010 and 2013, did not differ between fertilized and unfertilized plots ($F_{1,21}$ = 0.19; $P$ = 0.66; Fig. 1B). In contrast, seed addition significantly increased the magnitude of species composition change ($F_{1,21}$ = 4.7; $P$ = 0.04; Fig. 1B) but had no effect on shifts in ordination space ($F_{1,21}$ = 0.66; $P$ = 0.55; Fig. 2).

*Community-level trait shifts*

Fertilization had a positive effect on overall changes in community mean trait values between 2010 and 2013 ($\Delta$Comm) for vegetative height ($F_{1,17}$ = 8.0; $P$ = 0.01; Fig. 3A) and leaf area ($F_{1,17}$ = 6.8; $P$ = 0.02; Fig. 3B) but no effect on $\Delta$Comm SLA or LDMC (Fig. 3C,D). Seed addition had no effect on $\Delta$Comm for any trait. Changes in community mean traits occurred almost entirely through intraspecific trait shifts ($\Delta$Intra), whereas trait shifts due to species turnover ($\Delta$Turn) were negligible (Fig. 3A-D). Fertilization had a significant positive effect on $\Delta$Intra for height ($F_{1,17}$ = 23.4; $P < 0.001$; Fig. 3A), leaf area ($F_{1,17}$ = 18.5; $P < 0.001$; Fig. 3B), and SLA ($F_{1,17}$ = 4.7; $P$ = 0.04; Fig. 3C). There was no effect of fertilization on $\Delta$Turn for any trait except SLA, for which fertilization had a marginally negative effect ($F_{1,17}$ = 3.3; $P$ = 0.08; Fig. 3C).

Overall shifts in community mean trait values and the contributions of species turnover and intraspecific variation were influenced by initial interspecific and intraspecific FD and seed addition and their interactions with fertilization in several cases (Fig. 4). For ΔIntra in vegetative height, there was a significant negative interaction between initial interspecific FD and fertilization ($F_{1,17}$ = 9.1; $P$ = 0.008) and a significant positive interaction between intraspecific FD and fertilization ($F_{1,17}$ = 6.3; $P$ = 0.02; Fig. 4A). This indicates that intraspecific height responses to fertilization were strongest in communities that had high intraspecific variation in height at the start of the experiment and suppressed in communities with high initial interspecific variation. Intraspecific FD also had a significant positive effect on ΔIntra in leaf area ($F_{1,17}$ = 4.7; $P$ = 0.04; Fig. 4B). For shifts in community mean SLA, although the main effects of fertilization and seed addition were not significant, there was a significant negative fertilization by seed addition interaction ($F_{1,17}$ = 6.2; $P$ = 0.02), reflecting a weak positive effect of fertilization on SLA in the absence of seed addition and a negative effect with seed addition. For LDMC, initial interspecific FD had a positive effect on ΔTurn ($F_{1,17}$ = 7.4; $P$ = 0.01; Fig. 4C) and a negative effect on ΔIntra ($F_{1,17}$ = 11.8; $P$ = 0.003; Fig. 4D). Communities with high initial interspecific variation in LDMC had positive shifts in LDMC due to species turnover and negative shifts due to intraspecific responses.

Across all treatments, there were significant negative relationships between ΔIntra and ΔTurn for SLA ($R^2$ = 0.21; $P$ = 0.01; Fig. 5C) and LDMC ($R^2$ = 0.26; $P$ = 0.003; Fig. 5D) but no relationships for vegetative height or leaf area (Fig. 5A,B).

### *Single species trait responses to fertilization*

I examined intraspecific trait responses to fertilization for the 13 study species that occurred in at least three fertilized plots in both 2010 and 2013. Of these 13 species, 12 increased in height in response to fertilization (mean increase of 18.6 cm); 11 species increased in leaf area (mean increase of 1.06 $cm^2$); 11 species increased in SLA (mean increase of 1.8 $mm^2$ $mg^{-1}$); and 9 species decreased in LDMC (mean decrease of -17.2 mg $g^{-1}$). The strength of intraspecific responses of SLA and LDMC to fertilization increased with decreasing species mean vegetative height (Table 2). In contrast, leaf area responses were strongest for tall species and those with low initial mean and variance in leaf area (Table 2). The strength of intraspecific trait responses was not significantly related to species frequency or mean cover for any trait.

## Discussion

### *Community trait responses to fertilization*

Community trait shifts in response to three years of fertilization were mainly driven by intraspecific variation. Significant intraspecific responses to fertilization occurred in three of the four traits examined. Vegetative height, leaf area, and SLA increased within species in response to increasing nutrient availability, reflecting a shift toward a strategy of rapid resource uptake and growth (Wright et al. 2004, Reich 2014). Previous studies have also found that intraspecific variation plays a large role in community responses to resource availability. In a longer-term (10 yr) fertilization experiment in grasslands in the Czech Republic, Lepš et al. (2011) found that variation in community mean height, SLA, LDMC, and other leaf traits was mostly caused by intraspecific variation. Similarly, Jung et al. (2013) found that intraspecific variation contributed more than species turnover to changes in community mean trait values in subalpine meadows in response to simulated drought. Together with the findings of my study, these results highlight the importance of accounting for intraspecific trait variation when quantifying community functional responses to environmental change.

Previous studies examining intraspecific trait variation along environmental gradients have found that trait responses are highly idiosyncratic among species (e.g., Albert et al. 2010, Kichenin et al. 2013). Intraspecific trait responses also varied among species in this study, but some of this variation could be explained by species' functional characteristics. In particular, shifts in SLA and LDMC in response to fertilization were strongest for species of short stature, consistent with patterns observed across natural soil resource availability gradients in the same fields (Siefert 2012). These patterns may be explained if intraspecific shifts in SLA and LDMC are driven by decreasing light availability in the understory of fertilized plots due increased plant growth. Plants are known to respond to shading by increasing SLA and decreasing LDMC to maximize light capture per unit of leaf mass (Evans and Poorter 2001), and these responses are likely to be strongest in relatively short species, which are most subject to shading (Rozendaal et al. 2006). Leaf area showed the opposite pattern: intraspecific responses to fertilization were greater for tall species. Increases in leaf area are likely part of a general growth response to fertilization, which may be stronger for tall species that can take advantage of increased soil resource availability because they have greater access to light (Chapin et al. 1987). This finding is consistent with the "dominant plasticity" hypothesis, which predicts that competitive species have strong phenotypic plasticity to maximize resource capture and competitive ability (Ashton et al. 2010). Overall, the results of this experiment demonstrate that the strength of intraspecific trait responses may be partially explained by species' functional characteristics, but these relationships appear to be trait-specific.

There are several possible explanations for the weak contributions of species turnover to community traits shifts. First, the three- year duration of the experiment may not have been long enough for large changes in species composition to occur. This explanation may be partly discounted because fertilization did lead to significant shifts in species composition, and previous fertilization experiments in old fields have also seen significant changes in composition even within a single year (Mellinger and McNaughton 1975, Bakelaar and Odum 1978). Nevertheless, while short-term community trait responses to environmental manipulations have been shown to be driven primarily by intraspecific variation in this and previous experiments, species turnover is expected to play a more important role over longer time scales (Smith et al. 2009, Sandel et al. 2010). Second, although there were significant changes in the relative cover of species in response to fertilization, these changes were not explained by species' trait values. Species that had the most positive responses to fertilization included grasses such as *Poa pratensis*, *Dactylis glomerata*, and *Bromus inermis*, and species with negative responses included forbs such as *Solidago juncea*, *Euthamia graminifolia*, and *Trifolium repens*. Aside from the signal of growth form, there were no consistent differences in the measured traits between species that increased or decreased in response to fertilization, indicating that other traits or trait combinations mediated these responses. Finally, functional trade-offs among species generate multiple strategies with similar fitness in a given environment (Marks and Lechowicz 2006), leading to high interspecific trait variance within communities and blurring interspecific trait-environment relationships (Marks 2007). In contrast, multivariate trait combinations are likely more constrained within species, possibly allowed a stronger signal of environment on single traits at the intraspecific level.

The influence of species turnover on community trait shifts was further diluted by its negative relationship with intraspecific responses, particularly for SLA. A marginally significant negative response to fertilization due to species turnover was cancelled out by a positive response due to intraspecific variation, resulting in no overall trait response at the community level. Opposing trait shifts due to species turnover and intraspecific variation have been observed in previous studies, but the causes of these patterns appear to be context dependent (Lepš et al.

2011, Kichenin et al. 2013, Jung et al. 2014). The opposing changes in SLA observed in this study may be related to increasing aboveground competition for light in fertilized plots. The negative species turnover response was driven mainly by increasing cover of tall, competitive, relatively low-SLA grasses (e.g., *B. inermis*) and decreasing cover of small, subordinate, high-SLA forbs (e.g., *T. repens*), whereas the positive intraspecific shifts were likely driven by phenotypic plasticity of shaded individuals to increase light capture. This result is consistent with the idea that plastic responses that maximize short-term resource acquisition may oppose selection for trait values that maximize long-term competitive ability (Ryser and Eek 2000).

### *Effects of functional diversity and seed availability on community trait responses*

This study is the first to my knowledge to examine how community functional diversity mediates responses of community mean trait values to an environmental change. By analogy with models of evolutionary trait changes within populations (Lush 1937, Falconer 1960), I predicted that the magnitude of community-level trait changes would be positively related to the amount of within-community trait variation. In general, I found limited support for this hypothesis. Initial functional diversity did not influence overall changes in community mean trait values in response to fertilization for any trait. However, intraspecific changes in vegetative height and leaf area were strongest in communities with high initial intraspecific trait variance, indicating that communities with large reservoirs of intraspecific functional diversity, arising from phenotypic plasticity and possible heritable genetic variation, have greater capacity to respond to environmental change through intraspecific trait shifts. Interestingly, intraspecific shifts in height were suppressed in communities with high interspecific functional diversity. This finding suggests that when community trait space is occupied by multiple species with different mean trait values, there may be few openings for individual species to fill new regions of trait space through intraspecific trait shifts.

A major aim of this study was to test whether community functional composition and responses to fertilization were influenced by seed availability. Previous studies in grassland communities have found that seed addition enhances species diversity and species sorting along environmental gradients (e.g., Questad and Foster 2008, Houseman and Gross 2011, Foster et al. 2011), demonstrating that dispersal plays an important role in community assembly and responses to the environment. In the present study, seed addition had a modest positive effect on species richness and increased the strength of shifts in species composition in response to fertilization but had almost no effect on shifts in community mean traits. The only exception was a negative interaction between seed addition and fertilization on community mean SLA, likely due to increasing cover of competitive, low-SLA species (e.g., *B. inermis*) added to fertilized plots, which overwhelmed the positive response of SLA to fertilization in plots without seed addition. These results are consistent with previous findings that stochastic processes such as dispersal have a stronger influence on species composition than functional composition (Fukami et al. 2005, Swenson et al. 2012, Siefert et al. 2013). Dispersal limitation may prevent particular species with suitable trait values from establishing in a community, but this will only have a strong influence on community functional composition if no other species with suitable trait values are available. The high initial functional diversity and strong intraspecific responses observed in this experiment suggest that communities could track environmental changes without immigration from the local species pool. Dispersal is likely to have a more important influence on community responses to strong, long-term environmental shifts that favor trait values or trait combinations outside the range of values possessed by resident species (Ackerly

2003, Smith et al. 2009). However, there was a significant interaction between fertilization and seed addition

### *Implications*

The results of this study demonstrate that intraspecific trait shifts may play a key role in community functional responses to short-term environmental change, and that the capacity for such shifts may be greatest in communities with high initial intraspecific functional diversity. Future experiments manipulating inter- and intraspecific trait variation, including heritable variation among genotypes and plasticity within genotypes, are needed to further disentangle the effects of functional diversity on community functional responses to environmental change.

There is growing recognition that community functional composition exerts a strong influence on ecosystem processes (Diaz and Cabido 2001, Lavorel and Garnier 2002). Previous studies aimed at linking changes in community trait composition with changes in ecosystem function have focused exclusively on trait responses arising from species turnover (Garnier et al. 2004, Suding et al. 2008). In this experiment, fertilization and seed additions caused changes in species composition, but unlike intraspecific responses, these changes did not translate to directional shifts in community mean traits. These findings suggest that intraspecific trait shifts may track changing environmental conditions more reliably than trait shifts due to species turnover, highlighting the importance of accounting for intraspecific variation when quantifying and predicting community and ecosystem responses to environmental change.

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**Table 1.** Summary of seed additions.

| **Species** | **Mass (g $y^{-1}$)** | **No. seeds ($y^{-1}$)** |
|---|---:|---:|
| *Achillea millefolium* | 0.33 | 2000 |
| *Agrostis hyemalis* | 0.11 | 2000 |
| *Asclepias syriaca* | 1.30 | 200 |
| *Bromus inermis* | 1.00 | 313 |
| *Dactylis glomerata* | 1.00 | 941 |
| *Daucus carota* | 1.00 | 840 |
| *Euthamia graminifolia* | 0.16 | 2000 |
| *Hesperis matronalis* | 1.00 | 494 |
| *Hypericum perforatum* | 0.40 | 2000 |
| *Leucanthemum vulgare* | 1.00 | 441 |
| *Lotus corniculatus* | 1.00 | 816 |
| *Monarda fistulosa* | 0.71 | 2000 |
| *Phleum pretense* | 0.78 | 2000 |
| *Poa pratensis* | 0.65 | 2000 |
| *Solidago canadensis* | 0.20 | 2000 |
| *Solidago juncea* | 0.38 | 2000 |
| *Symphyotrichum laeve* | 0.89 | 2000 |
| *Trifolium pretense* | 1.00 | 600 |
| *Trifolium repens* | 1.00 | 1711 |

**Table 2.** Pearson's correlation coefficients for relationships between species' mean trait responses to fertilization and initial abundance, mean trait values, and trait variance. Bold text indicates that the relationship is statistically significant (α = 0.05).

| Response | Frequency | Cover | Trait mean | Trait variance | Mean height |
|---|---|---|---|---|---|
| Vegetative height | -0.52 | 0.23 | 0.49 | 0.29 | 0.49 |
| Leaf area | -0.17 | 0.24 | **-0.60** | **-0.70** | **0.58** |
| SLA | 0.51 | -0.15 | 0.49 | 0.38 | **-0.71** |
| LDMC | -0.51 | 0.13 | -0.02 | -0.16 | **0.64** |

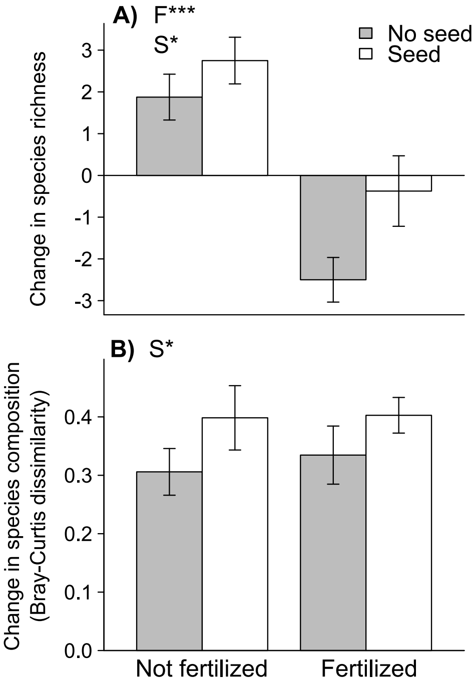

**Figure 1.** Effects of fertilization and seed addition on changes in (A) species richness and (B) species composition in experimental quadrats (n = 32) from 2010 to 2013. Significance of fertilization (F) and seed addition (S) effects is indicated as follows: *$P < 0.05$; ***$P < 0.001$.

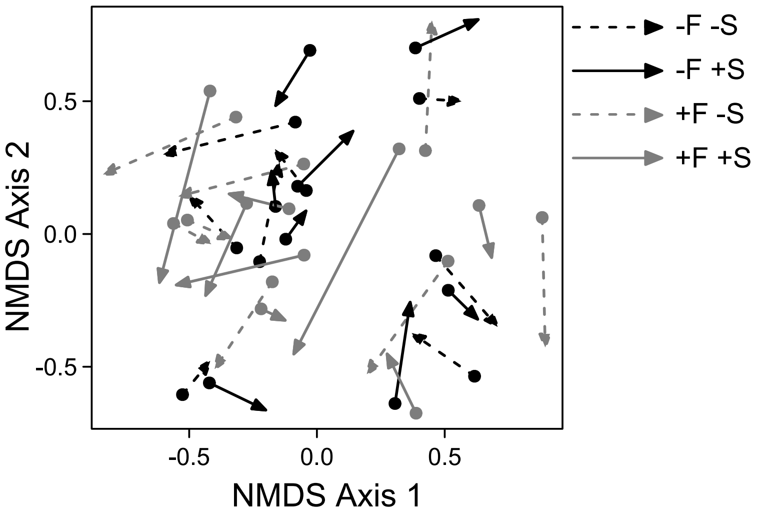

**Figure 2.** Shifts in species composition within experimental quadrats (n = 32) from 2010 (filled circles) to 2013 (arrows). F refers to fertilization level (-F, plots not fertilized; +F, plots fertilized). S refers to seed addition level (-S, no seeds added; +S, seeds added). Diagram was produced with two-axis non-metric multidimensional scaling (NMDS) of Bray-Curtis dissimilarity matrix.

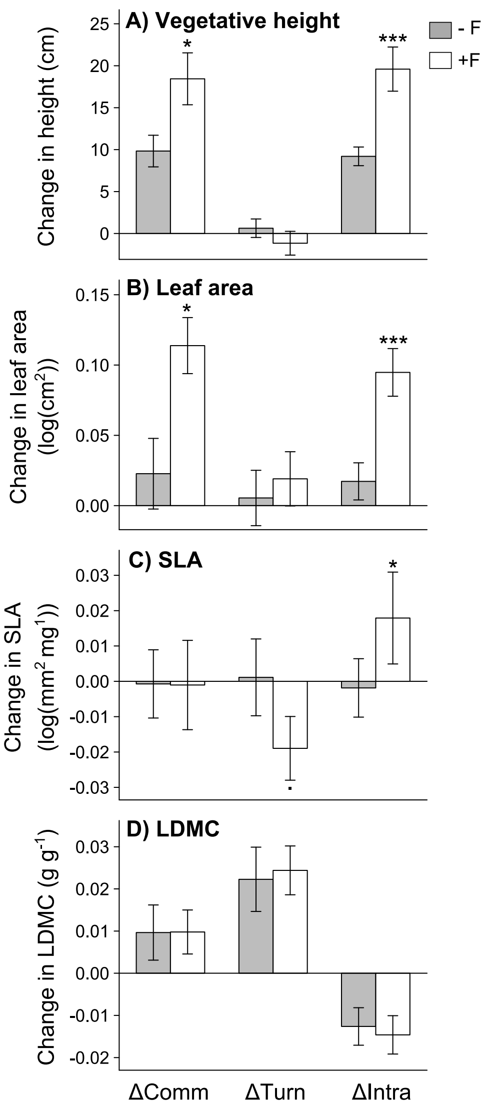

**Figure 3.** Effects of fertilization on changes in community mean trait values in experimental quadrats (n = 32) from 2010 to 2013. Results are shown for overall change in community mean traits (ΔComm), change due to species turnover (ΔTurn), and change due to intraspecific variation (ΔIntra). F refers to fertilization level (-F, plots not fertilized; +F, plots fertilized). Significance of fertilization effect is indicated as follows: $^{\cdot}P < 0.1$; $*P < 0.05$; $***P < 0.001$.

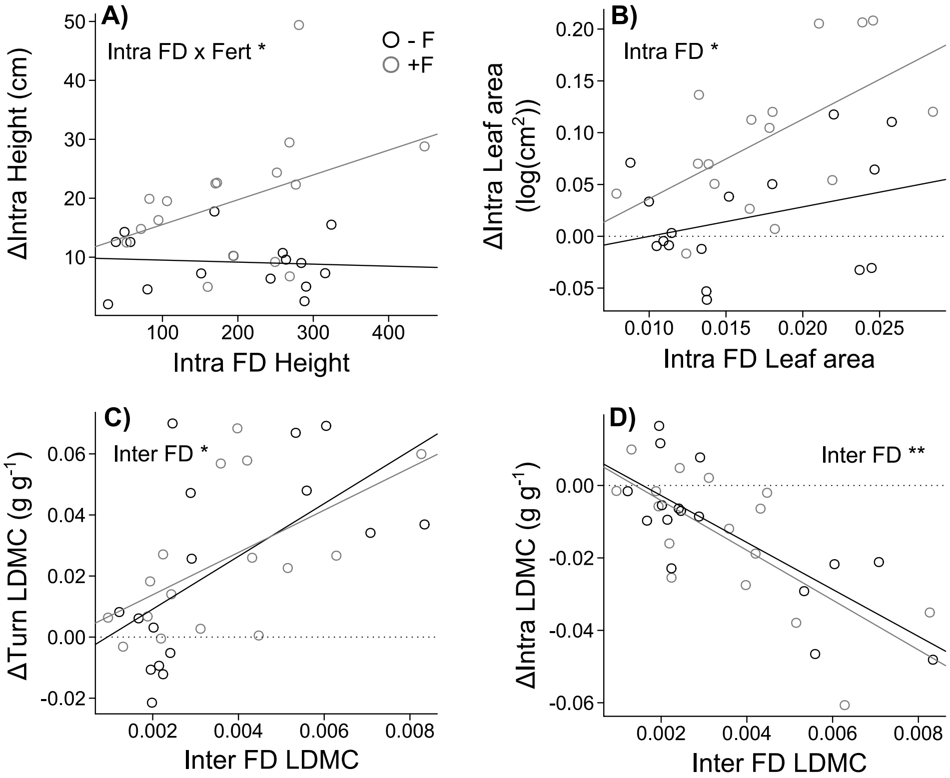

**Figure 4.** Effects of initial functional diversity on community trait shifts in experimental quadrats: (A) effect of initial intraspecific functional diversity (Intra FD) on intraspecific shift (ΔIntra) in vegetative height; (B) effect of initial Intra FD on ΔIntra in leaf area; (C) effect of initial interspecific functional diversity (Inter FD) on trait shift due to species turnover (ΔTurn) in leaf dry matter content (LDMC); (D) effect of initial Inter FD on ΔIntra in LDMC. F refers to fertilization level (-F, no fertilization; +F, fertilization). Significance of FD effects is indicated as follows: **P* < 0.05; ***P* < 0.01).

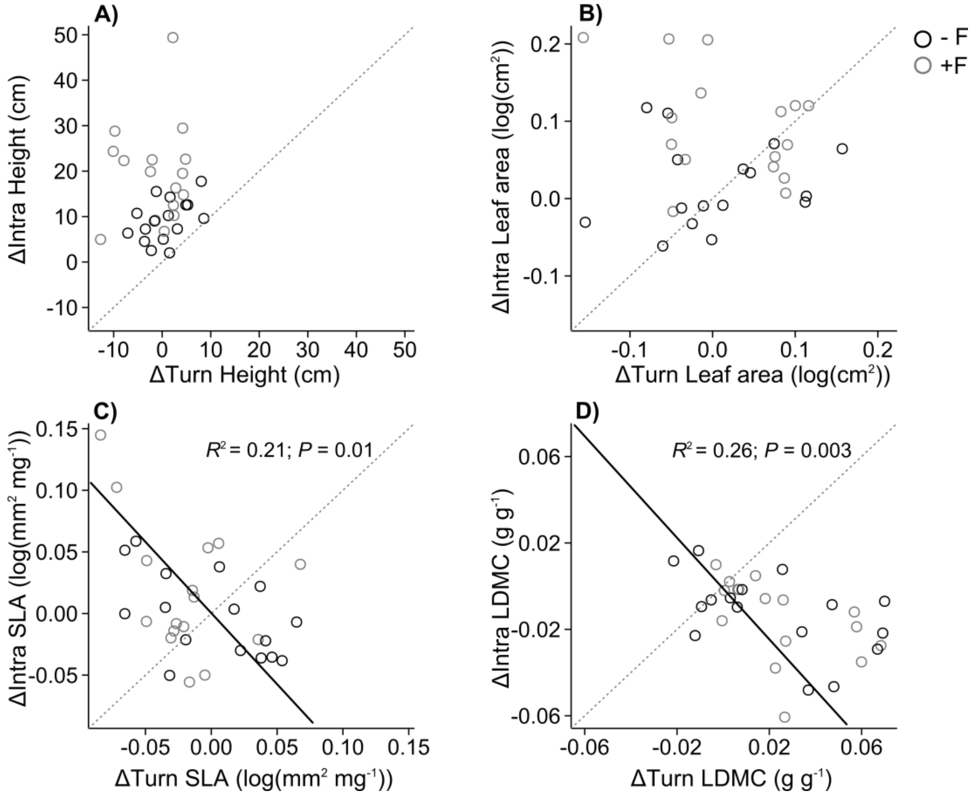

**Figure 5.** Relationship between trait shifts due to species turnover and intraspecific variation within experimental quadrats for (A) vegetative height, (B) leaf area, (C) specific leaf area, and (D) leaf dry matter content. Dotted line represents the 1:1 line. Major axis regression lines are shown for statistically significant relationships (α = 0.05).

# Chapter 6

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## Conclusions

Community assembly theory in recent decades has been built almost exclusively on interspecific niche differences (Weiher and Keddy 1995, Shipley et al. 2006, Vellend 2010). With the rise of trait-based approaches in community ecology, this has translated to a focus on interspecific differences in mean trait values and how selection or filtering processes act on those differences (McGill et al. 2006, Weiher et al. 2011). This view rests on the assumption that interspecific trait differences are much larger than intraspecific trait differences, which can therefore be safely ignored. The results of my dissertation research add to a growing body of work showing that this assumption is not met in many plant communities; intraspecific trait variation is substantial and contributes strongly to overall community-level trait variation in many cases (Jung et al. 2010, Messier et al. 2010, Hulshof and Swenson 2010). These findings have led to calls for intraspecific variation to be more fully considered and integrated in community ecology (Violle et al. 2012). An important initial step toward this goal is to assess the magnitude and structure of intraspecific trait variation within and among plant communities and its drivers (Albert et al. 2011).

A basic finding of my research is that intraspecific variation may account for a considerable amount of the total spatial and temporal trait variation in the old-field plant communities I investigated. The relative importance of intraspecific variation depended on a number of factors, and the results shed light on the circumstances in which intraspecific variation is large at the community level and therefore likely to influence community assembly and dynamics. First, the relative importance of intraspecific variation varied among traits. Across all studies, intraspecific variation tended to be relatively large for vegetative height and specific leaf area and smaller for leaf dry matter content and leaf area. These findings are consistent with previous work showing that some traits tend to be highly labile within species, reflecting strong phenotypic plasticity or genetic differentiation, while others are more conserved at the species level (Marks 2007, Donovan et al. 2014). Second, my results suggest that the relative importance of intraspecific variation depends on the spatial and temporal scale and type of environmental gradient being considered (Albert et al. 2011), with intraspecific variation playing a large role in community responses to edaphic variation on fine spatial and temporal scales. In contrast, community trait shifts along broad-scale climatic gradients were primarily driven by species turnover, supporting the hypothesis that interspecific trait differences become more important with increasing spatial scale and environmental gradient breadth (Albert et al. 2010, Auger and Shipley 2012).

This research represents possibly the most intensive examination to date of the magnitude and structure of intraspecific trait variation in plant communities, but generalizing these results requires comparing patterns across multiple community types and ecosystems. Toward this goal, I conducted a global meta-analysis (Siefert et al., unpublished data) using 45 studies, encompassing 630 plant communities, to assess the relative importance of intraspecific trait variation and the factors controlling it. The results largely supported and extended the findings of my dissertation research. The amount of intraspecific relative to interspecific trait variation within communities was greater for whole plant traits (e.g. height) than for stem and leaf traits and greater for leaf physiological traits (e.g., nutrient concentrations, SLA) than for leaf size-related traits such as leaf area. The relative importance of intraspecific variation also decreased with increasing spatial scale and species richness. Interestingly, patterns did not differ between growth forms (herbaceous vs. woody) or biomes (tropical vs. temperate), suggesting that the factors controlling intraspecific trait variation are consistent across plant communities worldwide.

Beyond quantifying the amount and structure of intraspecific trait variation, the ultimate goal for integrating intraspecific variation in trait-based ecology is to understand its consequences for community assembly and dynamics (Albert et al. 2011). The processes that underlie community assembly ultimately operate at the individual level (Violle et al. 2012); an individual plant's performance depends on its interactions with its abiotic environment and neighbors, and these interactions are in turn mediated by its functional traits. Given that traits may vary considerably among individuals within species due to genetic differences and phenotypic plasticity, accounting for intraspecific trait variation is critical for having a complete view of community assembly.

The results of my research and other recent work (e.g., Jung et al. 2010, 2014, Paine et al. 2011) demonstrate that intraspecific trait variation plays an important role in trait-based environmental filtering, one of the key processes implicated in plant community assembly. Evidence for within-species trait responses to environmental filtering comes from spatial patterns of intraspecific functional divergence (chapter 2), within-community trait dispersion patterns (chapter 3), and trait responses to environmental variation in space (chapter 4) and time (chapter 5). Ignoring intraspecific trait variation may result in underestimating or failing to detect the outcomes of environmental filtering (Violle et al. 2012), as in the case of old-field community responses to local edaphic gradients or experimental nutrient addition in my studies.

The role of intraspecific variation in niche differentiation, the other primary community assembly mechanism structuring plant communities, was less clear. Coexistence theory holds that species must have sufficiently different niches to coexist (MacArthur and Levins 1967, Chesson 2000), and it has been suggested more recently that intraspecific trait variation may promote coexistence by enhancing niche differentiation among neighboring individuals via genetic differences or phenotypic plasticity (Callaway et al. 2003, Vellend 2006, Ashton et al. 2010). Limited evidence for a role of intraspecific trait variation in niche differentiation in the old-field plant communities I studied came from the high intraspecific trait divergence observed at fine spatial scales (chapter 2) and from the finding that accounting for intraspecific trait variation improved detection of patterns of even trait spacing in null model analyses (chapter 3). Nevertheless, signals of niche differentiation were much weaker than those of environmental filtering in the studies communities, possibly due to not measuring the traits most importance for resource partitioning in plants, such as belowground and phenological traits (Cornwell and Ackerly 2009, Sun and Frelich 2011).

Most trait-based approaches currently used in community ecology focus on analyzing community trait dispersion patterns (e.g., community mean trait values and functional diversity indices) to infer community assembly processes (e.g., Stubbs and Wilson 2004, Swenson and Enquist 2009, Cornwell and Ackerly 2009, Kraft et al. 2011), and my research built on this work by incorporating intraspecific variation and spatial patterns of functional traits. These approaches are useful and have led to important advances, but they ultimately have limited ability to identify the specific processes that drive community assembly (Adler et al. 2013) and the role of intraspecific trait variation in these processes. A mechanistic understanding of community assembly requires understanding how trait differences among and within species influence differences in individual performance in specific environmental contexts, and how they mediate the competitive effects and responses of interacting individuals. The aim of future research should be to uncover the direct links between trait variation and individual performance that underlie community assembly mechanisms.

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Paine, C. E. T., C. Baraloto, J. Chave, and B. Hérault. 2011. Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. Oikos 120:720–727.

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Stubbs, W. J., and J. B. Wilson. 2004. Evidence for limiting similarity in a sand dune community. Journal of Ecology 92:557–567.

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Swenson, N. G., and B. J. Enquist. 2009. Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. Ecology 90:2161–2170.

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Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier. 2012. The return of the variance: intraspecific variability in community ecology. Trends in Ecology and Evolution 27:244–252.

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# Andrew Siefert

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## Education

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|---|---|
| 2009- | Ph.D. in Biology expected May 2014, Syracuse University (Mark Ritchie and Jason Fridley, advisors) |
| 2007 | B.S. in Environmental Resource Management, Pennsylvania State University |

## Grants and fellowships

| | |
|---|---|
| 2012-2014 | NSF Doctoral Dissertation Improvement Grant: “Community trait responses to environmental variation: assessing the roles of species turnover, genetic differentiation, and phenotypic plasticity”. $13,769 |
| 2011-2014 | NSF Graduate Research Fellowship. Project title: “Trait-based plant community assembly: incorporating space and intraspecific variation”. $125,500 |

## Research and professional experience

| | |
|---|---|
| 2009- | Future Professoriate Program, Syracuse University |
| 2008-2009 | Limnology Research Technician, Cornell Biol. Field Station, Bridgeport, NY |
| 2008 | Environmental Interpreter, Massachusetts Dept. of Conservation and Recreation |
| 2005-2007 | Stream Ecology Research Assistant, School of Forest Resources, Penn State University |
| 2005 | DOE Summer Undergraduate Laboratory Internship, Brookhaven National Laboratory, Upton, NY |

## Publications

**Siefert, A.**, Ravenscroft, C., Weiser, M. and Swenson, N.G. 2013. Patterns of functional beta diversity reveal deterministic community assembly processes in eastern North American tree communities. *Global Ecology and Biogeography* 22:682-691.

**Siefert, A.** 2012. Incorporating intraspecific variation in tests of trait-based community assembly. *Oecologia* 170:767-775.

**Siefert, A.**, Ravenscroft, C., *et al*. 2012. Scale dependence of vegetation-environment relationships: a meta-analysis of multivariate data. *Journal of Vegetation Science* 23: 942-951.

**Siefert, A.** 2012. Spatial patterns of functional divergence in old-field plant communities. *Oikos* 121:907-914.

Kattge, J. *et al*. 2011. TRY- a global database of plant traits. *Global Change Biology* 17: 2905-2935.

Carrick, H.J., Godwin, C.M., Johston-Greenwald, M., Rilk, C., **Siefert, A.**, and Tzilkowski, C.J. 2007. Evaluation of water quality in a spring fed stream based upon benthic algae and macroinvertebrates. *Journal of the Pennsylvania Academy of Sciences* 80:71-78.

## Manuscripts in review/preparation:

Li, Y., **Siefert, A**., and Wang, G**.** Community assembly and intraspecific trait variability between and within populations in a subalpine meadow (in review, *Journal of Plant Ecology*).

**Siefert, A.** and Fridley, J.D. Community functional responses to soil and climate at multiple spatial scales: when does intraspecific variation matter? (in review*, PLOS ONE*).

Moles, A. *et al*. Which is a better predictor of plant traits: temperature or precipitation? (in review, *Journal of Vegetation Science*).

**Siefert, A.** et al. Global meta-analysis of the relative magnitude of intraspecific trait variation in plant communities (in preparation for *Ecology Letters*).

**Siefert, A.** and Lesser, M. Up the mountain, North to the pole: do species' elevational and latitudinal limits match? (in preparation for *Global Ecology and Biogeography*).

## Selected presentations

**Siefert, A.**, Fridley, J.D., and Ritchie, M.E. 2013. Variation in plant functional traits across a latitudinal gradient: does intraspecific variation matter? 11th INTECOL Congress, London, UK.

**Siefert, A.**, Swenson, N.G., and Weiser, M. 2013. Scale dependence of vegetation-environment relationship: a case study on North American trees. International Biogeography Society Biennial Meeting, Miami, FL.

**Siefert, A.**, Ravenscroft, C., Weiser, M. and Swenson, N.G. 2012. Patterns of functional beta diversity reveal deterministic assembly processes in North American tree communities. Ecological Society of America Annual Meeting, Portland, OR.

**Siefert, A.** 2011. Spatial patterns of functional diversity in old-field plant communities. Ecological Society of America Annual Meeting, Austin, TX.

**Siefert. A.** and Mills, E.M. 2009. Temperature and nutrients influence interannual variability of phytoplankton succession in Oneida Lake, NY. Great Lakes Research Consortium Annual Meeting, Syracuse, NY.

**Siefert, A.** and Carrick, H.J. 2007. Effects of fish in stream food webs. International Association of Great Lakes Research Annual Conference, University Park, PA.

**Siefert, A.** and Carrick, H.J. 2007. Top-down trophic interactions in a benthic stream community. Environmental Chemistry Student Symposium, Pennsylvania State University.

**Siefert, A.** and Green, T. 2005. Effects of changes in canopy cover on understory vegetation in the Long Island Pine Barrens. Pine Barrens Research Forum, Brookhaven, NY.

**Siefert, A.**, Byrne, L., Bruns, M.A., and Kim, K.C. 2005. The communities within our communities: effects of urban landscape patterns on arthropods. Northeast Ecology and Evolution Conference, University Park, PA.

## Awards and honors

| | |
|---|---|
| 2012 | Best Poster Presentation, Syracuse University Life Sciences Symposium |
| 2007 | Best Undergraduate Oral Presentation, Penn State Environmental Chemistry Student Symposium |

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| 2007 | 2nd Place Poster in Health and Life Sciences, Penn State Undergraduate Research Exhibition |
| 2006 | Schreyer Honors College Summer Research Scholarship |
| 2004 | Dreibelbis Award for Excellence in Agriculture |
| 2003-2007 | Schreyer Honors College Academic Excellence Award |
| 2003-2006 | Gerald L. Bayles Memorial Scholarship |

## Teaching

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| 2013 | Exceptional Life (undergraduate seminar on “exceptions to the rules” across levels of biological organization), Syracuse University |
| 2013 | Guest lecturer, Multivariate Statistics (graduate), Syracuse University |
| 2011 | Teaching assistant, Integrative Biology (undergraduate lab), Syracuse University |
| 2009-2011 | Teach assistant, General Biology I & II (undergraduate lab), Syracuse University |

## Service and affiliations

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|---|---|
| 2014 | Organizer, working group on intraspecific trait variation in plant communities, Center for Functional and Evolutionary Ecology, Montpellier, France |
| 2012- | Ad hoc reviewer for *Australian Journal of Botany*, *Ecography*, *Ecological Monographs, Ecosphere, Functional Ecology*, *Global Ecology and Biogeography*, *Journal of Vegetation Science*, *New Phytologist*, *Oecologia*, *Oikos*, *PLOS ONE*, *Methods in Ecology and Evolution* |
| 2011- | Participant and data contributor, TRY Plant Trait Database |
| 2010- | Member of Ecological Society of America, International Biogeography Society, International Association of Vegetation Science |
| 2012-2013 | Vice President, Biology Graduate Student Organization, Syracuse University |
| 2009-2010 | Presenter, Environmental Fields Days (program for Syracuse area 6th grade students), Green Lakes State Park, Fayetteville, NY |