Trait-mediated community assembly: distinguishing the signatures of biotic and abiotic filters

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Conflicting hypotheses predict how traits mediate species establishment and community assembly. Traits of newly establishing individuals are predicted to converge, or be more similar to the resident, preexisting community, when the biotic or abiotic environment favors a single best phenotype, but are predicted to diverge when trait differences reduce competitive interactions. We tested these competing hypotheses using transplant seedlings in an old-field environment, and assessed the contribution of inter- and intra-specific transplant trait variation to community-level patterns. Using a soil moisture gradient and resident plant removals, we determined when traits of newly-establishing plants converge or diverge from the resident community by calculating community weighted mean traits for transplant and resident communities. We saw evidence of environmentally- and competitively-driven trait shifts that resulted in both trait convergence and divergence from the resident community, whose traits reflect the combined effects of both drivers. Leaf dry matter content (LDMC) of transplants diverged in the presence of competition, whereas plant height and stem-specific density (SSD) showed the opposite pattern, converging with the resident community in their presence. Specific leaf area (SLA) shifted with competition but did not reflect resident community SLA. All transplant traits were influenced by soil moisture, often in an interaction with competition, indicating that the strength of convergence or divergence is contingent on the abiotic environment. Intraspecific differences in transplant traits among treatments were evident in three of four traits; intraspecific height and SLA trends mirrored transplant community-level trends, whereas intraspecific shifts in SSD were distinct from community-level trends. Our study shows competition between plant species may cause traits of newly establishing plants to converge with the resident community, as frequently as it selects for trait divergence. These opposing effects of competition suggest that it plays a pervasive role in both intraspecific and species-level trait differences among communities.

A central goal of community ecology is to identify and develop general principles of community assembly (Grime 2006, McGill et al. 2006). Functional traits have proved useful for identifying successful strategies of species establishment and coexistence within plant communities, and are now widely applied (Violle et al. 2007). By assessing patterns of trait dispersion across ecological communities, environmental gradients and geographical scales, classic research on functional traits has focused on determining when niche differentiation and environmental filtering contribute to assembly (Weiher et al. 1998, Kraft et al. 2008, Maire et al. 2012). The underlying theory for this classic approach predicted that competition should limit the establishment of species with similar resource requirements (MacArthur and Levins 1967), resulting in the over-dispersion of trait values as plants with overlapping resource requirements are excluded (i.e. niche differentiation; Fig. 1A) (Weiher and Keddy 1995, Grime 2006, Cornwell and Ackerly 2009). In contrast, 'environmental filtering' was predicted to promote the establishment of new species that possess optimal traits

for underlying abiotic conditions, causing traits to converge towards a single optima (Fig. 1A; Weiher et al. 1998).

Despite evidence for both under- and over-dispersion of traits in plant communities, recent criticisms have challenged these classic interpretations of trait dispersion patterns (Funk et al. 2017). The application of coexistence theory to community assembly has raised the hypothesis that trait-based competitive differences may result in trait convergence (Fig. 1B; Mayfield and Levine 2010). Studies on tree community assembly, for example, show that most species establish when their traits match those of the surrounding community because of the competitive advantages conferred by these traits (Kunstler et al. 2016, Muscarella and Uriarte 2016). Such trends, however, remain difficult to detect in most observational studies, as it requires that responses to underlying abiotic factors and competition be disentangled statistically (Mayfield and Levine 2010, Gross et al. 2013, Kraft et al. 2015a). Furthermore, studies that attempt to detect this type of trait response by controlling for abiotic factors often utilize data from established communities in
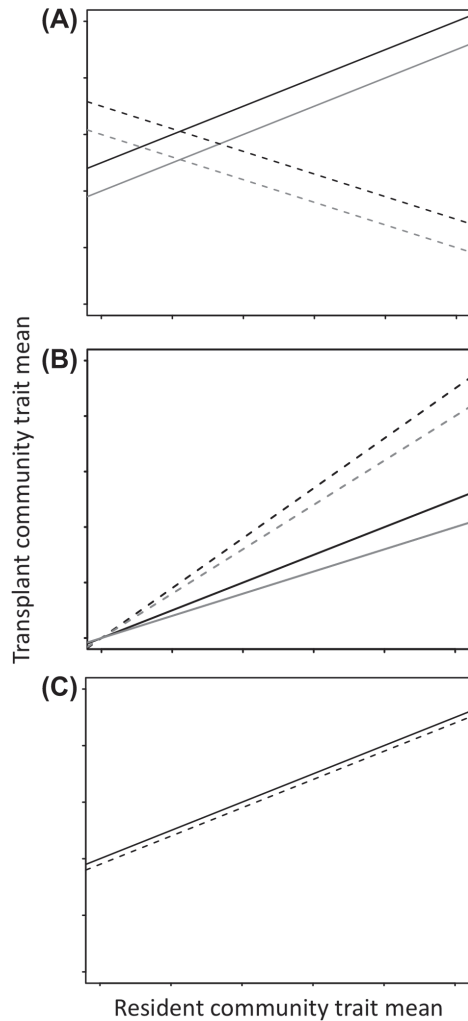
Figure 1. Interpreting trait responses to high or low soil moisture and presence or absence of competitors. (A) Classic hypothesis that competitive dynamics drive trait divergence, causing a negative correlation between transplants and the resident community when competitors are present (dashed lines). Environmental filters drive trait convergence, causing a positive correlation in the absence of competition (solid lines). Trait convergence is caused by unmeasured environmental factors – soil moisture has an additive effect, altering optimal trait levels (black versus grey lines). (B) Competition reinforces trait convergence, causing stronger convergence (slope closer to 1) when competitors are present than when they are absent. In this example, soil moisture has an interactive effect. (C) Competition and soil moisture do not alter trait convergence that is caused by unmeasured variables.

which species have already been excluded through competition. As discussed by de Bello et al. (2012), to accurately assess the effects of biotic processes using this approach requires all species that have the potential to exist within a community to be included in the species pool, as they may inhabit communities in the absence of existing selective pressures. Similarly, multivariate approaches may not detect differences in trait responses across gradients in biotic or abiotic conditions, as they may be canceled by opposition in the direction and strength of selection acting along these different niche axes (Spasojevic and Suding 2012). A better understanding of the causal relationships between traits

and the drivers of community assembly requires the application of experimental approaches that test the effect of abiotic constraints with and without competitors (Fig 1; Kraft et al. 2015a, Funk et al. 2017).

Many trait-based studies of community assembly assume that individuals of a single species show little or no variation in their traits, potentially obscuring the effects of traits on community assembly (Bolnick et al. 2011). The mechanisms driving community assembly act upon individuals (Clark et al. 2011), suggesting that intraspecific trait variation (ITV) may play an important role in community assembly when species express considerable phenotypic plasticity or genetic diversity (Albert et al. 2010). Indeed, studies that test the role of ITV have shown it can alter community assembly by altering biotic interactions with neighboring species and allowing greater resource use (Violle and Jiang 2009, Fridley and Grime 2010, Jung et al. 2010). The relative importance of this ITV varies in the proportion of total variation within or across communities, ranging from being relatively small (Garnier et al. 2001) to representing a substantial amount (Violle et al. 2007, Albert et al. 2010, Messier et al. 2010). A recent study by Lajoie and Vellend (2015) suggests that the importance of ITV in community assembly may differ with the environmental axis of interest, as they found ITV to respond more to non-climatic conditions and to variation in local species dominance. Furthermore, a recent meta-analysis by Siefert et al. (2015) found differences in the extent of ITV among trait categories, with organ-level traits having less ITV than whole-plant traits such as height or plant architecture. Intraspecific trait variation has also been demonstrated to influence interspecific trait differences, as greater within-species variation can cause greater trait overlap among species (Le Bagousse-Pinguet et al. 2014). Including intraspecific variation in studies of community assembly may therefore provide novel insights previously missed when it was assumed to be negligible (Jung et al. 2010, Thuiller et al. 2010, Bolnick et al. 2011, Violle et al. 2012).

In this study, we implement a recently-proposed, experimental approach for separating the effects of competition and the local environment on the traits of newly establishing plants. This approach tests whether traits of newly establishing species converge or diverge from the resident community when in the presence and absence of competition (Kraft et al. 2015a), and further assess when trait shifts reflect inter- and intraspecific differences among individuals. We selected sites along a soil moisture gradient and at each site established plots in which we either retained or removed the existing old-field plant community (hereafter termed the resident community). The traits of the resident community in these sites reflect the outcome of competitive dynamics within the local abiotic conditions. We introduced seedlings of four species that vary in commonly-measured traits (hereafter termed the transplant community), and used biomass-weighted mean trait values to compare traits of the transplant community to the traits of the resident community. Our goals were to determine: 1) when competition and local environmental conditions cause transplant traits to converge with or diverge from the resident community, and 2) whether shifts in transplant traits among treatments were driven by shifts in the success of different transplant species (species-level differences) or by intraspecific variation.

Our experimental approach allows us to assess the extent of trait convergence and divergence of newly establishing species in the initial stages of community assembly and, unlike in purely observational studies, this allows us to attribute these patterns to each of the competing hypotheses (Fig. 1). For example, if the hypotheses of environmental filtering and niche differentiation accurately predict traits of newly establishing plants, we would expect the traits of the transplant community to converge with the resident community in the absence of competition, but to show divergence when competitors are present (Fig. 1A). If, however, a trait confers a competitive advantage to an individual, we would expect to see trait convergence in our establishing transplants. This should produce a positive correlation between transplant trait means and those of the resident community even in the presence of competition (Fig. 1B). Various combinations of competitively-driven divergence or convergence with environmental filtering are expected to produce distinct patterns (Fig. 1B–C), and can therefore lead to a more mechanistic understanding of trait-based community assembly. We also note that traits expressed by the resident community are likely the outcome of both competition and the local environment, and in some cases competitive dynamics will cause these traits to differ from those that are most suited to the abiotic environment in the absence of competition. This scenario, not shown in Fig. 1, could cause transplant traits to be independent of resident community traits in the absence of competition.

Material and methods

Study species

The focal species selected for this study are perennial species native to tallgrass prairies, with some species occurring naturally at low abundances and all having established in other old-field experiments at our field site (Gilbert unpubl.). Our aim was to select species that were distinct in their growth rate and traits and would allow us to potentially detect a range in trait responses to our environmental gradient. Using published trait data (Reich et al. 2003, Tjoelker et al. 2005) we selected target species that varied in their relative growth rate, specific leaf area and measures of photosynthetic rate. Based on this criterion and germination rates, we selected three forb species, *Monarda fistulosa* (Lamiaceae), *Asclepias tuberosa* (Apocynaceae), *Liatris aspera* (Asteraceae) and the C_4 species, *Panicum virgatum* (Poaceae), for use in this transplant experiment. Although *P. virgatum* differs considerably in its growth form, this particular grass species has been noted as having traits more similar to forb species than other grasses (Craine et al. 2001).

As recommended by the seed supplier (Prairie Moon Nursery, Winona, MN), seeds of *M. fistulosa* and *P. virgatum* were cold stratified for six weeks, while the seeds of *A. tuberosa* and *L. aspera* were cold and moist stratified for the same duration. Transplants were started within a greenhouse, with seeds directly planted into a standard potting soil. Since germination was initially low, a solution of 0.5 g l⁻¹ gibberellic acid was applied to additional seeds in petri dishes and these seeds were transplanted into pots and included in the study. A simple bottom–up watering system was initially used, however, once grown, seedlings were moved out of the greenhouse and watered naturally by frequent rain. Prior to planting into experimental plots, plants were selected to exclude outliers (exceptionally large or small seedlings for a given species), and all remaining plants were randomized across treatments.

Experimental design

In the spring of 2013, 27 experimental sites were established at the Koffler Scientific Reserve, in Ontario, Canada (44°1′47.57″N, 79°32′3.23″W). Sites were spaced a minimum of 20 m apart and selected to utilize the natural variation in soil moisture across the reserve, with average seasonal soil moisture between sites ranging from 9–43%. The relative abundances of resident species within sites varied, but consistently included *Bromus inermis* (Poaceae), *Solidago canadensis* (Asteraceae) and *Vicia sativa* (Fabaceae), with other species such as *Conyza canadensis* (Asteraceae) and *Eupatorium maculatum* (Asteraceae) occurring in a smaller number of plots.

Each site consisted of three 1-m² plots all within 2 m of each other, with the three plots randomly assigned to receive one of three treatment groups: 'competition', 'no competition' and 'control'. For plots of the 'competition' group, the resident community was left intact, preserving naturally-occurring levels of biotic interactions as well as environmental selection. 'No competition' plots were cleared of above-ground vegetation and then maintained by weekly weeding through the duration of the experiment. The leaf litter was retained and replaced evenly over the plot to help preserve the soil moisture gradient. In removing competitors we altered the environmental conditions of the plot, removing the effects of competition for soil nutrients and light. As such trait variation in this plot will primarily reflect transplants' response to our primary environmental gradient, soil moisture (Kraft et al. 2015a). Finally, we did not manipulate the community in 'control' plots; these plots were measured to assess the trait distribution of the resident community under local biotic and abiotic conditions.

We planted 27 plants in each of the competitor-free and competition plots, with seven individuals of *L. aspera*, *A. tuberosa* and *P. virgatum* and six individuals of *M. fistulosa*, due to low seed germination for this species. To avoid interactions between transplants and the plants beyond the boundaries of the plots, we arranged plants in a grid formation, with individuals spaced 10 cm apart and a border of at least 25 cm left between our treatment plants and the plot edge. In the competition treatment, competitors were trimmed from a circular area 10 cm in diameter around each transplant at the time of planting, creating an initial period of reduced competition in which transplants could establish. These trimmed areas grew back quickly and were no longer apparent after three weeks. Transplants were randomly assigned to plots and to locations within plots. Individuals that did not survive transplantation were excluded from our analysis.

Traits were measured at the end of the season for each of our transplants. Four traits were selected to reflect different aspects of plant physiology and measured following

Cornelissen et al. (2003): specific leaf area (SLA), leaf dry matter content (LDMC), plant height, and stem-specific density (SSD). These traits have been well studied in the context of varying environments and competitive milieus of other ecosystems, allowing us to draw greater comparisons with our own results and a thorough understanding of the ecological consequences of trait selection. Both SLA and LDMC are measures of leaf economics, reflecting strategies of resource allocation and growth (Cornelissen et al. 2003). Height in turn, has been strongly associated with competitive abilities, particularly in the context of light absorption (Weiher et al. 1998, Cornelissen et al. 2003), while SSD reflects allocation to stem structure and defense against pathogens and environmental damage (Weiher et al. 1998, Cornelissen et al. 2003, Laughlin 2014).

Aboveground biomass was also measured for each plant and used to calculate community weighted means (CWM) of our traits, where the contribution that each plant makes to the community mean is weighted by its relative biomass. At the level of the resident community, these weighted means reflect the trait value of the dominant species within the community (Garnier et al. 2004), and at the level of the transplants they reflect the relative success of individuals. Traits, biomass and relative abundances were also measured for species in the control, resident community plots. When possible, we sampled up to five randomly-selected individuals for each species in the resident community (mean: 4.4, SD: 0.7). One species, *Festuca rubra*, was present in all plots but was excluded from our sampling, as it did not appear to vary predictably among plots and formed a low-level sward that was difficult to separate into individual plants. We did not measure individuals that were damaged (Cornelissen et al. 2003), and this precluded some rare species from being sampled in a control plot. Overall, we sampled an average of 3.5 species per control plot (SD: 0.64), whereas the total diversity on average was 5.2 species (SD: 1.6). This worked out to sampling species that made up over 85% of all individuals within a plot on average. For our CWM calculation, per-individual biomass was weighted by the relative abundance of the species, so that the sampled individuals were used to represent their species. We compared this first measure of CWM for the resident community to one in which all individuals sampled were considered equally – our results did not differ qualitatively, so we report only the first metric.

To determine leaf dry mass and plant biomass, plant matter was dried at 70°C for 24 h. Leaf area was determined from fresh leaf materials using the imaging software, ImageJ (ver. 1.47; Schneider et al. 2012). *Liatris aspera* was excluded from our analysis of SSD, as this species only produced basal leaves in its first growing season. Soil moisture was measured at each plot in two-week intervals using a TDR soil probe, with exact dates offset to ensure measurements were not taken within two days of the previous rain event.

Data analysis

To assess an overall response of transplant species to the traits of the resident community plots, we conducted a redundancy analysis (RDA) with the total aboveground biomass of each species as the response. This response incorporates both growth and survival by summing the biomass of all individuals within a species in each plot. The predictor matrix included plot soil moisture as well as the traits of individuals in the resident community plot, both alone and in an interaction with competition. In addition, we conducted a survival analysis of our focal species to assess the effects of competition and resident community traits on survival alone.

We began our trait-specific analyses by testing for correlations between traits, both at the community and species level. Since we observed low correlations between traits (all $r < 0.2$ for traits at the community-level and all $r < 0.25$ for traits within species), we considered traits to be independent of one another for our tests. Comparing PCA results from our traits to a broken stick model also indicated that a multivariate approach was not appropriate, and we therefore tested each trait separately.

Community weighted means of the transplant community were calculated for each trait by weighting trait values of each individual by its biomass relative to the total biomass of all transplants in a plot. Weighted means of the resident community were calculated using trait values of sampled individuals weighted by biomass and the relative abundance of each resident species. The weighted mean traits of the resident community were used as independent variables in our statistical models, with SLA of the resident community predicting SLA of the transplants, LDMC of the resident community predicting LDMC of the transplants, and so on. By including the CWM traits of the resident community, we were able to assess both the direction and relative strength of trait selection acting on our transplants. For example, if competitive interactions cause trait divergence, we would see a negative correlation between the mean trait values of the transplant and resident communities in our competition treatment. Our assumption is that transplants respond to the resident community but not each other because of the low abundances and small sizes of the transplants.

To meet test assumptions, transplant weighted means for height, LDMC and SSD were log transformed, and the weighted means for the resident community were also log transformed for these traits in order to compare on the same scale. Similarly, weighted mean SLA was square root transformed for transplants and the resident community. To test for community-wide responses in SLA and SSD, we applied linear-mixed-effects models using the lmer function in the R package lme4. In our models, we used site as a random effect and soil moisture, competition and the weighted mean of the resident community as fixed effects. Including site as a random effect generated patterns in the residuals for LDMC and height, and we therefore used linear models with site included as a fixed effect when analyzing these traits.

We tested for intraspecific shifts in traits and whether they converged or diverged with the resident community using similar methods as were used for the entire transplant community. Weighted-means were developed for each species in each plot (by weighting each individual by its biomass relative to the other individuals of the same species). Changes in traits due to interspecific shifts in species abundances (or relative biomass) do not change the weighted mean values within species, whereas phenotypic changes within species do. Statistical models were developed for each trait individually, with species identity, soil moisture, competition and

the resident community trait value included as fixed effects, and plot included as a random variable. Within-species trait responses were considered significant if there was a significant effect of soil moisture, competition or resident community trait (main effects or interactions), signifying that all species change in similar ways with these treatments. Within-species trait responses were also considered significant if there was an interactive effect between species and any of the other main effects, meaning that at least one species showed a shift in that trait. In the absence of detectable within-species response to our independent variables, we attributed differences in community-level traits to differences among species (as tested with the RDA).

For all analyses except height, we began with the most complex model (all interactions included), and used likelihood ratios to drop higher-level terms that did not improve model fit, until all terms remaining in the model were significant individually or in an interaction. There was a significant correlation between soil moisture and the weighted mean height of the resident community (no other traits showed this correlation). As a result, we did not test an interaction between soil moisture and the weighted mean height of the resident community, and instead tested each of these fixed effects in the presence and absence of the other (i.e. tested for the effect of soil moisture when community weighted mean height was present or absent from the model and vice versa). All analyses were conducted in R, ver. 3.2 (<www.r-project.org>).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.512p5> (Loughnan and Gilbert 2017).

Results

Traits of individual transplant species and the transplant community as a whole changed with traits of the resident community, with responses often depending on both the presence of competitors and on soil moisture (Table 1, Fig. 2, 3). We interpret the change in traits when competitors are present (versus absent) as the effect of competition, while the difference in traits when competitors are absent reflects the relative effect of the environment, as the seedlings were

planted at relatively low densities (Kraft et al. 2015a). The changes in transplant traits were driven in part by changes in the biomasses of transplant species among plots (Supplementary material Appendix 1 Table A1, $p < 0.01$), and could not be attributed to species-specific survival responses to our treatments or resident community traits (all $p > 0.3$). However, changes in transplant traits were also due to within-species shifts in some traits (Fig. 4, 5, Supplementary material Appendix 1 Table A3). Overall, we saw evidence of trait convergence in height and SSD when competitors were present, but not in the absence of competitors. We saw the opposite trend for LDMC, where transplants converged with the resident community in the absence of competitors, but diverged when competitors were present (Fig. 2). Due to the complexity of interactions with soil moisture, we consider each of the traits separately below, with all references to a mean trend referring to the biomass weighted mean at the appropriate level of weighting (community or species).

Specific leaf area was the only trait for which transplants did not converge or diverge with the resident community. Instead, transplant SLA increased significantly with both competition and soil moisture ($p < 0.001$ and $p = 0.037$; Supplementary material Appendix 1 Table A2). In the presence of competitors, transplant SLA increased by 10.30 mm^2 mg^{-1}, which was about the same increase observed across the soil moisture gradient (Fig. 2A). While transplant species differed in mean SLA, all showed a significant within-species increase in SLA in response to competition but not soil moisture ($p < 0.001$, Supplementary material Appendix 1 Table A3). Interestingly, the resident community SLA showed no trend with soil moisture ($p = 0.85$).

The other three traits showed different patterns of convergence or divergence with the resident community, with these patterns depending on whether competitors were present. Transplant LDMC showed a significant three-way interaction (soil moisture × competition × LDMC of resident community, $p = 0.026$; Supplementary material Appendix 1 Table A4). At mean soil moisture, transplant LDMC converged with that of the resident community in the absence of competition (positive slope), but diverged from the resident community when competitors were present (Fig. 2B). These trends were even stronger in high soil moisture plots, but reversed in low soil moisture plots, indicating that the effect of competition on LDMC convergence or divergence is contingent on abiotic conditions (Fig. 3A–B). Our test of intraspecific changes in LDMC showed that

Table 1. Summary of transplant trait convergence and divergence with the resident community. Environment effect refers to trends in weeded plots and Competitive effect refers to trends when the resident community was present. Dashed lines indicate no significant trend, and '+' indicates a trait response to the environment or competition that did not cause trait convergence or divergence with the resident community. * Trends were contingent on soil moisture (Fig. 3) with given trends apparent at mean soil moisture levels (Fig. 2). † Different species showed qualitatively different trends.

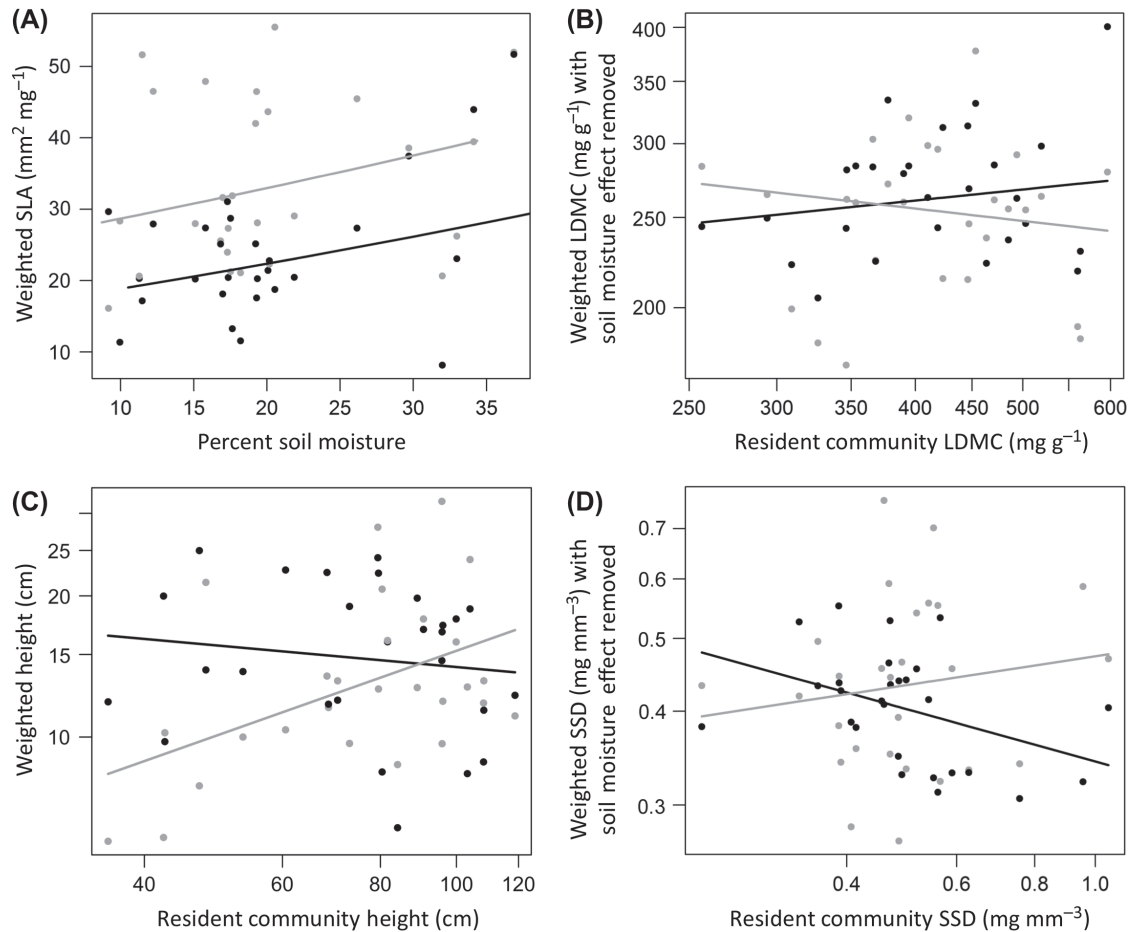| Level of organization	Trait	Environment effect	Competition effect
Interspecific	SLA	+	+
	LDMC	converge*	diverge*
	height	diverge	converge
	SSD	diverge*	converge*
Intraspecific	SLA	−	+
	LDMC	−	−
	height	−	converge
	SSD	converge and diverge†	converge and diverge†

Figure 2. Weighted mean trait values of transplant community in the presence (grey) and absence (black) of competition. (A) Specific leaf area (SLA) increases with soil moisture and in the presence of competitors but is unrelated to resident community SLA (not shown). (B) At mean soil moisture, leaf dry matter content (LDMC) converges with the resident community when competitors are absent, but shows the opposite trend in the presence of competition. (C) Plant height converges with the resident community when competitors are present but not when they are absent. (D) Stem-specific density (SSD) at mean soil moisture shows similar patterns as plant height. LDMC and SSD responses also depended on soil moisture (Fig. 3), but here we show patterns at mean soil moisture levels.

species differed significantly in LDMC (p < 0.001), but that LDMC within species did not respond to the resident community or treatments (Supplementary material Appendix 1 Table A5).

Plant height of the transplant community converged with the resident community when competitors were present, but showed no significant trend when competitors were absent (significant competition × resident community height interaction, p = 0.027; Fig. 2C). This response of the transplant community was mirrored by intraspecific trends in height, with all species showing convergence in the presence of competitors but no significant trend in the absence of competitors (Fig. 4, Supplementary material Appendix 1 Table A6–A7). We did not test for a three-way interaction for height because the height of the resident community increased with soil moisture (r = 0.32, p = 0.02). Instead, a separate analysis was run testing the effects of soil moisture when resident community height was not included; this analysis also showed no significant effect of soil moisture alone or in interaction (all p > 0.1).

Transplant community SSD showed a significant three-way interaction between soil moisture, competition, and the resident community SSD (p = 0.028; Supplementary material Appendix 1 Table A8). Transplant community SSD tended to diverge from SSD of the resident community in the absence of competitors, but converged with resident SSD when competitors were present (Fig. 2D). This trend of SSD convergence when transplants were in competition depended on soil moisture; it was strongest in dry plots but reversed (became divergent) in wet plots (Fig. 3C–D). Interestingly, intraspecific trends in SSD differed among species (Fig. 5, Supplementary material Appendix 1 Table A9) – only *P. virgatum* converged with the resident community when in competition (species × competition × resident community interaction p = 0.003; Fig. 5). However, all species responded to soil moisture in a consistent way by increasing divergence with the resident community at high soil moisture.

Discussion

The aim of our study was to understand when and why community assembly causes trait convergence or divergence among species. By using an experimental approach, we were
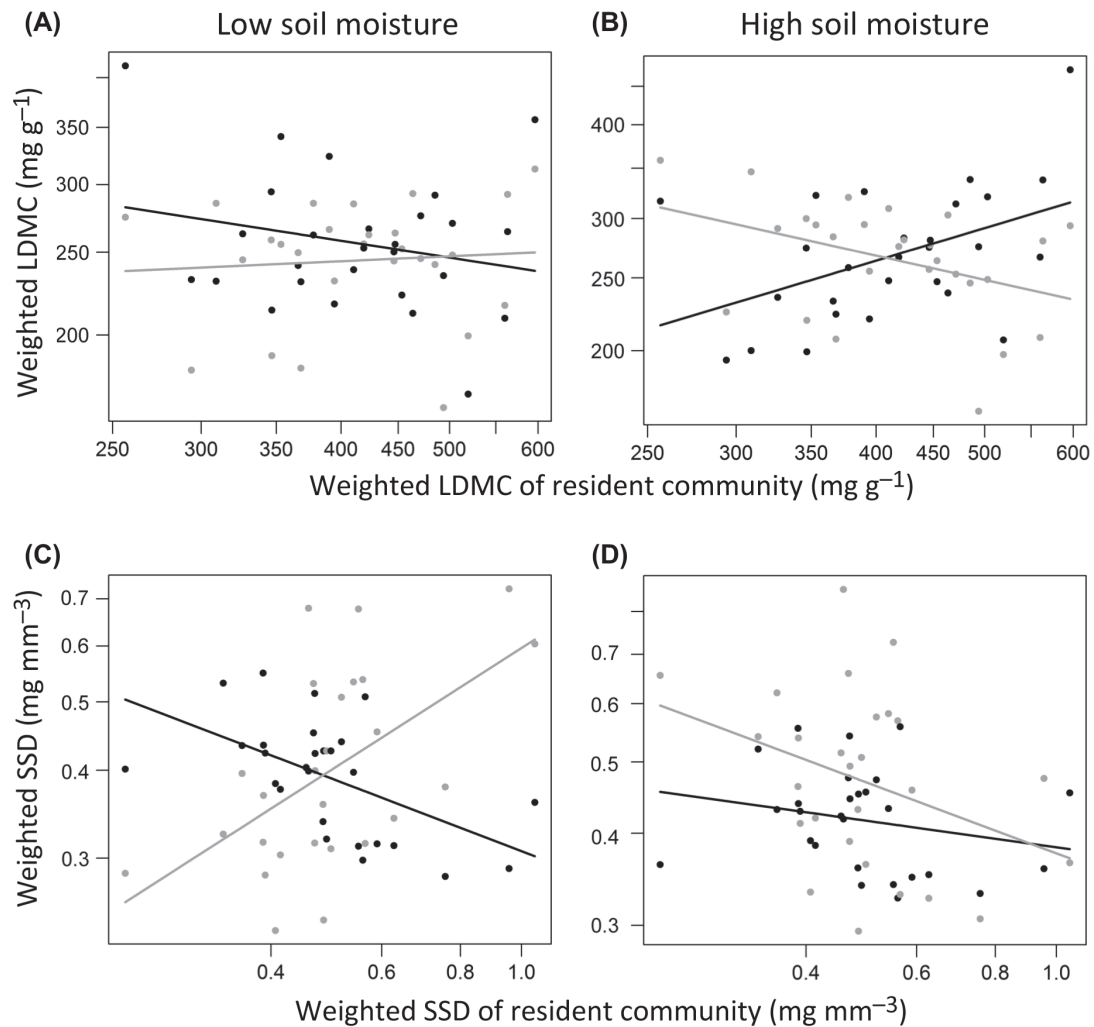
Figure 3. The effect of low soil moisture (mean – standard deviation; A, C) and high soil moisture (mean + standard deviation; B, D) on trait convergence for LDMC (A, B) and SSD (C, D). Figures display fitted trends in the presence of competitors (grey line) and in competitor-free treatments (black line). Points are fitted models plus residuals, with residuals taken from the original fit model that treats soil moisture as a continuous variable, and are included only to illustrate variation around the model fit.

able to determine when traits of transplanted, establishing species, and individuals within species, converged with the resident community. Our results clarify that both competitive interactions and the underlying environment can drive patterns of trait convergence and divergence, and that these outcomes differ among traits. Moreover, we were able to assess the degree to which intra-specific trait variation may augment or reduce community-level patterns. Taken together, our results support recent shifts in community assembly theory that recognize how competitive dynamics may lead to community-level patterns that differ from those predicted by classic theory, and that these patterns may be driven in part by intraspecific variation.

The results of our study help to resolve the debate about competitively- versus environmentally-driven trait convergence by showing that both processes act on newly-establishing species in a community. In average soil moisture conditions, competitive dynamics were found to cause trait convergence in height and SSD (Fig. 2C–D). This pattern of trait convergence is generated when differences in a trait drive competitive asymmetries, thus causing more similar

species to be more likely to coexist in a location (Mayfield and Levine 2010). Our results of trait convergence are consistent with both contemporary predictions about competitive interactions (Fig. 1B), and broadly supported in recent studies on annual plants and trees (Kraft et al. 2015b, Kunstler et al. 2016, Muscarella and Uriarte 2016). More broadly, our study supports a general shift in understanding how trait differences frequently lead to greater competitive asymmetries, whether competitive effects are measured in extant or invaded communities (Kunstler et al. 2016, Gross et al. 2015), over full generations (Kraft et al. 2015b), or in newly establishing species, as was done here.

Although trait divergence with the resident community is predicted by classic theory, recent research has suggested that divergence of single traits rarely promotes local coexistence (Kraft et al. 2015b, Kunstler et al. 2016, Muscarella and Uriarte 2016). In contrast, our study indicates that divergence along single trait axes can be important for maintaining diversity by allowing new species to establish, and also that the impact of trait divergence depends on underlying environmental conditions (Fig. 3). This environmental
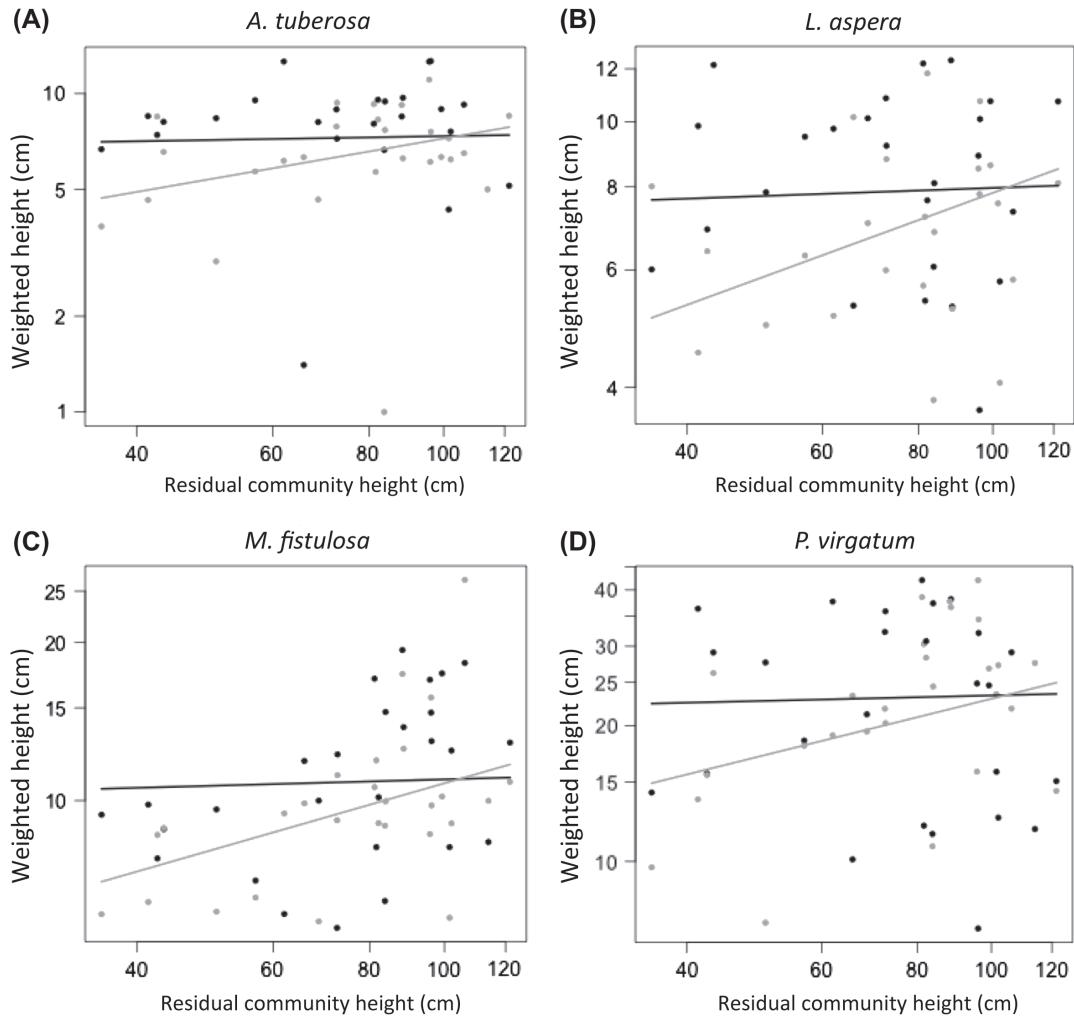
Figure 4. Intraspecific trends in the height of each transplant species in the presence (grey) and absence (black) of competition. *Asclepias tuberosa* (A), *Liatris aspera* (B), *Monarda Fistulosa* (C), and *Panicum virgatum* (D). All converge with the resident community when competitors are present, but not when they are absent. Note the different y-axes.

contingency of traits on competitive dynamics is hardly surprising; a large body of research has recognized the joint effects of environmental conditions and species interactions on traits at the species and community level (Dudley and Schmitt 1996, Suding et al. 2008, Poorter et al. 2009) and, similarly, species competitive dynamics rely on parameters that are sensitive to the underlying environment: maximum rates of increase, and both intra- and inter-specific density dependence (Germain et al. 2016). Our results highlight the need to better incorporate trait-specific competitive dynamics into research on coexistence and diversity, which in turn requires an explicit matching of environmental conditions to the effects of specific traits.

One approach to understanding trait-specific responses to competition and environmental conditions involves predicting the benefits and tradeoffs that traits confer under different environmental conditions, and understanding how these conditions change when species compete. For example, SLA is known to increase in response to soil moisture and shading, presumably because water losses from transpiration of thinner leaves become less costly relative to gains in carbon assimilation (Poorter et al. 2009, Jung et al. 2010). In

our study, plants invested less in leaf mass relative to leaf area as soil moisture increased, confirming the predicted effect of soil moisture on SLA in plant community assembly. The presence of above-ground competition drove a similar shift in SLA, causing an increase in this trait for each species and the transplant community as a whole. This response to above-ground competition suggests that shading caused by competitors had a stronger impact than competitor-driven reductions in soil moisture, as these constraints tend to produce opposite shifts in SLA (Poorter et al. 2009). Interestingly, SLA of the resident community did not show a clear relationship to soil moisture, suggesting that competition and other soil factors may have influenced the assembly of resident plants.

Just as SLA reflects leaf surface area relative to leaf mass, LDMC measures the ratio of dry to wet mass, having the opposite effect on leaf function than SLA; low LDMC can increase water loss from transpiration, but also the area of photosynthetic tissue available for light capture in low light conditions (Wilson et al. 1999). As with SLA, competition tended to cause a decrease in LDMC (more shade tolerance), but this was most pronounced in high soil moisture plots

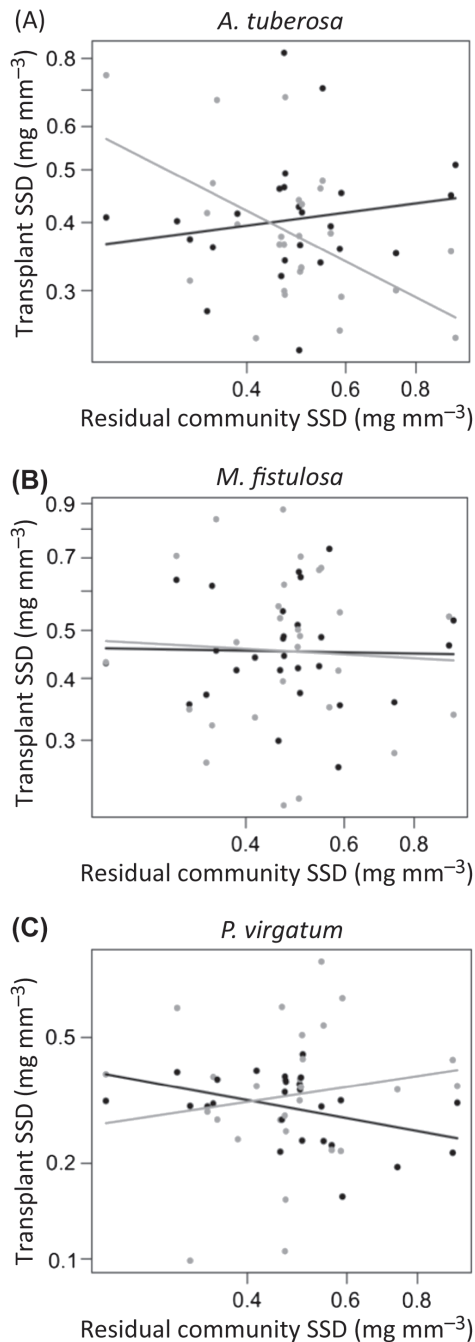(A) *A. tuberosa*

(B) *M. fistulosa*

(C) *P. virgatum*

Figure 5. Intraspecific trends in SSD *Asclepias tuberosa* (A), *Monarda Fistulosa* (B), and *Panicum virgatum* (C), in the presence (grey) and absence (black) of competition. Competitors caused divergent responses among transplant species.

when the resident community had low LDMC (Fig. 3B). In contrast, LDMC showed little variation in the presence of competitors in low soil moisture plots (Fig. 3A), suggesting that tradeoffs between shade tolerance and water use efficiency favored shade tolerant strategies more strongly when water was not limiting.

The observed shifts in stem traits in response to the competitive environments were less intuitive. Both height and SSD reflect tradeoffs in plant growth and structural investment (Laughlin 2014), however, only the shifts in height complied with our expectations. Transplant height converged

with resident community height, which also increased with soil moisture, likely indicating competition for light (Westoby 1998). In contrast, SSD showed both convergent and divergent trends that varied with soil moisture and competition (Fig. 3C–D). At lower SSD values, transplants are considered to have a less conservative growth strategy, and invest fewer resources in stem structure and water transfer potential to favor faster growth rates (Laughlin 2014). We only found SSD to converge in dry and mesic conditions and in the presence of competitors, suggesting that competition helps shape the optimal point in the SSD tradeoff between structure and growth (Fig. 2, 3). This interpretation is consistent with the shift in transplant SSD in the absence of competitors, from convergent to divergent, indicating that the relative benefits of faster growth change when competitors are absent.

There is increasing agreement that intraspecific trait variation also plays an important role in community dynamics (Bolnick et al. 2011), and may constitute a considerable proportion of trait variation within a community (Albert et al. 2011, Siefert et al. 2015). An unresolved question that emerges when intraspecific trait variation is present is whether it reinforces patterns seen at the community level or instead produces distinct patterns (Bolnick et al. 2011). Although some traits that we observed displayed intraspecific trends that were consistent with the transplant community as a whole, other traits highlighted species-level constraints. For example, despite consistent differences in height among transplant species, intraspecific responses in plant height mirrored the overall trends of the transplant community (Fig. 4). Siefert et al. (2015) found support for such responses in plant-level traits, such as height and plant architecture, that are less conserved and respond more to local environmental conditions. Increases in height in particular have been shown to be induced in some species when shading is present (Dudley and Schmitt 1996). Similarly, SLA increased for all species when competitors were present, mirroring the community-level response to competition but not to soil moisture. At the other extreme, SSD trends varied by species, with only one species (*Panicum virgatum*) showing similar patterns to community-level trends and the other species showing no trend (*Monarda fistulosa*) or even opposite trends (*Asclepias tuberosa*; Fig. 5). Such contrasting intraspecific responses across species were also found by Le Bagousse-Pinguet et al. (2015), who found opposing responses among target species across a rainfall gradient, but in relation to plant height. Finally, LDMC differed among species but showed no intraspecific trends, a result that is consistent with previous research showing that LDMC shows little intraspecific variation (Wilson et al. 1999). Taken together, our results differ from previous research that has found consistent similarities between intraspecific- and community-level trends (Jung et al. 2010; Carlucci et al. 2015). These differences suggest that patterns of intraspecific trait variation are dependent on both the traits and species considered, and are generally more muted than community-level patterns.

In interpreting the results of this study, it is important to recognize three limitations to the approach taken. First, by using a natural soil moisture gradient and removals, we tested the effects of one known environmental gradient and

contrasted these with the effects of competition. It could be that sampling over a broader range of abiotic conditions would cause the relative magnitude of environmental effects to differ. Second, in order to test both inter- and intra-specific trends in an experimental context, we used four species characteristic of tall grass prairie ecosystems. Although selecting species known to differ in their trait values likely minimized the effects of this limited species pool, a broader pool may also have generated a different magnitude or range of interspecific effects. Nonetheless, a broader pool would be unlikely to change our conclusion that intraspecific trait variation can mirror or counteract community-level trends for newly establishing species. Finally, our approach is consistent with models of trait-based community assembly and with coexistence theory, both of which emphasize the ability of new species to invade a community (MacArthur and Levins 1967, Chesson 2000, Webb et al. 2002). However, our focus on newly-establishing species in a community differs from many observational studies in that it does not offer inferences about the processes that structured the resident community. As such, our results are more applicable to the regeneration niche.

In summary, our study highlights the effects of environmental conditions and competition on community assembly, and shows how these factors often interact to produce different trait combinations. Both soil moisture and competition were found to drive the convergence or divergence of trait responses in establishing individuals relative to that of the resident community, with these different responses reflecting the functional roles of the traits measured. In other words, we found that the local environment and competition determined whether traits of individuals establishing in a community became more or less similar to those of individuals already present within the community. More generally, our study illustrates the limitations of using patterns of trait convergence to detect competitive interactions, and offers an experimental approach that can be broadly implemented to isolate the effects of competitive exclusion on trait convergence. Finally, we echo recent calls for quantifying within species variation in traits, which only sometimes reflects community-level trends. Combining these elements provides an important step towards isolating competitive and environmental determinants of inter and intra-specific trait variation, and brings us closer to understanding how community assembly structures species diversity.

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Supplementary material (available online as Appendix oik-03945 at <www.oikosjournal.org/appendix/oik-03945>). Appendix 1.