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Comment on “Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest”

Jeffrey K. Lake* and Annette Ostling

Kraft *et al.* (Reports, 24 October 2008, p. 580) used a variety of metrics describing the distribution of functional traits within a tropical forest community to demonstrate simultaneous environmental filtering and niche differentiation. We discuss how these results could have arisen from sampling design and statistical assumptions, suggesting alternative approaches that could better resolve these questions.

Kraft *et al.* (1) used the distribution of functional traits in a diverse tropical forest community to test hypotheses of community assembly. The study focused on six traits that drive diverse ecological functions. By comparing metrics of observed distributions of each trait with those expected under different null models, the authors showed evidence for both classical niche differentiation and environmental filtering at the scale of 20- by 20-m quadrats. Relative to null expectations, environmental filtering was indicated by shifting trait means, decreased trait range, and variance within quadrats, whereas differentiation was indicated by overdispersion, measured by standard deviation (SD) of nearest-neighbor distance in trait space, and kurtosis of the within-quadrat trait distribution. Combined, these tests were used to argue for the important role of stabilizing processes in the maintenance of biodiversity in a hyperdiverse tropical forest. This approach represents movement toward a more comprehensive use of functional traits in testing processes of community assembly. Nevertheless, there are some subtle problems in the Kraft *et al.* analysis that we expand upon here.

First, Kraft *et al.* (1) inappropriately tested for both environmental filtering and niche differentiation using null models that select randomly from the entire species pool. If environmental filtering limits the range of traits of species that can occur in a given quadrat, an accurate test of niche differentiation within quadrats must sample only from species that fall between the minimum and maximum traits present in a quadrat. The larger the available trait space, the larger the possible range of nearest-neighbor distances in trait space, and hence the bigger the SD of nearest-neighbor distances will be under a random draw from that available trait space. Thus, if limitations on the range of trait values in each quadrat due to habitat

filtering are not accounted for in the null trait distribution used in the niche differentiation test, one might artificially conclude that the observed SD of nearest-neighbor distances is smaller than expected by chance and that niche differentiation is occurring. Similar problems might arise in the comparison of kurtosis values.

Second, Kraft *et al.* ignored intraspecific variation. Due to the obvious difficulty of collecting trait data for all individuals, the authors targeted outer canopy leaves of trees in the 1- to 5-cm diameter at breast height (dbh) size class growing

under closed canopy that were readily accessed from the ground, leading to a collection of 2 to 5 leaves from 1 to 20 individuals for most of the 1089 species. Hence they had to generate observed quadrat-level trait distributions by assigning trait values to the occurrence of each species in each quadrat (known from the spatial tree data available for the plot), based on the limited information they have collected for the 1 to 20 individuals of that species across the plot. Based on three arguments—that a relatively low percentage of explained variance in traits is driven by individual and leaf sampled, that there is only limited correlation between traits and measured environmental gradients, and that species’ rank order of trait values measured from canopy trees is relatively similar to their rank ordering based on juvenile measurements—Kraft *et al.* assigned the species’ mean sapling trait values to all individuals of that species, regardless of individual size and light exposure.

Yet traits can vary 2- to 3-fold or more across ontogeny or light environment within a species, whereas the interspecific range within a community is similar or only moderately higher (2–5). This is not true for all traits (seed size varies intraspecifically, but not ontogenetically, and maximum size is a species-level trait), but for the traits related to leaf size, structure, and chemistry, intraspecific variation can be substantial. It is

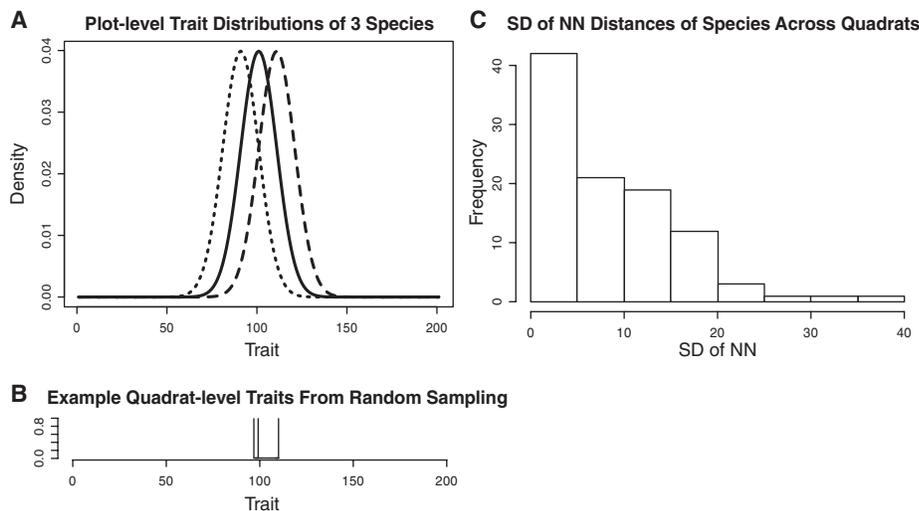


Fig. 1. Representation of the effect of sampling from intraspecific variability. (A) Hypothetical plot-level trait distributions of three species with a perfectly overdispersed, normally distributed trait, with means of 90, 100, and 110, respectively, and a SD of 10. (B) An example within-quadrat trait distribution that results when we sample one “real” individual from the distribution for each species instead of assuming that individual follows the species means, as Kraft *et al.* did. The height of the bars represents the number of occurrences, which is one for each species. (C) The resulting distribution of SD of nearest-neighbor distances (SD of NN) across 100 quadrats created in this way. The values of SD of NN if species means were used as Kraft *et al.* did is 0. Hence, intraspecific variation causes the SD of NN to go up on average. It will have this effect on both the observed and null model SD of NN. However the effect on the null model SD of NN will be extremely small because the species are so tightly packed in trait space at the plot level that traits sampled from species near one another in trait space become essentially interchangeable. The net result is that the observed SD of NN goes up, whereas the null SD of NN remains approximately the same, when intraspecific variation is accounted for, and the evidence for niche differentiation gets weaker.

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virtually certain that the individuals within a given quadrat are a mix of sizes (and light exposures) of different species. Hence, trait range and variance within quadrats, as well as the SD of nearest-neighbor distances and kurtosis of the trait distributions within quadrats, would all change dramatically if ontogenetic variation were included, and the impact on the observed trait distributions relative to the null predictions is highly unpredictable. The arguments of Kraft *et al.* for ignoring intraspecific variation do not alter this fact.

Furthermore, even the small amount of intraspecific variation among saplings could affect Kraft *et al.*'s more conservative test for niche differentiation, which uses only the spatial arrangement of individuals close in size to the size class for which trait data was actually collected (specifically 1- to 10-cm dbh individuals). A quadrat where species trait means are dispersed when occurrences are simply assumed to correspond to plot-level sapling means might really be randomly assembled based on the actual species' mean trait values for that quadrat. Consider, for example, the extreme case in which the traits of individuals of each species in a quadrat are a random draw from that species' plot-level trait distribution. The nearest-neighbor distances between species' quadrat mean trait values will then be more variable than the distances between the plot-level means of those species (Fig. 1). Here, there is much greater potential for shifts in the observed distribution than in the null, where the close packing of species should lead to little change after sampling from species trait distributions. Although it is impossible to know with certainty the impacts of ignoring intraspecific variation in traits without a good measure of that variability, it is certain that, at best, species means provide a first approximation of the trait distribution patterns resulting from the

community assembly processes acting in this forest.

The unfortunate solution to this problem seems to be sampling traits from many more individuals to gain spatially resolved trait data. This is a logistical hurdle, especially given the difficulty of sampling sun-exposed leaves of adults. However, because size structure can play an important role in competition (6, 7), overcoming these challenges seems necessary for understanding the assembly of a forest community where individuals vary so greatly in size. One alternative is to sample randomly from the known intraspecific distributions of traits for individuals within a given size class and light environment within each species when assigning trait values, that is, to consider the extreme case we described. Although this could mask the effects of niche differentiation driven by local competition—traits of individuals within a given quadrat may not be a random sample from that species' trait distribution—a rejection of the null even in this alternative analysis would provide clearer evidence for niche differentiation.

There are two final points we wish to make. First, as the authors note, the results they find for this forest are rather subtle. Although the statistical significance Kraft *et al.* found is high, effect size is often negligible or small. This is especially true for tests for overdispersion of traits at the quadrat level. Second, given how small this overdispersion is, ignoring intraspecific variation presents a problem more fundamental than the statistical issues we have raised. If intraspecific variation is high, species probably overlap a great deal in their trait distributions. If the strength of interspecific competition is proportional to this overlap, then interspecific competition may indeed be stronger than intraspecific competition, and the species may not be stably coexisting and hence not be truly niche differentiated even if there is a tendency for

overdispersion (8). Hence, evaluating process on the basis of overdispersion patterns in the absence of information about overlap may lead us to an invalid conclusion about the nature of community assembly. However, establishing a detailed relationship between the strength of interspecific competition and the amount of trait overlap requires a mechanistic understanding of competition in this forest that is currently unavailable, so Kraft *et al.* have carried out the most thorough analysis currently possible in this regard.

We applaud this overall approach and the substantial effort involved in moving toward tests of niche and neutral processes. These types of studies, particularly if combined with demographic data on individual trees, can move us toward a better understanding of the forces governing community assembly. However, we suggest that further analysis is needed before the signature of community assembly (in particular of niche differentiation) can be clearly detected in the observed trait distributions in this forest.

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