



Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests

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Niche differentiation and ecological filtering are primary ecological processes that shape community assembly, but their relative importance remains poorly understood. Analyses of the distributions of functional traits can provide insight into the community structure generated by these processes. We predicted the trait distributions expected under the ecological processes of niche differentiation and environmental filtering, then tested these predictions with a dataset of 4672 trees located in nine 1-ha plots of tropical rain forest in French Guiana. Five traits related to leaf function (foliar N concentration, chlorophyll content, toughness, tissue density and specific leaf area), and three traits related to stem function (trunk sapwood density, branch sapwood density, and trunk bark thickness), as well as laminar surface area, were measured on every individual tree. There was far more evidence for environmental filtering than for niche differentiation in these forests. Furthermore, we contrasted results from species-mean and individual-level trait values. Analyses that took within-species trait variation into account were far more sensitive indicators of niche differentiation and ecological filtering. Species-mean analyses, by contrast, may underestimate the effects of ecological processes on community assembly. Environmental filtering appeared somewhat more intense on leaf traits than on stem traits, whereas niche differentiation affected neither strongly. By accounting for within-species trait variation, we were able to more properly consider the ecological interactions among individual trees and between individual trees and their environment. In so doing, our results suggest that the ecological processes of niche differentiation and environmental filtering may be more pervasive than previously believed.

Over the past decade, ecological theory has witnessed major transitions, with the development of more rigorous frameworks to account for demographic stochasticity (Hubbell 2001), the redefinition of classic concepts such as the niche (Chase and Leibold 2003), a better conceptualization of the interplay between local and regional processes (Ricklefs 2004, Holyoak et al. 2005), and a deeper understanding on how physiological processes shape the assembly of ecological communities (McGill et al. 2006). This last line of research has led (among other things) to a quantification of ecological strategies through the measurement of functional traits, which capture key aspects of physiology (Wright et al. 2004, Baraloto et al. 2010b). From these advances, it has become evident that analyses of the distributions of trait values within and among communities yields insights into the ecological processes constraining their assembly (Stubbs and Wilson 2004, Kraft et al. 2008).

A primary community-wide process is niche differentiation, the evolutionary partitioning of niche conditions by species, which results from interactions among neighboring individuals within and among trophic levels. Niche differentiation is considered to incorporate the effects of both resource competition and shared natural enemies (Chase and

Leibold 2003). The second major ecological process shaping community assembly is environmental filtering (Harper 1977, also known as species sorting, Holyoak et al. 2005), which results from the interaction of plants with their abiotic environment.

Recent analyses have readdressed the issue of inferring the effects of ecological processes using the distributions of functional traits for tropical forest tree communities (Kraft et al. 2008, Swenson and Enquist 2009). In analyses of community assembly, functional traits may be used to quantify niche evenness (indicating niche differentiation) and niche breadth (indicating environmental filtering, Kraft and Ackerly 2010). According to competition theory, increasing similarity in functional trait values should lead to increased intensity of interactions among neighboring individuals, since these individuals then compete for more similar resources or have the same defenses, even as increasing proximity increases the likelihood of such interactions (Uriarte et al. 2004). Hence, communities shaped primarily by niche differentiation are predicted to have relatively evenly dispersed trait values, a pattern referred to as limiting similarity (MacArthur and Levins 1967). Environmental filtering, on the other hand, is inferred to be the dominant process shaping ecological communities

when observed ranges of trait values are narrower within than among local communities i. e. when observed ranges of trait values are narrower than expected. Environmental filtering is evident in many plant communities, in that the association of particular species with particular habitats or environmental characteristics is often explained by functional traits (Kraft et al. 2008, but not always: Stubbs and Wilson 2004, Mayfield et al. 2009).

Within-species variation in trait values has received little attention in studies of the assembly of tropical plant communities. Accounting for it, however, is important, as it can foster species coexistence (Lichstein et al. 2007, Jung et al. 2010). Many studies have measured functional traits on one or few individuals, which, it is assumed, are representative of all individuals of that species (Stubbs and Wilson 2004, Swenson and Enquist 2009). This method overlooks the within-species component of community-level variation in trait values, which recent studies have shown to be substantial (Albert et al. 2010a, Baraloto et al. 2010a, Hulshof and Swenson 2010). Studies in which trait values are measured only on a few individuals may thus underestimate the community-level variation in trait values. Another potential source of confusion introduced by summarizing data by species is the increased emphasis placed on rare species. Should rare species have unusual trait values, as has been shown for the morphology of passerine birds (Ricklefs 2005), analysis of species-mean trait values may cause the extent of ecological filtering to be underestimated.

This study has three objectives. First, we test the relative importance of niche differentiation and ecological filtering on community assembly in the species-rich rain forests of French Guiana. Second, we quantify the consequences of summarizing trait values at the species level by contrasting community-wide tests of trait distributions performed on species-mean data and individual-level data. Finally, we determine which functional traits are most affected by environmental filtering and niche differentiation. In tropical rainforests, most plant functional traits are associated with one of two orthogonal economic spectra. The leaf economics spectrum (LES) contrasts cheap leaves that provide quick return on investment, with expensive leaves that provide a longer-lasting revenue stream (Wright et al. 2004). The stem economics spectrum (SES), on the other hand, contrasts trunks with dense wood versus those with high volumetric moisture content and thick bark (Chave et al. 2009, Baraloto et al. 2010b). By separately assessing the breadth and evenness of traits associated with each economic spectrum, we may infer the extent to which environmental filtering and niche differentiation differentially affect leaves and stems.

Material and methods

Study sites and sampling

Nine 1-ha plots were censused in French Guiana. Plots were located in terra firme rain forest and spanned a gradient in precipitation (from 2 to 4 m year⁻¹). Inter-plot distances ranged from 0.5 to 300 km (mean = 117 km). Each tree was identified to species and sampled for functional traits. We measured nine functional traits (Table 1), five of which are

associated with the leaf economics spectrum (foliar N concentration, chlorophyll content, toughness, tissue density and specific leaf area). The remaining three (trunk sapwood density, branch sapwood density and trunk bark thickness) are associated with the stem economics spectrum (Wright et al. 2004, Baraloto et al. 2010b). A ninth trait, laminar surface area, is strongly correlated with neither spectrum (Baraloto et al. 2010b). In total, we sampled 4672 trees and 13 448 leaves. Details on field sampling and information about the traits examined can be found in Baraloto et al. (2010a).

We analyzed two datasets: raw individual values, and species-mean values, taken as the mean for each species present in each plot. In the species-level dataset, we corrected for the potential effects of individual stature on trait values, following the methods of Baraloto et al. (2010b). One of the nine traits, trunk bark thickness, varied strongly with individual stature (Paine et al. 2010), and so we corrected for this correlation in the species-level dataset by substituting the residuals from a linear regression of bark thickness against individual stature.

Statistical analyses

We explored the trait-based structure of local communities by comparing local trait distributions to pooled trait distributions, following the general strategy of Kraft et al. (2008). The ecological processes we investigate affect functional trait distributions simultaneously, but their effects can be assessed independently because they act upon different aspects of the trait distributions. Niche differentiation was assessed with a metric of trait evenness: the standard deviation of nearest neighbor distances in univariate or multivariate trait space. This metric is identical to the SDNN as defined by Kraft and Ackerly (2010). Environmental filtering was assessed with measures of trait breadth: range (for single traits), and volume of the convex hull (for multiple traits). A convex hull is the minimal (hyper-) volume that encloses a given set of points, which comprised individual trees arrayed in trait space (Cornwell et al. 2006). In all cases, we compared the metrics from observed communities to their equivalents computed from 1000 synthetic local communities. Synthetic communities were generated by permuting plot locations among species or among individuals, for the species-mean and individual-level analyses, respectively. This approach matches the species richness (or stem density) of observed to those of synthetic communities (Cornwell et al. 2006).

We assessed the significance of these comparisons with one-tailed tests, which were used because the hypotheses we tested were explicitly directional. If niche differentiation were strong, trait evenness would increase (i.e. the standard deviation of nearest neighbor distances in trait space would decrease). If environmental filtering were strong, trait ranges (or convex-hull volumes) would decrease, relative to communities assembled without regard to trait values. Because we performed many tests of significance, we used the step-up false discovery rate method to adjust the significance criterion and reduce the likelihood of type I errors (Garcia 2004). We compared the outcomes of individual-based and species-based analyses by comparing their respective p-values and number of significant results. For the former comparison we used paired t-tests, while for the latter we used proportion tests.

Table 1. Functional traits analyzed in the study.

Name	Spectrum	Range in dataset	Unit	Individuals sampled (%)	Species sampled (%)
Foliar N concentration	leaf economics	0.01–0.06	%	63	75
Foliar chlorophyll content	leaf economics	10.33–255.0	$\mu\text{g mm}^{-2}$	99	99
Leaf toughness	leaf economics	0.22–13.1	N	98	98
Leaf tissue density	leaf economics	0.084–2.86	g cm^{-3}	97	98
Specific leaf area	leaf economics	1.77–47.5	$\text{cm}^2 \text{g}^{-1}$	98	99
Trunk sapwood density	stem economics	0.23–0.98	g cm^{-3}	61	96
Branch sapwood density	stem economics	0.19–0.96	g cm^{-3}	51	75
Trunk bark thickness	stem economics	0.5–53	mm	81	95
Laminar surface area	uncertain affinity	2.03–640 497	cm^2	98	99

To avoid the possibility that any particular functional trait may bias our results, we separately analyzed the distributions of all possible combinations of the nine functional traits in each of the nine plots. As the analyses we conducted required datasets with no missing values, we used multiple imputation by chained equations (MICE) to impute missing data (17 and 7% of the individual and species-mean datasets, respectively). MICE imputes non-observed data based upon all of the other observed data using a Gibbs sampler (van Buuren et al. 2006). Previous studies have shown MICE to be an effective technique to impute unobserved data while maintaining the variance structure of the data (Baraloto et al. 2010b).

The comparison of local communities to randomized synthetic communities was predicated on the assumption that all nine plots lie within the same regional species pool – i.e. that all species have the capacity to disperse to all plots. We tested this assumption by correlating geographic distance among plots with species dissimilarity among plots. If species are dispersal limited, i.e. if there are sub-regional species pools, geographic distance should positively correlate with species dissimilarity. We used the Bray-Curtis index of compositional dissimilarity to create a floristic distance matrix. We then used a Mantel test to assess a correlation between the floristic distance matrix and the geographic distance matrix. We found no geographical structure in the floristic data (Mantel's $r = 0.15$, $p = 0.18$). Thus, we failed to reject the hypothesis that all plots lie within a single regional species pool.

Finally, we assessed the extent to which environmental filtering and niche differentiation differentially affected traits associated with the SES and LES. First, we assigned each trait combination to a economic spectrum if all the traits in the combination were associated with that spectrum. Any combination that included traits from both spectra was counted as 'Both'. Trait combinations that included laminar area were excluded, as this trait is only weakly associated with the two economic spectra (Baraloto et al. 2010b). A linear model predicted the p-value indicating the strength of filtering (or niche differentiation) on each trait combination as a function of the type of combination ('LES', 'SES' or 'Both') and the number of traits in the trait combination. Plot was included as a random term. The interaction between number of traits and type of trait combination was non-significant, and dropped from the model.

All analyses were performed in R ver. 2.11.1 (R Development Core Team 2009). Convex hull volumes were computed using the Quickhull algorithm, implemented with the 'geometry' package in R (Barber et al. 1996).

Results

Two primary patterns are evident in our results: there was more evidence of environmental filtering than niche differentiation, and individual-level data were more sensitive indicators of ecological processes than were species-mean data.

We detected significant reductions in univariate trait ranges and multivariate convex-hull volumes in eight of the nine studied plots, as compared with randomized communities (Fig. 1). This constitutes evidence for environmental filtering, and was strong in the multivariate analyses of many trait combinations in five plots, but weak or absent in the other four. In contrast, there was less evidence of reduction in the standard deviation of nearest neighbor distances in trait space in the nine plots (Fig. 2). These niche-differentiation effects were significant in four plots but only for a small fraction of trait combinations. Thus, there was little evidence for niche differentiation. One may expect that the two processes may be exclusive: plots substantially shaped by environmental filtering would not also be structured by niche differentiation. Our results belie that supposition, as two plots (Nouragues-11L and Trésor) showed substantial evidence of being shaped by both processes. Conversely, the functional trait distributions of two plots (Lavilette and Nouragues-20H) were consistent with the hypothesis that they were assembled randomly with regard to trait values.

Individual-based analyses were more sensitive indicators of environmental filtering (Fig. 1) and niche differentiation (Fig. 2) than were analyses of species-mean trait values, both in terms of mean p-values (evaluated with paired t-tests), and in terms of the frequency at which significant effects of the ecological processes were detected (evaluated with proportion tests). This difference was only evident in multivariate analyses, whereas univariate analyses of trait evenness and trait range were no more sensitive on individual-level or species-mean data (paired t-tests: $p > 0.05$).

We evaluated the extent to which traits associated with the LES and SES were differentially shaped by ecological processes. These effects were slight, and we note that the majority of trait combinations showed no evidence of filtering at all. Nevertheless, trait combinations associated with the SES were significantly less strongly filtered than were those associated with the LES and those that included traits from both spectra (Fig. 3a). There were no significant differences among the three types of trait combinations in terms of the intensity of niche differentiation (Fig. 3b).

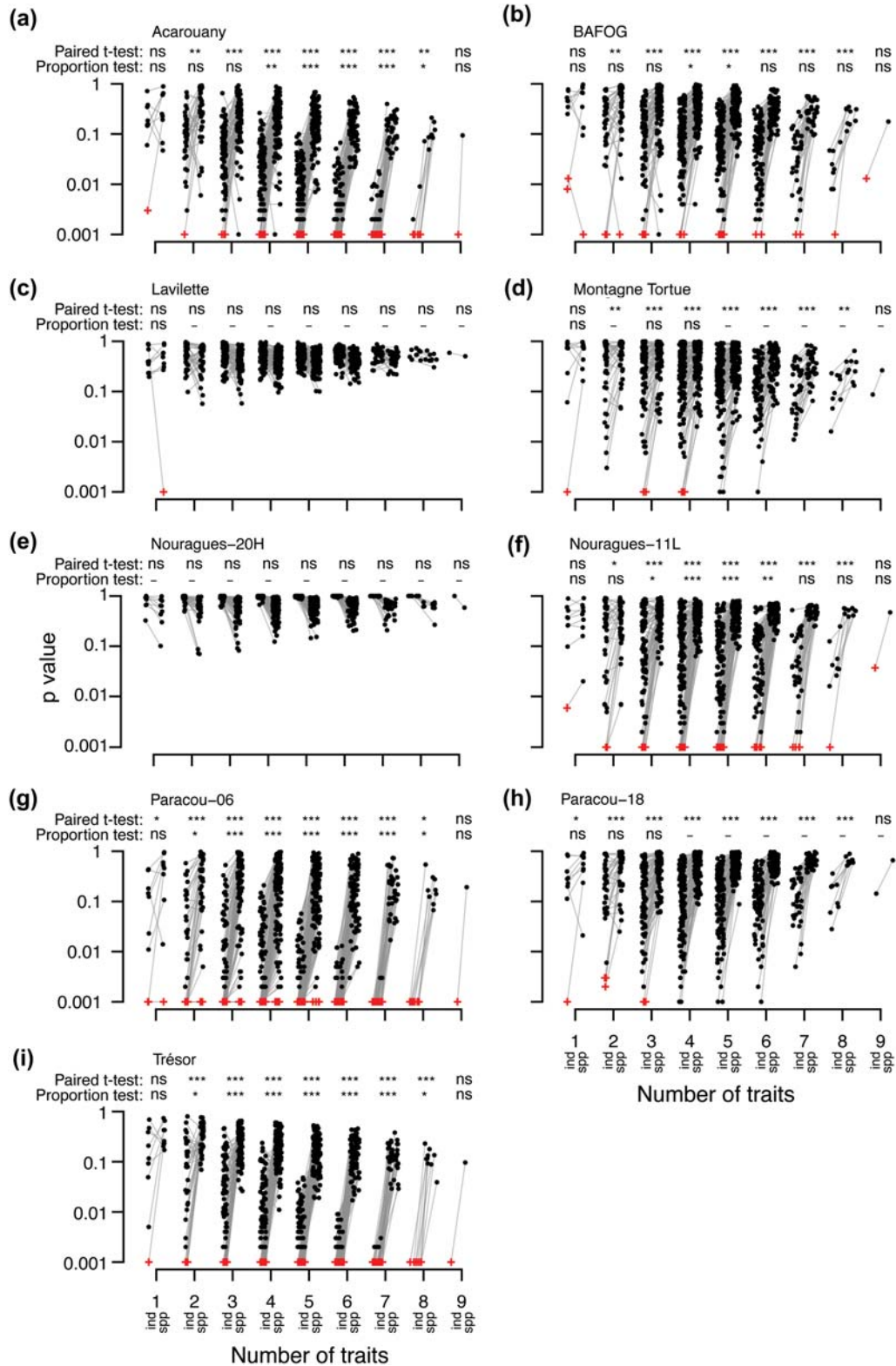


Figure 1. Individual-level functional traits are more sensitive indicators of environmental filtering than are species-mean traits. Points indicate the significance of the deviation between observed convex-hull volumes in trait space and those expected in communities assembled without regard to trait values. The observed and expected values were computed for every possible combination of nine functional traits, and are grouped by the number of traits included in each combination. Plus signs indicate combinations of traits significantly affected by environmental filtering, whereas circles indicate non-significantly filtered combinations. The significance threshold was determined by the step-up false discovery rate method (Garcia 2004). Lines connect identical combinations of traits, which were calculated both on individual-level and species-mean data. Paired t-tests weigh the hypothesis that for each combination of traits, individual-level data yields a more sensitive measure of niche differentiation than does species-mean data. Proportion tests weigh the hypothesis that individual data yields a greater proportion of significant results than does species-mean data. “ns”: $p > 0.05$, “*”: $p \leq 0.05$, “**”: $p \leq 0.01$, “***”: $p \leq 0.0001$, “-”: insufficient data. Note log scale on y-axes.

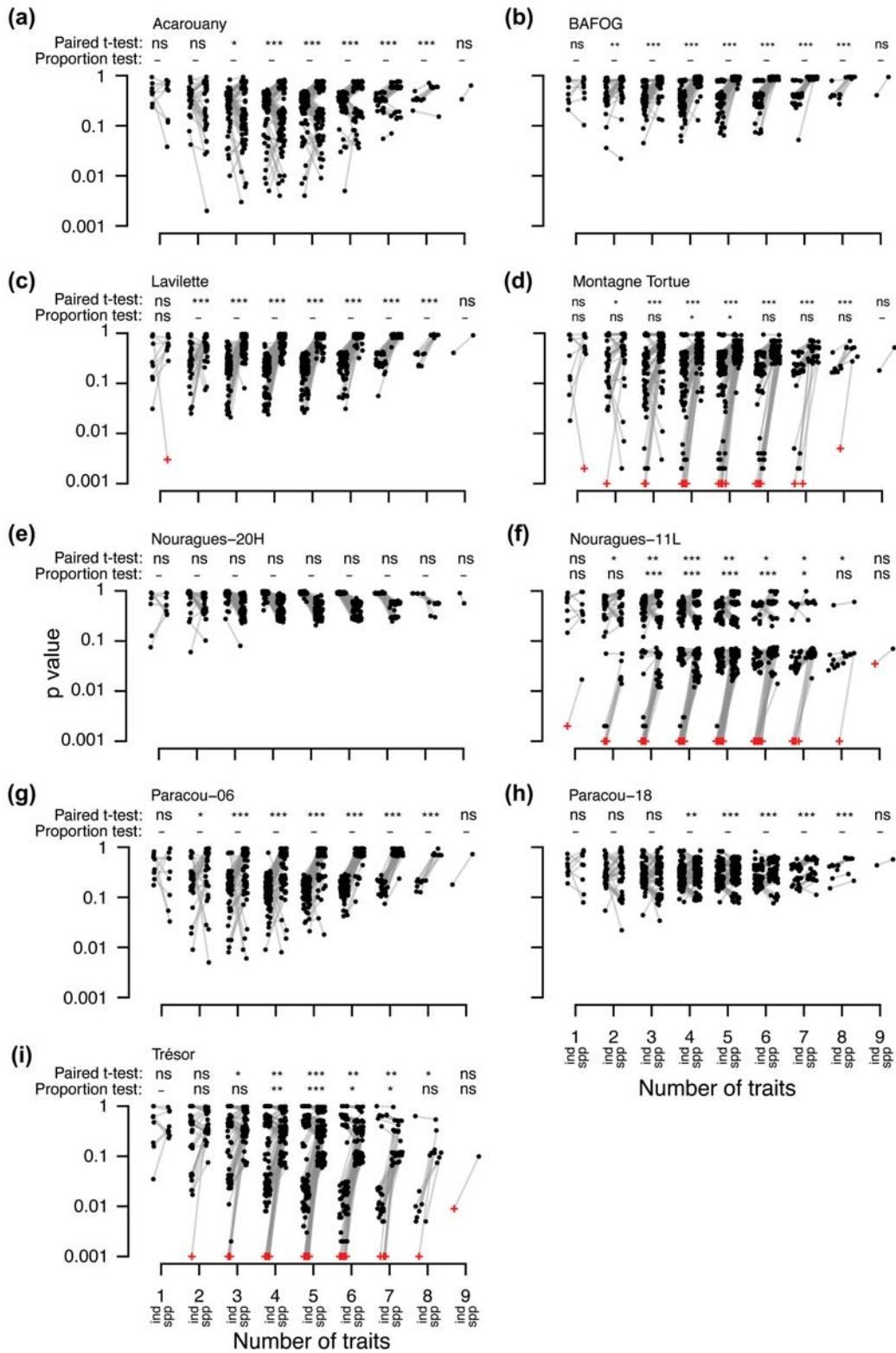


Figure 2. Individual data are more sensitive indicators of niche differentiation than are species-mean data. Points indicate the significance of the deviation between observed standard deviation of nearest neighbor distances in trait space and those expected in communities assembled without regard to trait values. Pluses indicate combinations of traits significantly affected by niche differentiation, whereas black circles indicate non-significant combinations. Other features are as described in the legend to Fig. 1.

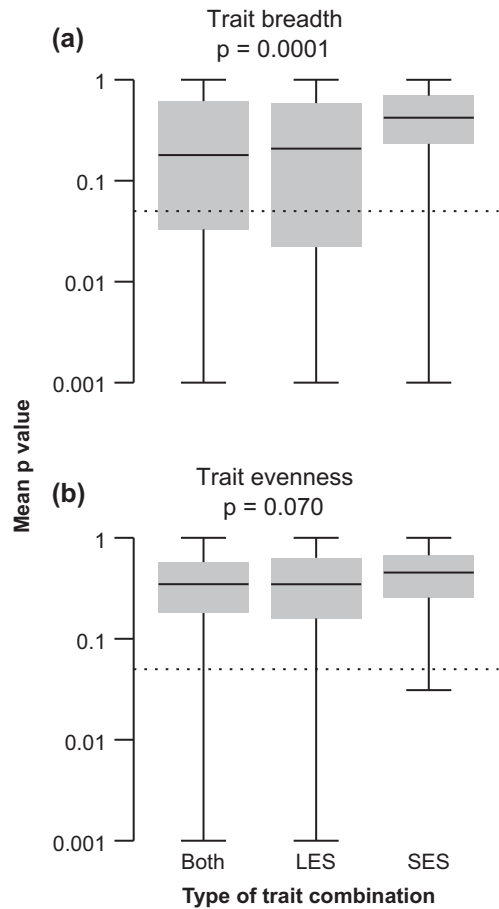


Figure 3. (a) Combinations of traits associated with the stem economics spectrum (SES) are significantly less strongly shaped by ecological filtration than are those associated with the leaf-economics spectrum, or those that include traits from both spectra. (b) In terms of trait evenness, indicating the effects of niche differentiation, there were no significant differences between combinations of traits from the SES, LES or mixtures. Dotted lines indicate $\alpha = 0.05$. Note log scale on y-axes.

Discussion

Relative importance of ecological processes

Environmental filtering appears to more strongly constrain the assembly of tree communities in French Guiana rain forests than does niche differentiation. Environmental filtering was widespread, limiting the range of at least some traits in eight of nine plots (Fig. 1). There was also evidence of niche differentiation in five plots, though it was less substantial than environmental filtering (Fig. 2).

Nevertheless, the relative roles imputed to filtering and differentiation are somewhat difficult to infer. They depend in part on the heterogeneity of environmental conditions in the study plots. Though precipitation varied widely among our plots – between 2 and 4 m annually – all the plots were located in never-flooded (terra firme) forest and on igneous substrates. Had we sampled a wider range of habitats, including, for example, forests on floodplains or white-sand substrates, we undoubtedly would have detected an even stronger signal of environmental filtering (Fine et al. 2006).

Overall, we detected little evidence of niche differentiation. And even this weak evidence of niche differentiation may overstate its role, since our metric of trait evenness, the standard deviation of nearest neighbor distances in trait space can confound the effects of niche differentiation with those of habitat filtering (Kraft and Ackerly 2010). Despite this limitation, we use it because it is the metric best suited to the multivariate analyses we emphasize in this contribution. Another complication for interpretation is that analyses of habitat filtering tend to have greater statistical power than do those of niche differentiation (Kraft and Ackerly 2010). Thus, the interpretation of the weak pattern of trait evenness is somewhat ambiguous: it may be that niches are in fact weakly differentiated, or it may be that we failed to detect differentiation that is, in reality, substantial. However, analyses of the same plots at smaller spatial scales (where power should be greater, Kraft and Ackerly 2010) also revealed little evidence of niche differentiation (results not shown). Together, these lines of evidence suggest that environmental filtering more strongly affects the community assembly of French Guiana rain forests than does niche differentiation.

We note that multivariate analyses are more sensitive indicators of the effects of ecological processes than are univariate analyses. In the case of environmental filtering, this suggests that filtering causes both increases in inter-trait correlations and reductions in trait ranges (Cornwell et al. 2006, Baraloto et al. 2010b). Convex-hull volumes are sensitive to changes in trait ranges, and also to changes in the strength of correlation among traits. In other words, if the variance in the relationship between traits is reduced, ranges would remain equal even as the convex-hull volume would shrink. A corollary of this observation is that convex-hull volumes are highly sensitive to outliers. One way to increase the robustness of this method would be the use of empirical density smoothing, which grids trait space, then estimates the density of points around every grid vertex (F. Jabot unpubl.). Such an approach would allow the volume of the intersection of two convex hulls to be precisely calculated. Unfortunately, the data required to accurately estimate the empirical density mounts rapidly with increases in the number of traits examined.

Contrasting inferences from individual and species-mean data

The second principal result of this study is that, for all plots and most trait combinations, individual-level data was a more sensitive indicator of niche differentiation and environmental filtering than was species-mean data (Jung et al. 2010). We note that we used per-plot species means, rather than an overall species means. Species means taken over all plots would probably have indicated an even weaker effect of niche differentiation and environmental filtering. Summarizing trait data by species can have substantial consequences. The first is a loss of detail: Intra-specific variation in trait values is often substantial, both within and among populations, and particularly over environmental gradients (Patiño et al. 2009, Albert et al. 2010b, Baraloto et al. 2010a). Summarizing data by species also reduces the apparent contribution of common species while emphasizing that of rare species. Analyses of individual data, by contrast, are more representative of the bulk of individuals in the community. Summarizing by

species has consequences for our understanding of community assembly, since intra-specific trait variation can affect community structure and promote species coexistence (Lichstein et al. 2007, Jung et al. 2010). Collecting individual-level data is laborious, and we note that species-mean trait data is suitable for a wide range of ecological studies (Baraloto et al. 2010a). For studies of community assembly, however, we concur with Albert et al. (2010a), that individual-level data is most appropriate. Even in ecosystems such as grasslands where individual genets may be difficult to distinguish, it may be possible to weight species-mean trait values by their relative abundance to more accurately evaluate the extent to which ecological processes generate community structure.

Our results warrant a re-evaluation of the conclusions of previous trait-based community-assembly studies. For example, in Ecuador, Kraft et al. (2008) detected environmental filtering, and in Costa Rica, Swenson and Enquist (2009) detected significant clustering of functional traits. In both cases, the incidence of significant deviations from the null expectation of communities assembled without regard to trait values was quite low. These studies were methodologically quite different from our work, including differences in plot size and the minimum sizes of trees studied. Nevertheless, a key difference is that their analyses were conducted at the species level. Previous studies measured traits on up to 20 individuals per species, then calculated mean trait values, which were applied to all individuals of that species (Stubbs and Wilson 2004, Kraft et al. 2008, Mayfield et al. 2009, Swenson and Enquist 2009). In contrast, we explicitly compare results from species-mean and individual-level data. Because individual-level data indicate substantially stronger effects of environmental processes on community assembly than do species-mean data, we suggest that previous authors may have inadvertently under-estimated the effects of niche differentiation and environmental filtering.

Differential effects on leaf traits and stem traits

Which traits underlie the observed patterns of trait breadth and trait evenness? A clean answer to this question would suggest mechanisms by which niche differentiation and ecological filtering shape community assembly. Our results suggest that environmental filtering more strongly acts upon traits associated with the leaf economics spectrum than traits associated with the stem economics spectrum. Combinations of traits associated with the LES, and combinations that included both LES and SES traits, were more strongly shaped by environmental filtering than were combinations comprised solely of SES traits (Fig. 3a). Even though the majority of trait combinations were not significantly filtered, this pattern suggests that the expression of unusual LES trait values is more likely to lead to filtering than is the expression of unusual SES trait values. This pattern also suggests a sampling effect: the inclusion of a strongly filtered trait in a particular set of traits was sufficient to cause the larger set of traits to be filtered. The overall effect of niche-differentiation in these communities appeared slight (Fig. 2), and LES-associated traits appeared to be no more indicative of niche differentiation than were SES-associated traits (Fig. 3b). In ecosystems where niche differentiation plays a stronger role, such as competition-dominated grasslands,

a clearer signal may be detected. Such signals would be useful to indicate, for example, the relative importance of above- and below-ground competition. To better understand the mechanistic bases of ecological processes on community assembly, we recommend that traits associated with both spectra of plant economics be included in future analyses.

Conclusions

In this study, we assessed the degree to which niche differentiation and environmental filtering affect functional trait distributions in nine 1-ha plots of tropical rain forest using species-mean and individual-level data. Environmental filtering appeared to more strongly shape these forests than did niche differentiation. Individual-based analyses of functional traits of individual trees indicate that ecological processes strongly structure the forests of French Guiana, a conclusion that would have been obscured by analyses focusing solely on species-mean data. As intra-specific variation may be critical in allowing species coexistence in diverse forests, it is essential to account for it in studies of community assembly. The mechanistic bases of the observed ecological filtration remain murky, but may be more related to leaf traits than to stem traits. The geographic separation of our plots, and the large number of individual trees studied suggest that our conclusions should apply to a wide range of diverse forests.

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