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Ontogenetic trait variation influences tree community assembly across environmental gradients

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Abstract.   Intraspecific trait variation is hypothesized to influence the relative importance of community assembly mechanisms. However, few studies have explicitly considered how intraspecific trait variation among ontogenetic stages influences community assembly across environmental gradients. Because the relative importance of abiotic and biotic assembly mechanisms can differ among ontogenetic stages within and across environments, ontogenetic trait variation may have an important influence on patterns of functional diversity and inferred assembly mechanisms. We tested the hypothesis that variation in functional diversity across a topo-edaphic gradient differs among ontogenetic stages and that these patterns reflect a shift in the relative importance of different assembly mechanisms. In a temperate forest in the Missouri Ozarks, USA, we compared functional diversity of leaf size and specific leaf area (SLA) of 34 woody plant species at two ontogenetic stages (adults and saplings) to test predictions about how the relative importance of abiotic and biotic filtering changes among adult and sapling communities. Local communities of adults had lower mean SLA and lower functional dispersion of SLA than expected by chance, particularly at the resource-limited end of the topo-edaphic gradient, suggesting an important role for abiotic filtering among co-occurring adults. In contrast, local communities of saplings often had higher functional dispersion of leaf size and SLA than expected by chance regardless of their location along the topo-edaphic gradient, suggesting an important role for biotic filtering among co-occurring saplings. Moreover, the overall strength of trait-environment relationships varied between saplings and adults for both leaf traits, generally resulting in stronger environmental shifts in mean trait values and trait dispersion for adults relative to saplings. Our results illustrate how community assembly mechanisms may shift in their relative importance during ontogeny, leading to variable patterns of functional diversity across environmental gradients. Moreover, our results highlight the importance of integrating ontogeny, an important axis of intraspecific trait variability, into approaches that use plant functional traits to understand community assembly and species coexistence.

Key words: abiotic filtering; biotic filtering; community assembly; functional diversity; intraspecific trait variation; leaf size; ontogeny; oak-hickory temperate forest; Ozarks; plant functional traits; specific leaf area; Tyson Research Center Plot.

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Introduction

The ecological-filter concept is central to trait-based ecology and has proved useful for under-standing mechanisms of community assembly and species coexistence (Weiher et al. 2011, HilleRisLambers et al. 2012). Trait-based models of community assembly often view local com-

munities as limited-membership assemblages in which local abiotic conditions and biotic interactions impose deterministic filters on the functional trait diversity of co-occurring species (Belyea and Lancaster 1999, Diaz et al. 1999). Abiotic filtering has been found to increase species similarity through abiotic constraints in more stressful environments, resulting in low functional diversity among coexisting species (Weiher and Keddy 1995, Weiher et al. 2011). Biotic filtering, on the other hand, has been found to generate more complex patterns due to multiple mechanisms. In more benign environments limiting similarity can increase functional diversity among coexisting species (Cornwell and Ackerly 2009, Weiher et al. 2011) whereas equalizing-fitness processes can decrease functional diversity among coexisting species (Chesson 2000, Spasojevic and Suding 2012), and in stressful environments, facilitation can act to prevent coexisting species from being too similar and increase functional diversity (Brooker et al. 2008, Butterfield 2009). Empirical tests of these models are critical not only for understanding the relative importance of community assembly processes in natural communities, but also for the conservation and restoration of biodiversity in human-altered ecosystems (Funk et al. 2008, Wainwright et al. 2012).

Central to the trait-based framework is the idea that community-wide trait patterns accurately reflect the strength and signature of abiotic and biotic assembly mechanisms across environmental gradients (Diaz et al. 1999, Westoby et al. 2002, Mason and de Bello 2013). However, mechanistic inferences based on patterns of functional diversity are complicated by the fact that trait variation can emerge through a combination of interspecific trait variation, intraspecific trait variation across environmental gradients (Jung et al. 2010, Violle et al. 2012), and intraspecific trait variation across ontogenetic stages (Poorter 2007, Yang et al. 2014). Yet, most studies of trait-based assembly have focused on interspecific trait variation typically measured at a single ontogenetic stage (e.g., Cornwell and Ackerly 2009, Spasojevic and Suding 2012) or extracted from floras or trait databases with limited information on intraspecific trait variation (e.g., Schamp and Aarssen 2009, Liu et al. 2013). More recently, ecologists have incorporat-

ed intraspecific trait variation into this framework by comparing how traits of individual species vary across environments (e.g., Fernandez-Going et al. 2012, Spasojevic et al. 2014) or by partitioning trait variation within and among species to help infer the relative importance of different assembly mechanisms (e.g., Messier et al. 2010, Violle et al. 2012, Hulshof et al. 2013). In contrast, little is known about how ontogenetic trait variation influences community assembly across environmental gradients (e.g., Poorter 2007, Yang et al. 2014). If assembly mechanisms vary in their relative importance across ontogenetic stages (Webb and Peart 2000, Comita et al. 2007), community-wide patterns of functional diversity may mask the signature of abiotic and biotic mechanisms during community assembly.

Ontogenetic trait variation may play an especially strong role in mediating the strength of assembly mechanisms across environmental gradients. In plant communities one of the most conspicuous axes of trait variation is the shift from conservative or 'stress-tolerant' traits at lower resource availability to opportunistic or 'fast-growing' traits at higher resource availability (Reich et al. 1997, Wright et al. 2004, Adler et al. 2014). Communities vary along this trait axis in response to gradients in climate, light availability, soil fertility and soil moisture (Reich et al. 1997, Westoby et al. 2002, Cornwell and Ackerly 2009, Spasojevic et al. 2014). Importantly, the strength of these patterns may depend on ontogenetic shifts in traits (e.g., Poorter et al. 2005) or assembly mechanisms (e.g., Dent et al. 2013) across environmental gradients. For example, early ontogenetic stages such as seedlings and saplings typically have leaf traits that allow them to maintain positive carbon balance in light-limited environments (Dalling et al. 1998, Thomas and Winner 2002, Poorter et al. 2005), often resulting in stronger abiotic filtering of leaf traits in low-light environments for saplings relative to adults (Laurans et al. 2012, Dent et al. 2013). In contrast, canopy adults in high-light environments may be more strongly limited by soil resources, resulting in stronger abiotic filtering of leaf traits across soil-resource gradients (Russo et al. 2012). In addition, the strength of abiotic filtering may vary among ontogenetic stages if seedlings and saplings are more sensitive to density-dependent biotic interactions

(Webb and Peart 1999, Harms et al. 2000, Wright 2002, Metz et al. 2010), resulting in stronger biotic filtering of traits in early life-history stages (Paine et al. 2012). Thus, patterns of functional diversity based on single ontogenetic stages may obscure inferences about the relative importance of community assembly processes across complex environmental gradients.

Here, we test the hypothesis that variation in functional diversity across environmental gradients differs among ontogenetic stages and that these patterns reflect a shift in the relative importance of different mechanisms of community assembly. In a temperate forest-dynamics plot in the Missouri Ozarks, USA, we compared functional diversity of leaf size and SLA of 34 woody plant species between two ontogenetic stages (adults and saplings) to test predictions about changes in the relative importance of abiotic and biotic filtering across a topo-edaphic gradient. If abiotic filtering has a stronger influence on adults across the gradient, we predicted lower functional diversity of leaf traits for adults relative to saplings, particularly in local communities with lower resource availability. In contrast, if biotic filtering has a stronger influence on saplings, we predicted higher functional diversity of leaf traits for saplings relative to adults, particularly in local communities with higher resource availability. Alternatively, if community assembly processes operate similarly across ontogenetic stages, we predicted similar trait-environment relationships for adults and saplings. We tested our predictions by comparing patterns of functional diversity across the topo-edaphic gradient for local communities of adults using adult traits and local communities of saplings using sapling traits. We then compare our results to the commonly used approach of applying adult trait values to all individuals (both saplings and adults) in the community. In contrast to previous studies that typically infer the importance of community assembly mechanisms based on functional traits measured at a single ontogenetic stage (Cornwell and Ackerly 2009, Spasojevic and Suding 2012), our approach allowed us to examine the influence of ontogenetic trait variation on patterns of functional diversity and inferred assembly mechanisms across environmental gradients.

METHODS

Study site: The Tyson Research Center Forest Dynamics Plot

Our study was conducted at Washington University in St. Louis' Tyson Research Center, located 25 miles (40 km) southwest of Saint Louis, Missouri (38°31′ N, 90°33′ W; mean annual temperature 13.5°C; mean annual precipitation 957 mm). The 800-ha research center is located on the northeastern edge of the Ozark ecoregion and is largely dominated by deciduous oak-hickory forest. Following moderate grazing and selective logging during the early 1900s, the property was acquired by the U.S. military for munitions storage in 1942, and then purchased by Washington University in 1962 (Zimmerman and Wagner 1979). The property has been relatively undisturbed for ~80 years and tree cores collected from large individuals of dominant species indicated tree ages of 120–160 years in the early 1980s (Hampe 1984). Soils types include silty loams and silty clays that develop from shale limestone, limestone, cherty limestone and chert formations (Zimmerman and Wagner 1979).

Our study was conducted in the Tyson Research Center Plot (TRCP), a 25-ha (500 × 500 m), stem-mapped, forest-dynamics plot (Fig. 1) that is part of a global network of forest-ecology plots coordinated through the Smithsonian Institution Center for Tropical Forest Science (CTFS) and Forest Global Earth Observatories (ForestGEO). The TRCP includes strong edaphic and topographic gradients characteristic of oak-hickory forests in the Ozark region. Elevation in the TRCP ranges from 172–233 m (mean = 206 m) and slope ranges from 0.8° to 26.9° (mean = 13.8°) at the 20 × 20 m scale. The plot includes a representative range of habitat types found in oak-hickory forests (e.g., east-facing slopes, ridges, west-facing slopes, valleys). As of May 2014, all free-standing stems of woody species greater than 1 cm diameter at breast height (DBH) in the central 20 ha of the plot have been tagged, identified, measured and mapped following CTFS-ForestGEO protocols (Condit 1998). For this study, we use data from a 12-ha (460 × 260 m) section of the TRCP that was censused from 2011–2012 and in which plant trait data and soils data were collected between the summers of 2011
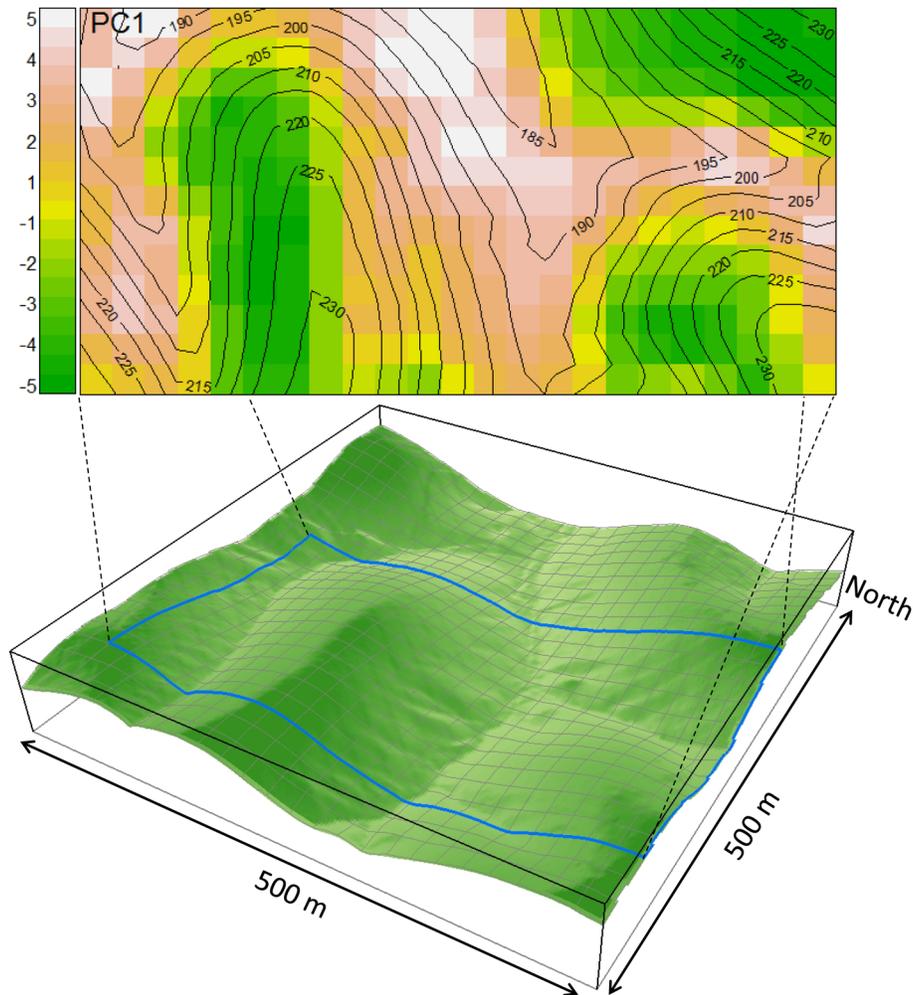
Fig. 1. Topo-edaphic gradients in the Tyson Research Center Plot, Missouri, USA. The bottom map shows topographic variation from a digital elevation model based on LIDAR data, with 20 × 20 m quadrats overlaid as a grid. The blue outline shows the 12-ha section (460 × 260 m) used in this study. The top map shows variation among 20 × 20 m quadrats in Principal Component (PC1), an axis that describes variation in soil (Al, base saturation, Ca, cation exchange capacity, Fe, Mg, Mn, NO_3^+ mineralization, P, pH) and topographic variables (aspect). PC1 explained 51.3% of the variation in the environmental data (Appendix: Fig. A1). Bottom map credit: Francis J. Baum, GIS Certificate Program, Washington University in St. Louis.

and 2013 (Fig. 1). The 12-ha section contains 299 20 × 20 m quadrats, ~18,400 main stems and 40 total species. Species richness varies from 3 to 15 species (mean = 8 species) per quadrat, with the greatest richness in the valleys and the lowest richness on west-facing slopes (Appendix: Fig. A1A). Simpson's diversity varies among quadrats as well, with the highest diversity on ridge tops and east facing slopes and the lowest diversity in valleys (Appendix: Fig. A1B). Additional infor-

mation on the TRCP is available on the CTFS-ForestGEO website (http://www.ctfs.si.edu).

Environmental gradients

Following the sampling design described in John et al. (2007), we measured spatial variation in 14 soil variables: available nitrogen (N), N mineralization rates, base saturation, effective cation exchange capacity (ECEC), exchangeable cations (Al, Ca, Fe, K, Mg, Mn, Na), pH, plant-

available phosphorous (P), and total exchangeable bases (TEB). We collected a sample of 10 soil cores (0- to 10-cm depth, ~500 total g/sample) every 40 m along a regular grid of points using a 2.5-cm diameter, open-end soil probe (AMS, number 401.10, American Falls, Idaho, USA), excluding the top organic horizon. To measure variation in soil properties at finer scales, each alternate grid point was paired with an additional sample point at 2, 8, or 20 m in a random compass direction (John et al. 2007), resulting in 126 total samples (10.5 samples/ha) for the 12-ha section of the plot. As samples were collected in the field, we extracted N using 2.0 M KCl on 2 g of field-moist soil. N was measured as NH_4^+ and NO_3^- in the KCl extracts by automated colorimetry using a Lachat Quikchem 8500 (Hach, Loveland, Colorado, USA). We then estimated N mineralization from a second KCL extract using a simple laboratory-incubation procedure (Robertson et al. 1999). For each sample, we incubated 2 g of field-moist soil inside an aluminum-foil packet placed in a sealed plastic bag for 10 days at room temperature, without adjusting the soil moisture. N mineralization rate was calculated as the difference in NH_4^+ and NO_3^- between the first sample (field sample) and second sample (incubated sample) after the 10-day incubation period.

We measured exchangeable cations, pH, and plant-available P on soils that had been air-dried at ambient laboratory temperature and sieved <2 mm. Exchangeable cations were measured by extraction in 0.1 M $BaCl_2$ (2 h, 1:30 soil to solution ratio), with detection by inductively-coupled plasma optical-emission spectrometry on an Optima 7300 DV (Perkin-Elmer, Shelton, Connecticut, USA) (Hendershot et al. 2008). Soil pH was measured in a 1:2 soil to solution ratio in both water and 10 mM $CaCl_2$ using a glass electrode. Plant-available P was extracted in Bray-1 solution, with detection by automated molybdate colorimetry on a Lachat Quikchem 8500 (Hach). Total exchangeable bases (TEB) were calculated as the sum of Ca, K, Mg, and Na, effective cation exchange capacity (ECEC) was calculated as the sum of Al, Ca, Fe, K, Mg, Mn, and Na, and base saturation was calculated as (TEB/ECEC) × 100. Finally, we used kriging to estimate values of all soil variables in each 20 × 20 m quadrat (John et al. 2007, Baldeck et al. 2013) using the geoR package (Ribeiro and Diggle 2001) in R (R Core Team 2012). All soil analyses were performed at the Soils Laboratory at the Smithsonian Tropical Research Institute, Panama (http://stri.si.edu/sites/soil/).

For each 20 × 20 m quadrat, we calculated 4 topographic variables: aspect, convexity, mean elevation, and slope. Mean elevation above sea level was quantified as the mean elevation of the four corners of each quadrat. Slope and aspect were quantified using the slope and aspect tools in ArcGIS 10.1. Aspect was measured as the direction of the steepest slope within each quadrat. Because aspect is a circular variable, we used cosine(aspect) in our analyses (Legendre et al. 2009). Convexity was measured as the elevation of a given quadrat minus the mean elevation of the eight surrounding quadrats (Legendre et al. 2009). For the edge cells, convexity was measured as the elevation of the center point minus the mean of the four corners (Legendre et al. 2009).

Trait sampling

We measured traits of 34 woody species in the TRCP. For 28 species, we measured traits on both saplings and adults (Appendix: Tables A1 and A2). The six other species are absent or rare as adults or saplings. Consequently, traits of one species were only measured on an adult (*Juglans nigra*) and traits of five species were only measured on saplings (*Acer negundo*, *Celtis tenuifolia*, *Ostrya virginiana*, *Prunus americana*, *Quercus muehlenbergii*). Together, these 34 species comprise ≥99% of the total number of individual stems in the TRCP. Traits were not measured on an additional 6 rare species with only 1 or 2 individual stems in the entire TRCP. For tree species we classified saplings as any individual less than 10 cm DBH and adults as any individual 10 cm DBH or greater. For shrub species we classified saplings as any individual less than 5 cm DBH and adults as any individual 5 cm DBH or greater. These classifications were based on the literature (e.g., Held and Winstead 1975) and our knowledge of the natural history of our species. However, we do acknowledge that these cut-offs are imperfect. Classification of ontogenetic stages based on species specific growth and age are likely to provide a more accurate estimate of ontogenetic stage, but are

likely not tractable in large scale studies such as ours.

We measured two key plant functional traits on 795 total individuals: leaf size and specific leaf area (SLA). Leaf area is associated with leaf energy and water balance, where small leaf size represents a strategy to cope with heat stress, drought stress, cold stress and photo-oxidative stress (Perez-Harguindeguy et al. 2013). Specific leaf area is associated with resource uptake strategy and tissue N (Reich et al. 1997), where high SLA represents a strategy to maximize carbon gain and relative growth rate (Westoby et al. 2002). For both adults and saplings, we measured traits on fully-developed leaves with minimal damage or senescence. For adults we collected 3 sun-exposed leaves from each of 3–8 representative individuals of each species (Appendix: Tables A1 and A2), typically in the habitat in which they are most abundant. For saplings we collected three leaves from the upper-crowns of 1–57 individuals of each species in one or more habitats, where the sample size for each species varied according to the relative abundances of saplings within the TRCP (e.g., 10 species had less than five total individual adults or saplings in the 12-ha section of the plot and all of those individuals were sampled). Due to differences in sample sizes between ontogenetic stages and species, we focus here on species-level trait means for each ontogenetic stage, calculated as the mean trait value across all the measured individuals of a given ontogenetic stage. We calculated leaf area (cm^2) from scanned leaves and petioles using Image-J (Rasband 2007). For compound species, we calculated leaf area as the mean leaflet area per leaf including petiolules (Perez-Harguindeguy et al. 2013). We calculated SLA (cm^2/g) as leaf area per unit dry mass after leaves were dried in an oven at 60°C for 4 days. In our data set these two traits were not correlated (P = 0.51).

Statistical analyses

Environmental gradients.—To describe variation in the environmental conditions among the 299 quadrats we used a principal component analysis (PCA) of the soil and topographic variables described above. Since our primary focus was to test the influence of ontogenetic trait variation on patterns of functional diversity, rather than to compare the importance of different environmental variables, we focus on results for PC1, the axis that described the most variation among the environmental variables (51.3%) and which includes both soil and topographic variables. The PCA was conducted in JMP version 10 (SAS Institute, Cary, North Carolina, USA).

Ontogenetic trait variation.—The hypothesis that variation in functional diversity across environmental gradients differs among ontogenetic stages depends on adults and sapling differing in their traits. Thus, we first tested whether adults and saplings generally differed in mean leaf size and SLA. For the 28 species for which we had trait data at both stages, we tested for differences in mean leaf size and SLA between ontogenetic stages using a linear mixed model with species as a random factor and ontogenetic stage as a fixed factor. We additionally examined species specific ontogenetic trait differences using separate t-tests on each trait for each species individually, applying Bonferroni corrections to our P-values to account for multiple comparisons (Nakagawa and Cuthill 2007). Lastly, we examined if ranked values of species traits remain the same or change with ontogeny by plotting the relationship between mean species ranks for adults and saplings. The slope of this relationship represents the degree to which interspecific trait hierarchies are maintained between ontogenetic stages, whereas the magnitude of deviations from the one-to-one line represents the degree to which individual species change ranks between ontogenetic stages.

Functional diversity across environmental gradients.—To test our hypotheses we examined patterns of functional diversity across the environmental gradient for local communities of (1) adults using only adult traits, (2) saplings using only sapling traits, and (3) the commonly used approach of applying adult trait values to all individuals in the community (both saplings and adults). For each of the 299 quadrats we calculated two complementary metrics: community-weighted mean (CWM) trait values (Garnier et al. 2004) and functional dispersion (FDis; Laliberte and Legendre 2010) for each of the three derivations of local communities. CWM trait values were calculated as the sum across all species of species' trait values weighted by their relative abundance (Garnier et al. 2004). Follow-

ing Laliberte and Legendre (2010), we calculated FDis as the mean distance of each species, weighted by relative abundances, to the centroid of all species in a quadrat. Although there are many metrics of functional diversity (reviewed in Mouchet et al. 2010, Schleuter et al. 2010), we focused here on FDis because it is independent of species richness, takes into account species abundances, and can be used for single traits or multiple traits (Laliberte and Legendre 2010). Moreover, Ricotta and Moretti (2011) recently proposed a unified analytical framework that combines CWM and a close analog of FDis (Rao's Q). We then compared FDis for each trait individually and for both traits combined to a null model based on random trait assembly. The null model simulates trait assembly in each quadrat by randomly shuffling trait values among species in the plot while preserving the species richness and species relative abundance within each quadrat. For each quadrat, we calculated the mean null-expected FDis and 95% confidence intervals (CI) based on 9999 iterations of the null model. Finally, we calculated the difference between the observed FDis and the mean null FDis, where positive values indicate quadrats with trait values more dissimilar than expected by chance and negative values indicate quadrats with trait values more similar than expected by chance (Spasojevic and Suding 2012). Functional diversity calculations were conducted using the FD package (Laliberte and Legendre 2010) in R. For all calculations we only included main stems; we only counted one stem for multi-stemmed individuals. Functional diversity patterns were qualitatively unchanged if calculations were conducted with basal area instead of relative abundance.

Finally, we tested our hypotheses that trait-environment relationships differ between ontogenetic stages (adults and saplings) using a linear mixed model with PC1 as a continuous variable, ontogenetic stage as a fixed factor, the interaction of PC1 and ontogenetic stage, quadrat as a random factor, and CWM trait values and FDis as response variables in JMP version 10 (SAS Institute, Cary, North Carolina, USA). For this analysis we only used CWMs and FDis calculated for the adult community and for the sapling community individually and did not include the combined community approach. Here, a signifi-

cant effect of ontogenetic stage would indicate that functional diversity differs between adults and saplings, whereas an interaction between ontogenetic stage and PC1 would indicate that adults and saplings respond differently to the same environmental gradient. Lastly, to contrast trait-environment patterns among the three derivations of the local community (adults, saplings, combined community) we compared the strength of trait-environment relationships (r^2) for CWM trait values and FDis across the topo-edaphic gradient described by PC1. While r^2 values can be derived from mixed models (Nakagawa and Schielzeth 2013), our mixed model does not include the combined community of adults and saplings. Thus we used calculated r^2 values from separate linear models for adults, saplings, and the combined community of adults and saplings to qualitatively compare the strength of trait-environment relationships among these three approaches.

RESULTS

Environmental gradients and ontogenetic trait variation

Soil resources and topography vary strongly across the 12-ha plot (Fig. 1). Using a principal components analysis (PCA), we found that the first four PC axes explained 75% of the variation in soil and topographic variables (Appendix: Fig. A2). PC1 (51.3% of the explained variation) characterizes a gradient ranging from low soil-resource availability (e.g., low N, P, K) and more south-facing aspects to high soil-resource availability (e.g., high N, P, K) and more north-facing aspects (Fig. 1; Appendix: Fig. A1). PC2 (11.1%) characterizes gradients in elevation and convexity (Appendix: Fig. A2). PC3 (7.4%) and PC4 (6.8%) characterize gradients in Na and slope, respectively.

Adults and saplings differed significantly in both leaf size ($F_{1, 806} = 97.85$, $P < 0.01$) and SLA ($F_{1, 806} = 105.87$, $P < 0.01$) with saplings generally having 26% greater leaf size and 47% higher SLA than adults. While we found a general trend of greater leaf size and SLA among ontogenetic stages, only 8 species (31%) had significantly different leaf sizes between ontogenetic stages and 12 species (46%) had significantly different SLA between stages (Appendix: Tables A1 and A2,
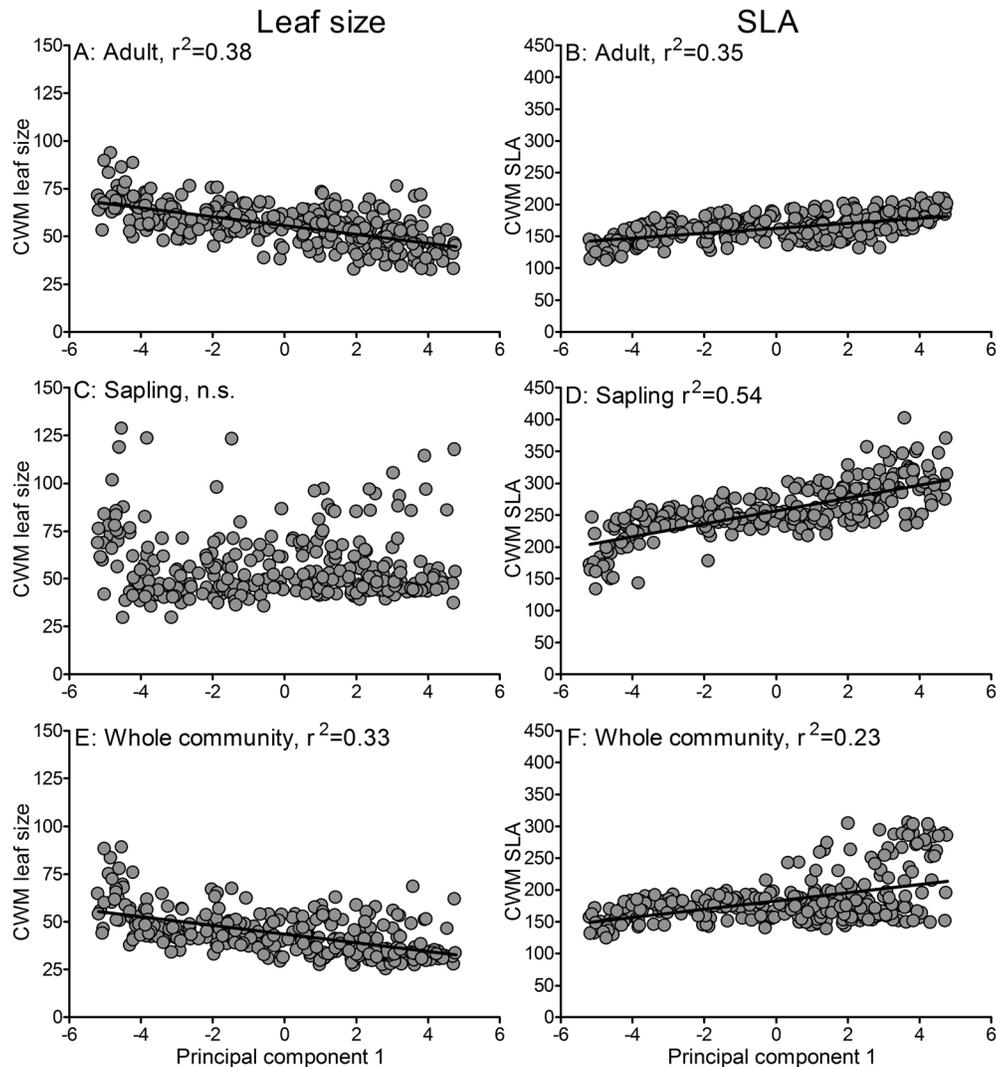
Fig. 2. Variation in community-weighted mean (CWM) leaf size (left column) and specific leaf area (SLA) (right column) across a topo-edaphic gradient characterized by Principal Component 1 (Fig. 1; Appendix: Fig. A1). Each point represents a 20×20 m quadrat. Relationships are plotted for (A, B) adults only using adult traits, (C, D) saplings only using sapling traits and (E, F) the combined community of adults and saplings using adult traits. Regression lines indicate significant linear relationships ($P < 0.05$) between CWMs and the topo-edaphic gradient from simple linear regressions.

respectively). Ranked values of species traits were positively correlated between adults and saplings (Appendix: Fig. A3). However, individual species showed large shifts in their rank trait values between ontogenetic stages (Appendix: Fig. A3).

Functional diversity across environmental gradients

The trait-environment relationships varied between saplings and adults for both leaf traits (Fig. 2). Community-weighted mean (CWM) leaf size decreased across the topo-edaphic gradient for adults (Fig. 2A) and the combined community of adults and saplings (Fig. 2E), indicating larger leaf size in low-nutrient and more south-facing quadrats (Appendix: Fig. A2). In contrast, there was no significant change in CWM leaf size across the same gradient for saplings (Fig. 2C),

resulting in an interaction between ontogenetic stage and PC1 on leaf size ($F_{1,595} = 296.92$, $P < 0.01$) in our mixed model. CWM SLA increased across the topo-edaphic gradient for adults, saplings, and the combined community of adults and sapling (Fig. 2), indicating higher SLA in high-nutrient and more north-facing quadrats (Appendix: Fig. A1). However, this relationship was almost twice as strong for saplings (Fig. 2D; $r^2 = 0.54$) compared to adults (Fig. 2B; $r^2 = 0.35$) as demonstrated by the interaction between ontogenetic stage and PC1 on SLA ($F_{1,595} = 126.17$, $P < 0.01$) in our mixed model. The combined community of adults and saplings showed a weaker relationship with PC1 (Fig. 2F; $r^2 = 0.23$) than either the adult or sapling portion of the communities.

Functional dispersion (FDis) also varied significantly across the topo-edaphic gradient for both leaf traits. FDis of leaf size decreased across the topo-edaphic gradient for adults and saplings (Fig. 3), indicating less diversity in leaf size in high-nutrient and more north-facing quadrats (Appendix: Fig. A1). In contrast, FDis of SLA increased across the topo-edaphic gradient for adults and saplings (Fig. 3), indicating greater diversity in SLA in high-nutrient and more north-facing quadrats (Appendix: Fig. A1). Changes in FDis along the gradient were similar for adults and saplings, resulting in no significant interaction between ontogenetic stage and PC1 in our mixed models for either trait (leaf size: $F_{1,595} = 0.38$, $P = 0.54$; SLA: $F_{1,595} = 2.71$, $P = 0.10$). There was also no significant relationship between multivariate FDis and PC1 ($F_{1,298} = 0.18$, $P = 0.66$).

Despite similar patterns of FDis across the topo-edaphic gradient for adults and saplings, the two ontogenetic stages differed in their overall patterns of trait dispersion. For adults, 27% of local communities had lower FDis of SLA than expected by chance (Fig. 3B), whereas FDis of leaf size did not differ from the null model (Fig. 3A). For saplings, in contrast, 6% of quadrats had higher FDis of SLA than expected by chance (Fig. 3D) and 7% of quadrats had higher FDis of leaf size than expected by chance (Fig. 3C). Moreover, these patterns were generally absent in the combined community of adults and saplings, where FDis of leaf size never differed from the null model (Fig. 3E) and only

3% of quadrats had lower FDis of SLA than expected by chance (Fig. 3F).

DISCUSSION

Our results support the hypothesis that ontogenetic trait variation influences community assembly across environmental gradients. We found that saplings generally had higher leaf size and higher SLA than adults (Appendix: Fig. A3), a pattern often observed in closed-canopy forests where saplings experience low light availability in the shaded understory and selection for leaf traits that increase carbon gain (Poorter 2001, Shipley 2002). Given the strong influence of light limitation on sapling leaf traits (Laurans et al. 2012, Dent et al. 2013), we expected to find a weaker effect of the topo-edaphic gradient on abiotic filtering of sapling leaf traits relative to adult leaf traits. Consistent with this prediction, we found that local communities of adults had lower mean SLA and lower functional dispersion in SLA than expected by chance, suggesting an important role for abiotic filtering among co-occurring adults. In contrast, a few local communities of saplings exhibited higher functional dispersion of leaf size and SLA than expected by chance, suggesting a role for biotic filtering for saplings not present in adults. Moreover, the overall strength of trait-environment relationships varied between saplings and adults for both leaf traits, generally resulting in stronger environmental shifts in mean trait values and trait dispersion for adults relative to saplings. Collectively, these results suggest that contrasting patterns of functional diversity for adults and saplings reflect shifts in the relative importance of abiotic and biotic filtering during community assembly.

Our results suggest that the functional diversity of adults is more strongly influenced by abiotic filtering across topo-edaphic environmental gradients than the functional diversity of saplings. We found that 27% of local communities of adults had lower FDis of SLA than expected by chance and that the majority of these communities were located toward the resource-poor end of the topo-edaphic gradient (Fig. 3B). This pattern, coupled with the systematic change in CWM SLA across the gradient (Fig. 2B), suggests a stronger influence of abiotic
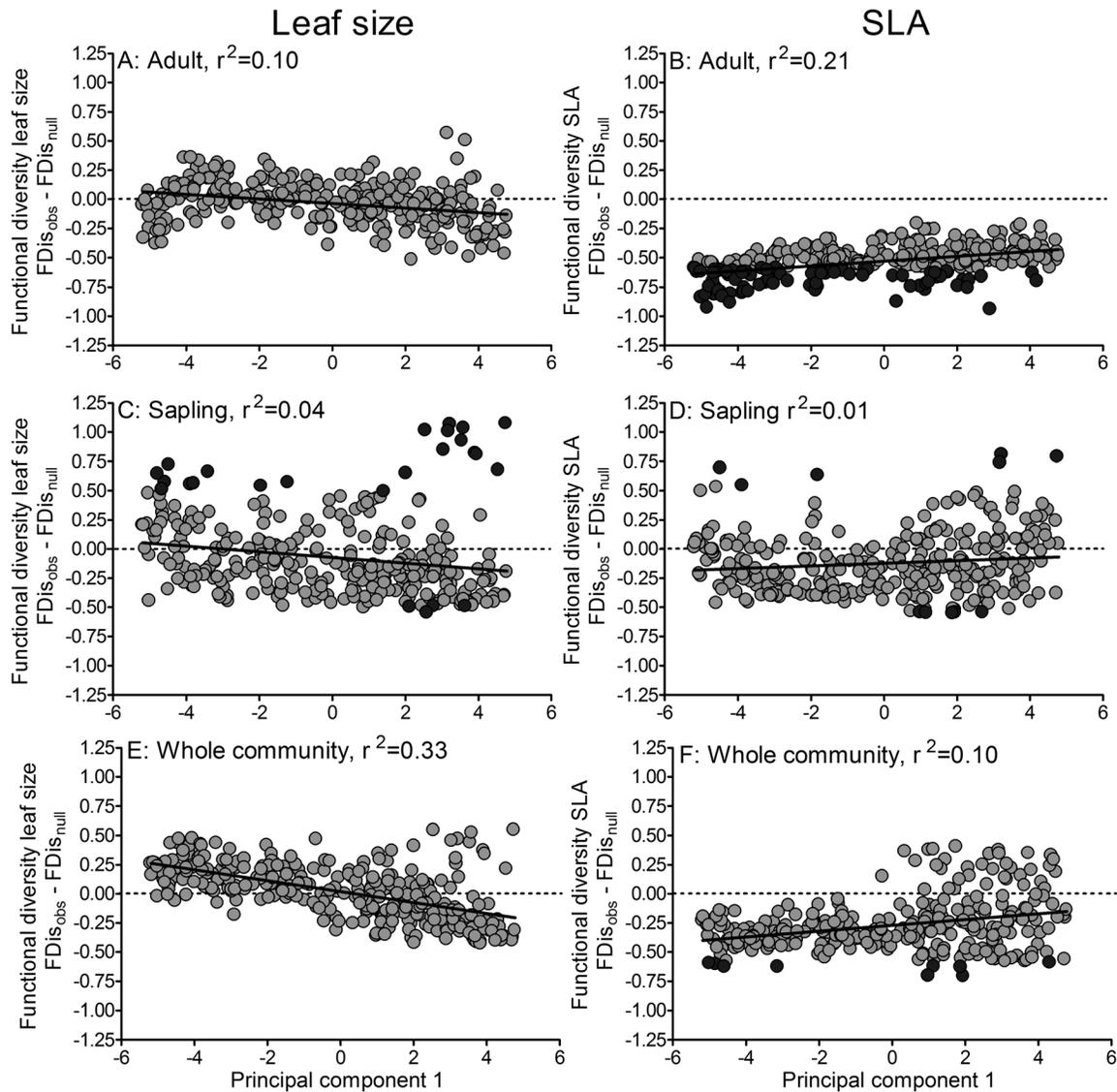
Fig. 3. Variation in functional dispersion (FDis) of leaf size (left column) and SLA (right column) across a topo-edaphic gradient characterized by principal component 1 (Fig. 1; Appendix: Fig. A1). Each point represents a 20 × 20 m quadrat. Relationships are plotted for (A, B) adults only using adult traits, (C, D) saplings only using sapling traits and (E, F) the combined community of adults and saplings using adult traits. The dashed line represents no difference between the observed FDis and a null model of random trait assembly, positive values indicate higher FDis than expected from the null model (trait overdispersion), and negative values indicate lower FDis than expected from the null model (trait underdispersion). Black symbols represent local assemblages where the observed FDis is significantly higher or lower than expected by chance, whereas grey symbols represent local assemblages where the observed FDis is not significantly different from the null expectation. Regression lines indicate significant linear relationships ($P < 0.05$) between FDis and the topo-edaphic gradient from simple linear regressions.

filtering at lower resource availability and a potential shift towards stronger competition via limiting similarity at higher resource availability (Weiher and Keddy 1995, Spasojevic and Suding 2012); patterns consistent with other forests (e.g., Lebrija-Trejos et al. 2010, Mason et al. 2012). Abiotic filtering of SLA in adult communities may result from increased water stress in low-resource environments as these habitats tend to occur on exposed ridge tops and more southerly facing slopes with low water availability (Fig. 1; Appendix: Fig. A2) (Olivero and Hix 1998, Ruiz-Sinoga and Martinez-Murillo 2009). In contrast, FDis of adult leaf area was never different than expected by chance at any location across the topo-edaphic gradient. This pattern could be explained by stronger stochastic assembly of this trait in adult communities (Hubbell 2001, Weiher et al. 2011) or a simultaneous influence of both biotic filtering and abiotic filtering leading to intermediate values of FDis (Spasojevic and Suding 2012).

In contrast to adults, the functional diversity of saplings was only weakly influenced by abiotic filtering across the topo-edaphic gradient with only a few local communities exhibiting lower functional dispersion than expected by chance. Instead, we found greater evidence of a role for biotic filtering in sapling relative to adult communities regardless of their location across the gradient—biotic filtering was present for some sapling communities, but never for adult communities. In several local communities of saplings, FDis of leaf size and SLA was greater than expected by chance, suggesting an important influence of biotic filtering through limiting similarity owing to increased competitive interactions (Weiher et al. 2011, Spasojevic and Suding 2012) or negative-density dependent mortality from natural enemies (Paine et al. 2012). However, since the sapling communities with non-random functional diversity patterns were evenly spaced across the environment gradient we cannot discern the specific processes that may contribute to biotic filtering. Nonetheless, these patterns suggest a biotic assembly mechanism for saplings that is absent or weak in the adult community. Moreover, soil resources and topography explained ~20% more variation in CWM SLA for saplings than for adults, suggesting a shift in the strength of this trait-

environment relationship during ontogeny. SLA may be higher in more resource-rich, north-facing habitats due to similar selection on adults and saplings for fast-growing species with high photosynthetic rates (Reich et al. 1997, Westoby et al. 2002). The difference between saplings and adults may occur because higher resource availability selects for fast-growing adults, which increase light limitation for saplings, resulting in selection for increased SLA in saplings (Poorter 2001, 2007) that allow them to maintain positive carbon balance in light-limited environments (Dalling et al. 1998, Thomas and Winner 2002, Poorter et al. 2005). While the importance of light on sapling leaf traits is not a new finding (e.g., Poorter 2001, Rozendaal et al. 2006), our finding suggest that ontogeny is a key axis of intraspecific trait variation which may influence inferences based on patterns of functional diversity in studies of community assembly.

Although our results suggest an important influence of ontogenetic trait variation in this community, it is important to recognize that the relative importance of ontogenetic trait variation is likely to vary systematically among different plant functional traits. While our study only focused on two traits (leaf size and SLA), other traits similarly associated with resource acquisition strategies and stress tolerance (e.g., plant height, leaf dry matter content, tissue chemistry, specific root length; Westoby 1998, Reich et al. 2003, Laughlin 2014) are likely to exhibit ontogenetic trait variation as the allocation and acquisition of resources changes with ontogeny (Lilles and Astrup 2012, Martin and Thomas 2013). Some traits, however, may not vary through ontogeny. For example, categorical traits such as lifespan (e.g., annual or perennial), dispersal syndrome (e.g., wind, water, animal), clonality and N-fixation are relatively invariant throughout the life of an individual (Perez-Harguindeguy et al. 2013). Additionally, some traits are only present at particular life stages, such as floral traits or seed traits, and it may not be possible to quantify these at different life stages (Perez-Harguindeguy et al. 2013).

Moreover, the importance of ontogenetic trait variation in community assembly may potentially vary across broad-scale environmental gradients. For example, in low-productivity ecosystems the relative difference in traits be-

tween early and late life stages has the potential to be quite small relative to the difference in high-productivity ecosystems (e.g., Lilles and Astrup 2012). The relative importance of ontogenetic trait variation may therefore increase with increasing productivity across broad-scale ecological gradients. However, empirical data testing this idea is lacking and examining ontogenetic trait variation along broad ecological gradients will help illuminate how widespread the importance of ontogenetic trait variation is for trait-based community assembly.

Conclusions

Our results highlight the importance of ontogeny as a key axis of intraspecific trait variation in studies of trait-based community ecology (Bolnick et al. 2011, Violle et al. 2012). Despite growing interest in the role of intraspecific trait variation in community assembly and species coexistence (Albert et al. 2011, Bolnick et al. 2011, Violle et al. 2012), many studies in trait-based ecology infer mechanisms based on patterns of functional diversity at a single ontogenetic stage. Although adult plant communities may potentially represent the final outcome of community assembly, this approach assumes that assembly is not a dynamic, continual process (e.g., Mouquet et al. 2003, Canning-Clode et al. 2010) and that assembly mechanisms that act at early life stages are less important. Here, we show that the strength of trait-environment relationships vary between co-occurring adults and saplings in a temperate forest, suggesting shifts in the relative importance of community assembly mechanisms through ontogeny. Importantly, these processes would be obscured using more traditional approaches that do not incorporate ontogenetic influences on patterns of functional diversity. Our results highlight the importance of incorporating ontogenetic trait variation, an important axis of intraspecific trait variability, into approaches that use plant functional traits to understand community assembly and species coexistence across complex environmental gradients.

Acknowledgments

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SUPPLEMENTAL MATERIAL

APPENDIX

A: Species richness

B: Simpson's diversity
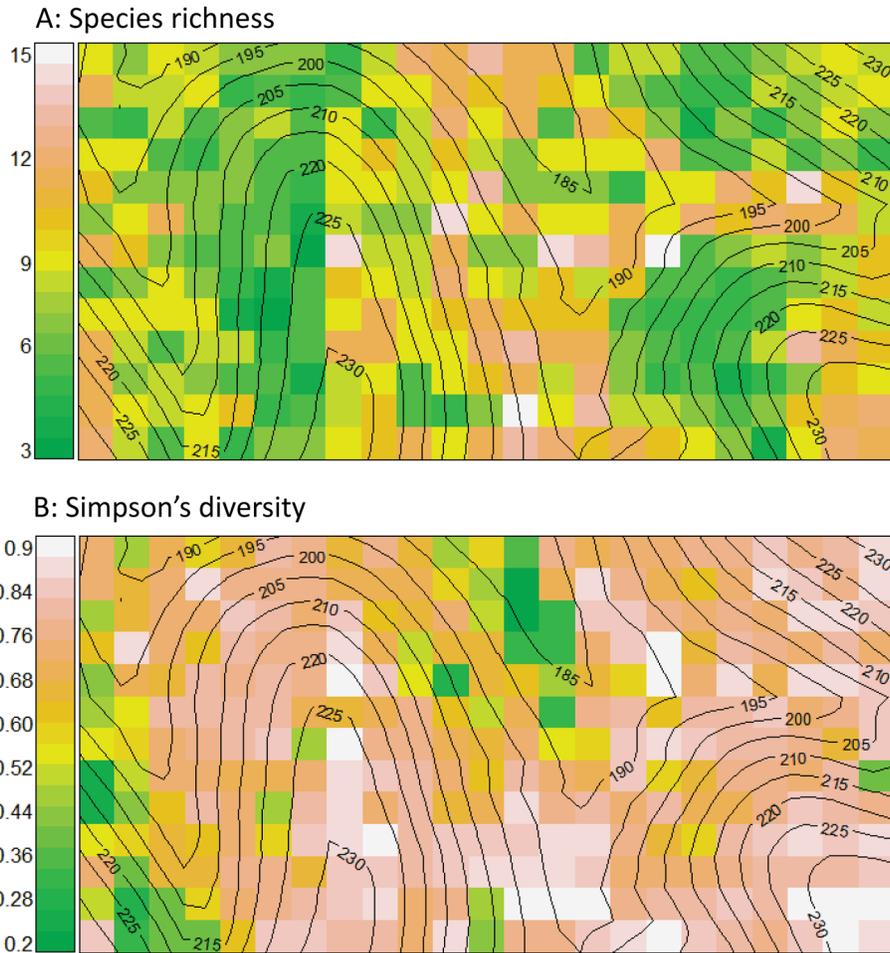
Fig. A1. Gradients in (A) species richness and (B) Simpson's diversity calculated for the 20 × 20-m quadrats of the 12-ha section (Fig. 1) of the Tyson Research Center Plot, Missouri, USA.
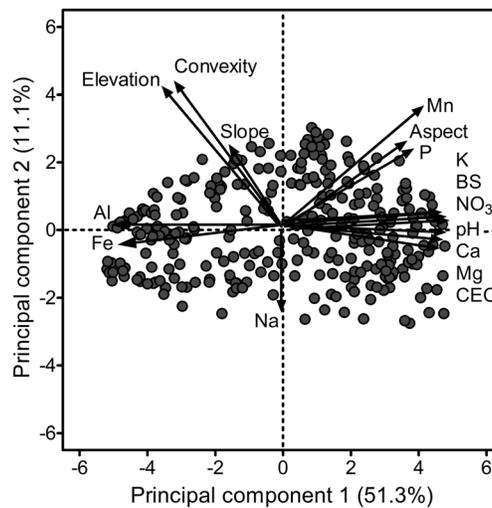
Fig. A2. Principal components analysis (PCA) of soil and topographic variables in 20×20 m quadrats across a 12-ha section of the Tyson Research Center Plot, Missouri, USA. Soil variables included aluminum (Al), base saturation (BS), calcium (Ca), cation exchange capacity (CEC), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na), nitrate mineralization (NO_3^+ mineralization), pH, and Bray phosphorus (P). Topographic variables included mean elevation, slope, cosine (aspect) and convexity. The first principal component (PC1) described 51.3% of the variation among quadrats, whereas PC2 described 11.1% of the variation. Al, BS, Ca, CEC, Fe, Mg, Mn, NO_3^+ mineralization, P, pH, and aspect loaded strongly on PC1, whereas elevation and convexity loaded strongly on PC2. PC3, representing variation in Na, described 7.4% of the variation, and PC4, representing variation in slope, described 6.8% of the variation (data not shown).
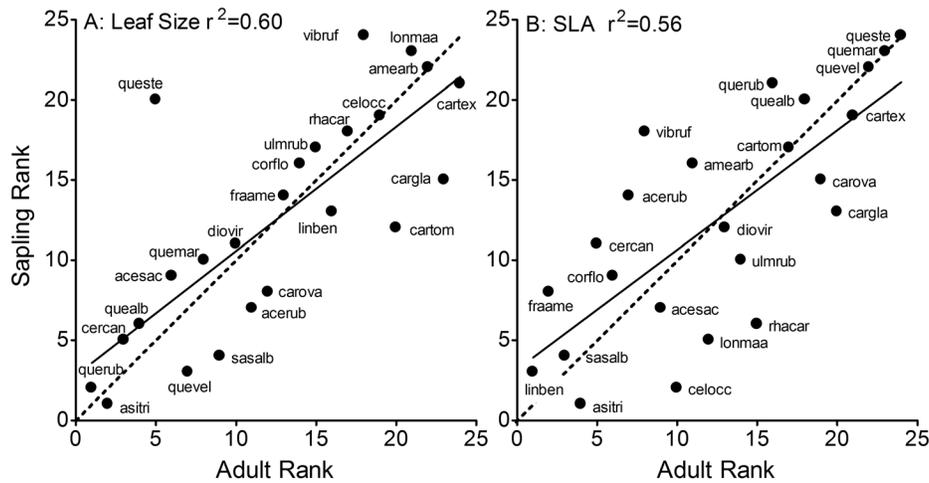
Fig. A3. Trait ranks for adults and saplings of 28 woody species for (A) leaf size and (B) specific leaf area (SLA). Low numbers indicate that a species has a high trait value (e.g., high leaf area) and high numbers indicate a species has a low trait value relative to other species in the community. Deviations from the one-to-one line (dashed line) indicate that species do not have the same trait rank at different ontogenetic stages. Positive correlations between ranked trait values between different ontogenetic stages may suggest that traits measured at one ontogenetic stage are representative of community-wide trait patterns (e.g., Paine et al. 2012). Consistent with this idea, we found positive correlations between adult and sapling trait-ranks for both leaf size ($r^2 = 0.56$) and SLA ($r^2 = 0.50$). Importantly, however, the strength of functional diversity-environment relationships differed for adult and sapling traits. These results suggest that correlations between traits at different ontogenetic stages do not necessarily imply similar patterns or processes across stages. Instead, our results highlight the importance of explicitly comparing trait-environment relationships among ontogenetic stages when drawing community-wide inferences about assembly mechanisms. Species names are included in Appendix: Table A1.

Table A1. Summary statistics (means and standard errors [SE]) for leaf size of 34 woody species in the Tyson Research Center Plot, Missouri, USA. Results from t-tests of trait differences between ontogenetic stages (adults versus saplings) are shown in the last column; values in boldface indicate significant differences after Bonferroni corrections applied.

Species	Code	Family	Sapling			Adult			T-ratio
			N	Mean	SE	N	Mean	SE	
Acer negundo	aceneg	Aceraceae	1	35.90	...	...	...	...	...
Acer rubrum	acerub	Aceraceae	32	83.12	3.27	5	49.62	2.61	**6.45**
Acer saccharum	acesac	Aceraceae	9	74.69	4.24	5	68.41	1.65	1.38
Ailanthus altissima	ailalt	Simaroubaceae	5	32.58	1.90	8	30.19	1.77	1.24
Amelanchier arborea	amearb	Rosaceae	55	24.66	0.83	5	19.88	1.95	1.05
Asimina triloba	asitri	Annonaceae	27	180.69	5.75	5	97.27	4.50	**9.69**
Bumelia lanuginosa	bumlan	Sapotaceae	1	21.37	...	3	22.82	2.49	...
Carya glabra	cargla	Juglandaceae	8	49.94	7.44	5	12.58	2.23	**4.81**
Carya ovata	carova	Juglandaceae	20	78.02	5.78	5	41.86	4.05	**5.12**
Carya texana	cartex	Juglandaceae	17	32.23	2.83	5	11.28	0.87	**7.09**
Carya tomentosa	cartom	Juglandaceae	27	60.75	3.37	5	22.11	4.25	**6.60**
Celtis occidentalis	celocc	Ulmaceae	11	37.51	3.70	5	22.78	5.56	1.77
Celtis tenuifolia	celten	Ulmaceae	1	27.14	...	...	...	...	...
Cercis canadensis	cercan	Fabaceae	10	102.06	5.79	5	75.97	7.65	1.70
Cornus drummondii	cordru	Cornaceae	1	19.05	n/a	3	48.45	5.68	...
Cornus florida	corflo	Cornaceae	57	45.21	1.23	5	36.88	4.52	0.80
Diospyros virginiana	diovir	Ebenaceae	18	67.00	5.50	5	52.34	4.82	1.08
Fraxinus americana	fraame	Oleaceae	49	51.24	1.94	5	40.23	3.39	1.46
Juglans nigra	jugnig	Juglandaceae	...	...	...	5	24.35	1.25	...
Lindera benzoin	linben	Lauraceae	23	53.76	2.67	5	32.01	0.93	**7.69**
Lonicera maackii	lonmaa	Caprifoliaceae	25	23.09	1.11	5	21.15	0.33	1.68
Ostrya virginiana	ostvir	Betulaceae	2	33.79	...	...	...	...	...
Prunus americana	pruame	Rosaceae	2	29.92	...	...	...	...	...
Quercus alba	quealb	Fagaceae	42	98.11	3.97	5	70.18	10.42	2.50
Quercus marilandica	quemar	Fagaceae	8	70.84	8.02	5	65.69	14.77	0.31
Quercus muehlenbergii	quemue	Fagaceae	1	55.58	...	...	...	...	...
Quercus rubra	querub	Fagaceae	44	137.72	5.73	5	98.07	11.70	2.12
Quercus stellata	queste	Fagaceae	1	33.98	...	5	69.94	7.91	...
Quercus velutina	quevel	Fagaceae	19	132.56	8.62	5	66.05	13.65	3.60
Rhamnus caroliniana	rhacar	Rhamnaceae	43	42.32	1.05	5	26.24	3.04	5.00
Sassafras albidum	sasalb	Lauraceae	42	106.99	4.45	5	60.98	1.93	**3.93**
Tilia americana	tilame	Tiliaceae	1	145.67	...	3	189.53	27.80	...
Ulmus rubra	ulmrub	Ulmaceae	34	45.13	3.07	5	32.52	2.46	2.21
Viburnum rufidulum	vibruf	Caprifoliaceae	17	21.69	1.13	5	23.05	2.67	−0.40

Table A2. Summary statistics (means and standard errors [SE]) for specific leaf area of 34 woody species in the Tyson Research Center Plot, Missouri, USA. Results from t-tests of trait differences between ontogenetic stages (adults versus saplings) are shown in the last column; values in boldface indicate significant differences after Bonferroni corrections applied.

Species	Code	Family	Sapling			Adult			T-ratio
			N	Mean	SE	N	Mean	SE	
Acer negundo	aceneg	Aceraceae	1	318.55	...	...	...	...	...
Acer rubrum	acerub	Aceraceae	32	226.68	5.31	5	208.01	24.03	−0.36
Acer saccharum	acesac	Aceraceae	9	274.54	12.38	5	181.17	6.96	**6.57**
Ailanthus altissima	ailalt	Simaroubaceae	5	362.76	22.15	8	327.91	36.91	1.45
Amelanchier arborea	amearb	Rosaceae	55	221.27	7.06	5	171.33	6.35	2.94
Asimina triloba	asitri	Annonaceae	27	432.80	14.19	5	231.07	20.33	**6.92**
Bumelia lanuginosa	bumlan	Sapotaceae	1	248.89	...	3	233.73	19.59	...
Carya glabra	cargla	Juglandaceae	8	232.37	12.55	5	114.33	7.68	**8.02**
Carya ovata	carova	Juglandaceae	20	225.93	5.72	5	124.14	7.42	**10.86**
Carya texana	cartex	Juglandaceae	17	201.85	10.26	5	112.54	7.12	**7.15**
Carya tomentosa	cartom	Juglandaceae	27	219.52	4.71	5	129.89	9.80	**6.71**
Celtis occidentalis	celocc	Ulmaceae	11	346.37	20.11	5	171.65	17.77	**5.69**
Celtis tenuifolia	celten	Ulmaceae	1	814.16	...	...	...	...	...
Cercis canadensis	cercan	Fabaceae	10	257.46	7.54	5	228.34	20.87	−0.01
Cornus drummondii	cordru	Cornaceae	1	231.42	...	3	255.19	10.08	...
Cornus florida	corflo	Cornaceae	57	259.57	4.42	5	210.62	13.97	1.56
Diospyros virginiana	diovir	Ebenaceae	18	246.56	9.73	5	156.57	20.90	3.02
Fraxinus americana	fraame	Oleaceae	49	268.60	5.80	5	249.14	48.27	−0.27
Juglans nigra	jugnig	Juglandaceae	...	...	...	5	167.45	15.19	...
Lindera benzoin	linben	Lauraceae	23	345.48	8.65	5	313.54	34.63	0.89
Lonicera maackii	lonmaa	Caprifoliaceae	25	280.79	11.84	5	160.64	7.28	**8.64**
Ostrya virginiana	ostvir	Betulaceae	2	344.89	...	...	...	...	...
Prunus americana	pruame	Rosaceae	2	307.35	...	...	...	...	...
Quercus alba	quealb	Fagaceae	42	160.75	3.12	5	126.74	8.69	3.68
Quercus marilandica	quemar	Fagaceae	8	112.61	3.82	5	87.06	4.97	4.07
Quercus muehlenbergii	quemue	Fagaceae	1	193.04	...	...	...	...	...
Quercus rubra	querub	Fagaceae	44	159.61	2.56	5	139.55	8.39	0.56
Quercus stellata	queste	Fagaceae	1	96.00	...	5	77.05	4.54	...
Quercus velutina	quevel	Fagaceae	19	134.05	3.57	5	97.56	2.63	**7.95**
Rhamnus caroliniana	rhacar	Rhamnaceae	43	276.51	7.50	5	141.15	7.73	**12.56**
Sassafras albidum	sasalb	Lauraceae	42	281.08	5.52	5	236.77	6.37	**8.73**
Tilia americana	tilame	Tiliaceae	1	273.52	...	3	275.86	29.15	...
Ulmus rubra	ulmrub	Ulmaceae	34	259.57	11.72	5	147.06	10.65	**10.58**
Viburnum rufidulum	vibruf	Caprifoliaceae	17	201.97	10.27	5	183.57	12.58	1.51