

Incorporating intraspecific variation in tests of trait-based community assembly

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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.

Keywords Environmental filtering · Functional trait · Intraspecific variation · Old field · Niche differentiation

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

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(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 mean, plot-specific species mean, and individual-level trait data. 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 canadensis*, *Bromus inermis*, and *Poa pratensis*.

Materials and methods

Study site

I collected functional trait data in old-field plant communities in Green Lakes State Park, Fayetteville, NY, USA (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 C₃ 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-m² 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 to 1,500 m, and distances between plots within fields ranged from 4 to 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 2,337 individuals representing 55 species (mean species richness = 9.0 species per 1-m² 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 mean, plot-specific species mean, 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 trade-off 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; 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 canadensis*, 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. canadensis*, 11 for *B. inermis*, 12 for *P. pratensis*), since estimates of trait metrics are probably 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):

$$\text{SES} = (I_{\text{obs}} - I_{\text{null}}) / \sigma_{\text{null}} \quad (1)$$

where I_{obs} is the observed metric, I_{null} is the mean of the null distribution, and σ_{null} is the standard deviation of the null distribution. A negative SES value indicates 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 1 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 canadensis*, *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*, 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. canadensis* (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

Table 1 Results of site- and plot-level community assembly tests based on fixed species mean, plot-specific species mean, and individual trait values

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	6.3
Plot-specific mean	-0.24	6.3	-0.05	8.3	-0.38	18.8	-0.20	6.3
Individual	-0.47	8.3	-0.29	8.3	0.31	16.7	0.09	8.3
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

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 1 errors across multiple tests

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 canadensis* 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-m² 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 demonstrate that non-random 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

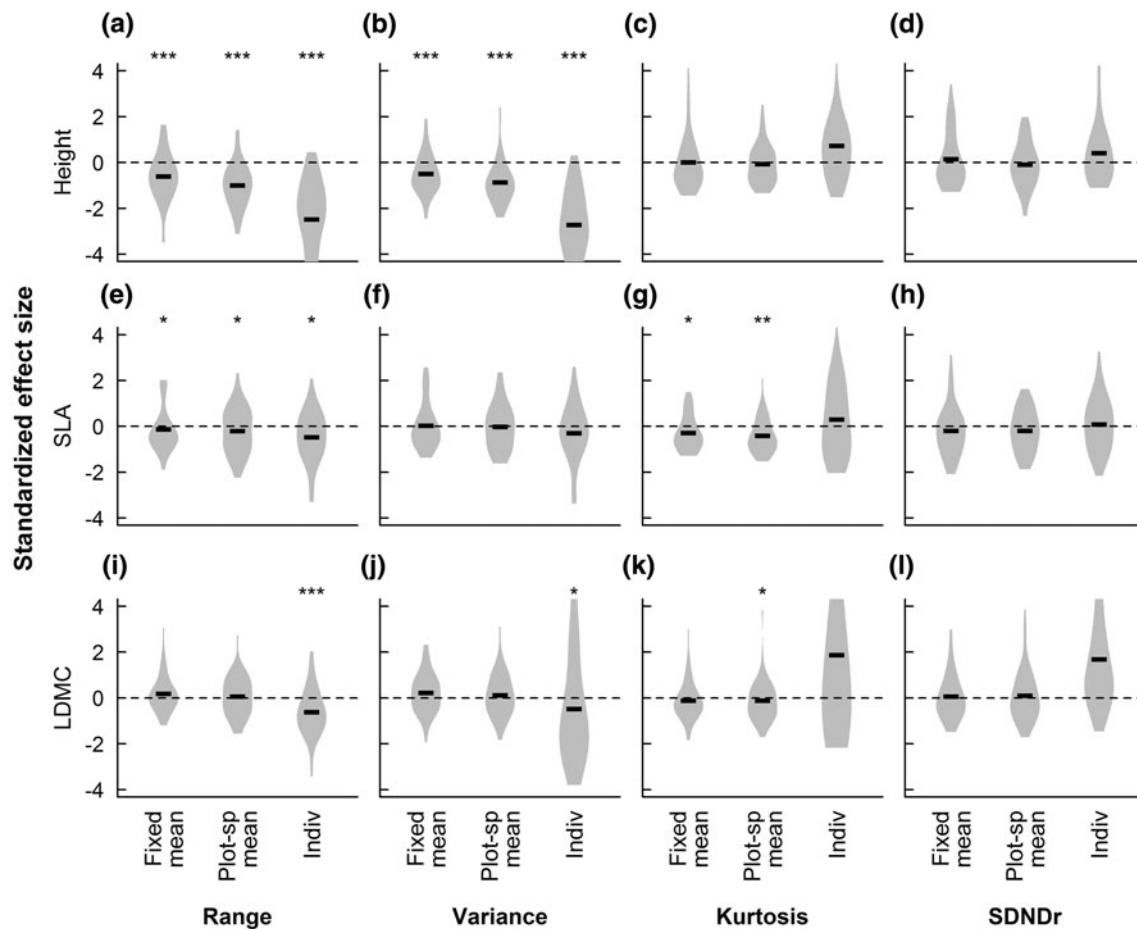


Fig. 1 Results of community assembly tests using fixed species mean, plot-specific species mean, and individual trait values. *Gray areas* show the distribution of standardized effect sizes (SES; deviation of observed values from mean of the null distribution) of community trait metrics in observed plots ($n = 48$) 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

site, *Solidago canadensis*, *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. canadensis* 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 (Gubsch et al. 2011; Roscher 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 (Albert et al. 2010; Thuiller 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; Uriarte 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

Table 2 Results of site- and plot-level assembly tests for single species

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								
<i>S. canadensis</i>	-1.53	33.3	-1.31	26.7	-0.46	0.0	-0.23	6.7
<i>B. inermis</i>	-2.12	36.4	-2.10	54.6	0.08	0.0	-0.05	0.0
<i>P. pratensis</i>	-1.26	33.3	-1.25	33.3	0.33	0.0	0.40	0.0
Specific leaf area								
<i>S. canadensis</i>	-0.24	6.7	-0.23	13.3	0.00	6.7	-0.13	0.0
<i>B. inermis</i>	-0.35	9.1	-0.29	18.2	-0.09	0.0	-0.15	9.1
<i>P. pratensis</i>	-1.55	41.7	-1.44	50.0	0.53	0.0	0.27	0.0
Leaf dry matter content								
<i>S. canadensis</i>	-0.27	20.0	-0.31	26.7	0.29	0.0	0.07	0.0
<i>B. inermis</i>	-0.87	36.4	-0.78	36.4	-0.24	8.3	-0.04	8.3
<i>P. pratensis</i>	-2.24	50.0	-1.86	66.7	0.59	0.0	0.15	0.0

Mean SES values refer to average standardized effect sizes across all neighborhoods of a given species in the study site ($n = 15$ for *S. canadensis*, 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 1 errors across multiple tests

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 4–1,500 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-m² 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) and 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.

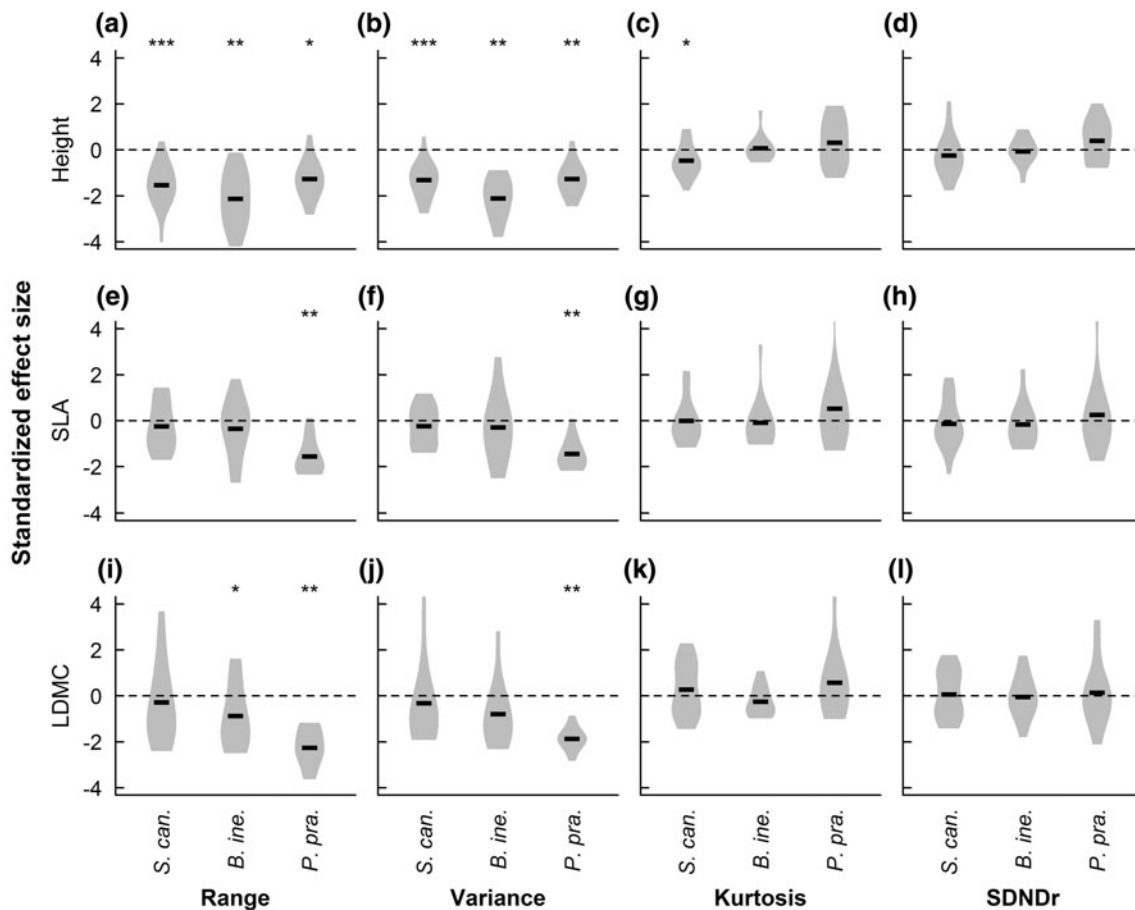


Fig. 2 Results of single-species assembly tests. Results are shown for the three most abundant species in the study site: *Solidago canadensis* (*S. can.*), *Bromus inermis* (*B. ine.*), and *Poa pratensis* (*P. pra.*). Only plots containing at least eight individuals per species were included in

the analysis. *S. canadensis*, $n = 15$; *B. inermis*, $n = 11$; *P. pratensis*, $n = 12$. *SLA* specific leaf area, *LDMC* leaf dry matter content. For explanation of graphs, see Fig. 1

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 advance our 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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Conflict of interest The author declares that he has no conflict of interest.

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