

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

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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 non-random 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<sup>2</sup> 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 canadensis*, *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.

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 (Weiher et al. 1998, Cornwell et al. 2006, Kraft and Ackerly 2010). 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

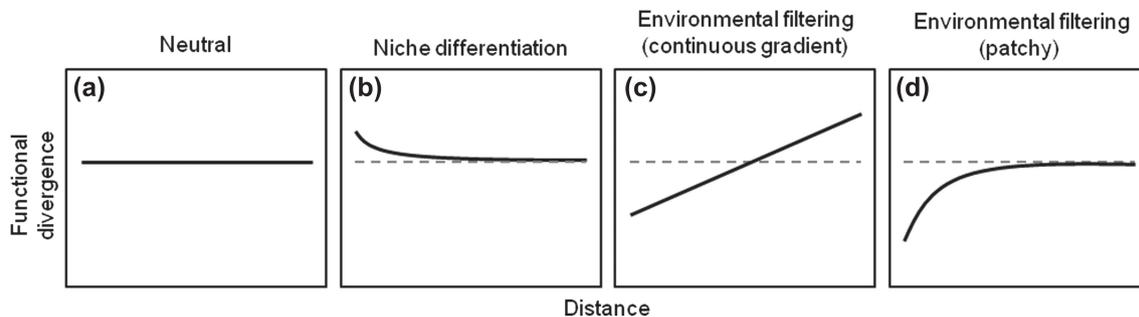


Figure 1. Hypotheses for spatial patterns of functional divergence. (a) neutral hypothesis- functional traits are neutral with regard to plant fitness and individuals disperse randomly; no relationship between functional divergence and distance. (b) niche differentiation hypothesis- resource competition 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.

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 canadensis*, *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 × 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<sup>2</sup> 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 et al. 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 h 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  $\text{NH}_4^+$  and  $\text{NO}_3^-$  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 1998) 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<sup>2</sup> plots and individual plants. At the 1-m<sup>2</sup> 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 canadensis*, *Bromus inermis*, *Galium mollugo* and *Poa pratensis*. *Solidago canadensis*, 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 Development Core Team 2010).

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).

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

	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.

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<sup>2</sup> 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<sup>2</sup> 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).

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
<i>S. canadensis</i>	371	621	40	211
<i>B. inermis</i>	130	413	69	16
<i>G. mollugo</i>	53	145	64	414
<i>P. pratensis</i>	48	132	64	314
SLA				
Plot mean	1.9	4.2	55	95
Individual	67.1	69.3	3	17
<i>S. canadensis</i>	11.3	12.0	6	21
<i>B. inermis</i>	10.3	12.6	18	30
<i>G. mollugo</i>	77.6	185.6	58	28
<i>P. pratensis</i>	14.5	38.2	62	13
LDMC				
Plot mean	0.0002	0.0005	57	74
Individual	0.0046	0.0049	6	32
<i>S. canadensis</i>	0.0007	0.0009	21	$< 1$
<i>B. inermis</i>	0.0007	0.0010	37	$< 1$
<i>G. mollugo</i>	0.0015	0.0017	12	$< 1$
<i>P. pratensis</i>	0.0013	0.0032	60	18

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

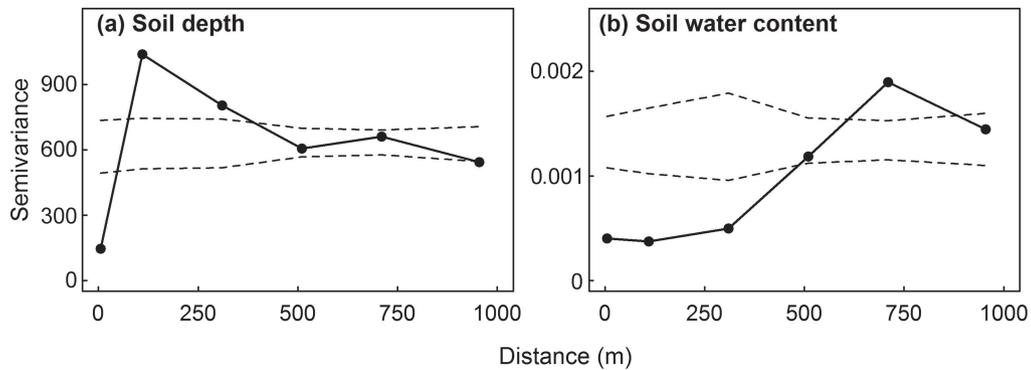


Figure 2. Semivariograms of environmental variables (1-m<sup>2</sup> plot grain size, n = 48 plots). Distance classes are 0–10 m, 10–200 m, 200–400 m, 400–600 m, 600–800 m, 800–1200 m. Dashed lines define 95% confidence envelope based on 10000 randomizations of the data. Semivariance values below confidence envelope indicate positive spatial autocorrelation; values above confidence envelope indicate negative spatial autocorrelation.

Spatial patterns of intraspecific functional divergence varied among species. At all distances, intraspecific divergence in height was 200–400% stronger in competitive dominants (*S. canadensis*, *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 4 times 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 may play a key role in shaping spatial patterns of functional divergence.

Vegetative height, SLA, and LDMC all exhibited non-random 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

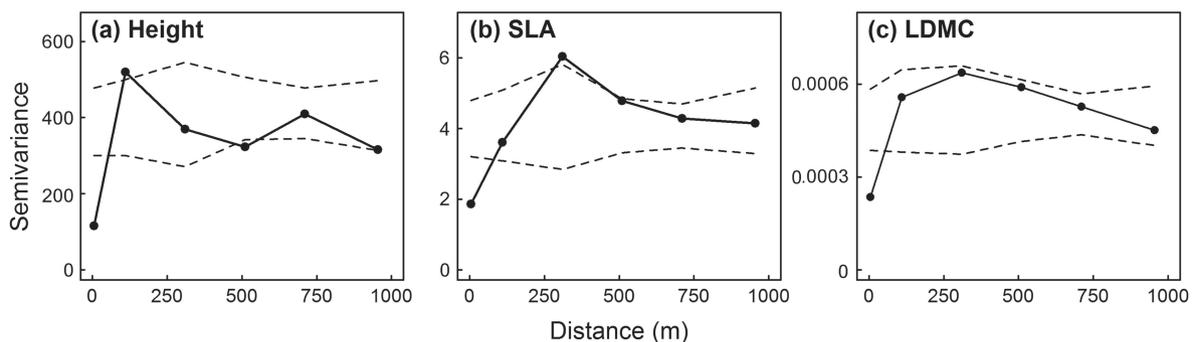


Figure 3. Semivariograms of plant functional traits (1-m<sup>2</sup> plot grain size, n = 48 plots). Distance classes are same as in Figure 2. Dashed lines define 95% confidence envelope based on 10000 randomizations of the data. Semivariance values below confidence envelope indicate positive spatial 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).

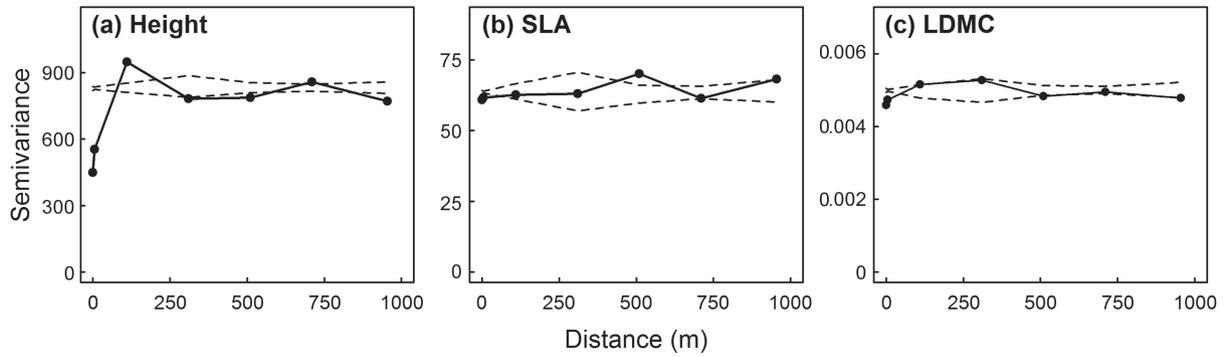


Figure 4. Semivariograms of plant functional traits (individual grain size,  $n = 2337$  individuals). Distance classes are same as in Fig. 2, with extra bin at distance = 0 for co-located plants (within same 1-m<sup>2</sup> plot). Dashed lines define 95% confidence envelope based on 10000 randomizations 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).

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<sup>2</sup> 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 (Wright et al. 2004, de Bello et al. 2009, Freschet et al. 2011, Messier et al. 2010). There are two likely explanations for this pattern. First, functional traits such as SLA and LDMC may be involved in complex tradeoffs 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

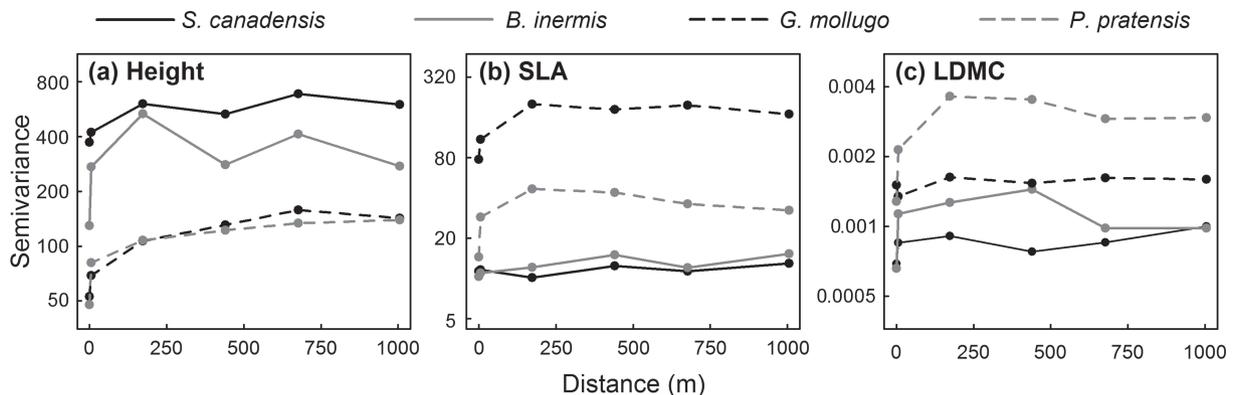


Figure 5. Semivariograms of plant functional traits (individual grain size) in common species: *Solidago canadensis* ( $n = 606$ ), *Bromus inermis* ( $n = 308$ ), *Poa pratensis* ( $n = 239$ ), *Galium mollugo* ( $n = 107$ ). Distance classes are same as in Fig. 2, with extra bin at distance = 0 for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

variation in plant communities (Albert et al. 2010, Hulshof 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 (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. Though spatial patterns of functional divergence were qualitatively similar in the four species analyzed in this study, 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. canadensis* 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 canadensis* and *Bromus inermis*, are clonal and grow in dense patches up to at least several meters in diameter (Siefert unpubl.), 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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