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

Nathan J. B. Kraft* and David D. Ackerly

Lake and Ostling address several issues that they suggest could influence our analyses of tropical forest community assembly. Some of the issues have already been considered, whereas others appear to arise from misunderstandings. We offer clarification of our analyses and additional discussion of our results.

Lake and Ostling (1) express several concerns that they suggest could influence our analyses of tropical forest community assembly (2). Here, we address each comment in turn.

Lake and Ostling point out, as others have previously (3, 4), that an appropriate null model for detecting even spacing may need to incorporate the effects of habitat filtering. In some instances, habitat filtering, which reduces the range and possibly the variance of trait values among co-occurring species, may also produce nonrandom patterns in trait spacing, when compared to a null model including species from multiple habitats. In our analyses (2), we addressed the interaction between habitat filtering and niche differentiation by using habitat-restricted null models. Previous analyses of the Yasuní plot (5) identified two primary habitat types within the plot, ridgetops and valley bottoms, and our tests of trait averages strongly mirrored the distribution of these habitats [figures 1A and S1 in (2)]. We therefore expected that limiting the species pool to just species occurring within each habitat should reduce the habitat filtering signal for plots within the respective habitats, which it did in many cases. If Lake and Ostling were correct that our even spacing results were driven entirely by habitat filtering, using a habitat-restricted pool also should have reduced the signal of niche differentiation. In many cases, the niche differentiation signal was stronger under habitat-specific null models (2), which suggests that there are at least two distinct nonrandom processes occurring.

There are additional ways to address the interaction between habitat filtering and niche differentiation that we did not present. One way (3) is to standardize spacing metrics by the observed range of trait values within a quadrat. Thus, instead of the standard deviation of nearest-neighbor distances (SDNN), one can use SDNN divided by the range as the test metric. Using this metric to

repeat the analyses shown in table 1 in (2), we detect even spacing in three traits (leaf nitrogen Wilcoxon $P = 0.011$; leaf size $P < 0.0001$; maximum diameter at breast high (dbh) $P = 0.0005$), although specific leaf area (SLA, leaf area divided by dry mass) is no longer significant (6). Alternatively, the null model can be restricted to include only species that occur within the range of values found within the quadrat (4). This approach, which treats each quadrat as if it is located at a distinct position along a continuous environmental gradient, seems biologically implausible given what we know about habitat associations at Yasuní and other tropical forests (5, 7); however, it can be applied. Repeating the analyses summarized in table 1 in (2), modified to include a restricted range null model in quadrats where significant filtering was detected, our basic conclusions about the presence of even spacing hold (leaf nitrogen Wilcoxon $P = 0.01$; leaf size $P = 0.007$; maximum

dbh $P < 0.0001$; other traits not significant). Both of these alternative analyses offer the same general result as our main analysis, with the exception of SLA, which was significant in our main analysis but had a very small effect size.

Next, Lake and Ostling suggest that intra-specific variation should be considered. We heartily agree that greater sampling and study of intra-specific variation in forests like Yasuní would be valuable, but we are doubtful that the effect of such variation in a properly specified null model analysis of Yasuní would be as dramatic as they envision.

First, there is an important general point about what individual trait variation represents. Variability in measurements between individuals can be due to plastic phenotypic responses to the environment, ontogenetic changes, genetic variation, sampling error, and other sources. Plastic phenotypic and ontogenetic responses are often correlated among species, and we contend that a proper null model that incorporates intraspecific variation should apply this type of variation in a correlated way across species. This would reduce the degree of intraspecific variability in analyses relative to the figures that Lake and Ostling cite. For example, they cite 2- to 3-fold variation in leaf traits across ontogeny in other studies, whereas we find an average of 1.7-fold variation in SLA within well-sampled species [table S6 in (2)] of similar stature and light exposure. This is in contrast to the 9-fold variation we find in mean SLA across species of similar stature and light exposure, 6-fold variation in species mean leaf nitrogen, >5000-fold variation in species mean leaf size (we measured minimum photosynthetic units), 6-fold variation in adult wood density, 180-fold

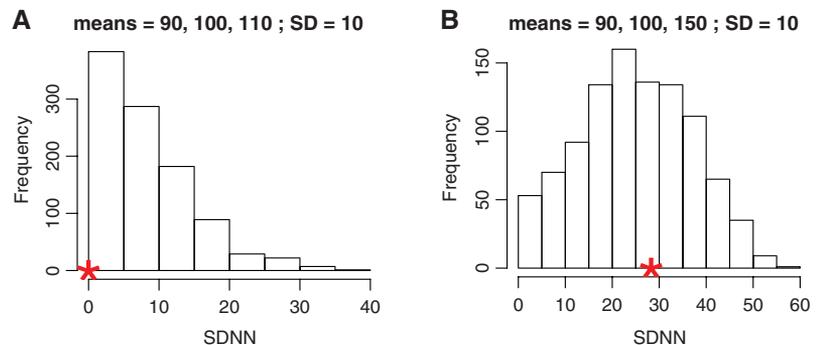


Fig. 1. Effect of including intraspecific trait variability in the estimation of SDNN in two cases, following Lake and Ostling’s (1) example. (A) Same case as figure 1C in (1), where one individual of three species with trait means of 90, 100, and 110, and each with a trait SD of 10, is randomly sampled and the SDNN is calculated. Here the process is repeated 1000 times to generate a distribution of SDNN values. The asterisk (*) indicates the SDNN value calculated from the species mean alone (which is 0). In this case, stochastic sampling from intraspecific trait distributions can only increase SDNN relative to the value calculated from means, as the species means are perfectly spaced already (and because SD values are bounded at 0). However, in any instance where species mean values are less than perfectly spaced (and therefore SDNN calculated from species means is greater than 0) (B), as is the case in every trait in every quadrat of our study (2), adding stochastic sampling of intraspecific variation can result in either larger or smaller estimates of SDNN than would be produced by simply using species means. Therefore, in real communities, using species means should not systematically underestimate SDNN calculated from intraspecific data, as Lake and Ostling suggest.

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variation in maximum dbh, and >209,000-fold variation in seed size.

Second, we disagree with Lake and Ostling that measures of species spacing, such as SDNN, are the ideal metric for use with intraspecific variation. They suggest adding stochastic sampling variation to species means, which seems to bypass a history in ecology of using niche overlap indices (8) when considering intraspecific variation. Recent work (3), for example, uses spacing metrics similar to ours for species means and niche overlap metrics for analyses with intraspecific data, and we find this distinction useful.

Third, Lake and Ostling argue that incorporating intraspecific variation will dramatically alter the outcome of our tests of even spacing using SDNN. This is in part because they incorrectly assume that stochastically applied intraspecific variation will result in a distribution of SDNN values in which all values are equal to or greater than SDNN calculated from species means, indicating less even spacing [figure 1 in (1)]. This result arises from a biologically implausible parameter choice in their example (Fig. 1A). In all other cases, adding intraspecific variation can either increase or decrease estimates of SDNN, making communities appear either more or less randomly assembled (Fig. 1B). This is hard to construe as a systematic bias, particularly for abundant species within communities, where Lake and Ostling's approach would be no different from using species means. This issue aside, it should be noted that the magnitude or variability of SDNN values have little bearing in any absolute sense; the key is the value of the observed SDNN relative to the null expectation. As the variation should

be added to both the null and the observed data, the effect on the test outcome, if any, will likely be small when intraspecific variation is small relative to interspecific differences.

Lake and Ostling's comments in this area raise an interesting question: Do the functional traits of leaves, seeds, and wood directly influence plant establishment and community assembly, or are the traits proxies or correlates of overall strategies that may be assembling nonrandomly within these communities? We would argue that it is the latter, whereas Lake and Ostling's concerns regarding intraspecific variation seem to presume the former, in which it is the actual trait value of the individuals in a plot that is responsible for the community assembly processes. This distinction is most apparent for some of the traits included in our analysis that Lake and Ostling did not focus on, such as seed size and maximum dbh. In both of these cases, actual values cannot be applied to the tens of thousands of immature individuals within the plot, so species averages serve as a proxy for associated ecological strategies.

Lake and Ostling state, as we did in (2), that the evidence for nonrandom assembly processes at Yasuní is subtle. They go on to suggest that nonrandom assembly processes are therefore unimportant or negligible. We contend that the difference between a fully neutral community and a largely equalized community with weak stabilizing forces (9), as both our habitat filtering and even spacing results suggest, lies at the heart of the argument over the importance of neutral theory. As Purves and Pacala (10) have shown, the patterns in relative abundance that have been used to support neutral theory arise

from stochastic demographic processes, not from ecological equivalence of species (two distinct aspects of the neutral theory that are often conflated). A combination of gap dynamics, soil and topographically based habitat filtering, impacts of natural enemies, and strategy differentiation at local scales all may act in concert to produce the patterns that we reported. These nonrandom stabilizing processes, even if they are subtle, have important implications for the fate of rare species within communities, the turnover of communities in space and time, and the structure and function of ecosystems.

References and Notes

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11. We have benefited from conversations with J. Lake, A. Ostling, W. Cornwell, and S. Kembel about these and related issues. Our response was improved by the comments of two anonymous reviewers.

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