Response to Comment on "Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest"
Nathan J. B. Kraft, et al.
Science 324, 1015-d (2009);
DOI: 10.1126/science.1169885

The following resources related to this article are available online at www.sciencemag.org (this information is current as of July 17, 2009):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:
http://www.sciencemag.org/cgi/content/full/324/5930/1015-d

A list of selected additional articles on the Science Web sites related to this article can be found at:
http://www.sciencemag.org/cgi/content/full/324/5930/1015-d#related-content

This article cites 7 articles, 2 of which can be accessed for free:
http://www.sciencemag.org/cgi/content/full/324/5930/1015-d#otherarticles

This article appears in the following subject collections:
Ecology
http://www.sciencemag.org/cgi/collection/ecology
Technical Comments
http://www.sciencemag.org/cgi/collection/tech_comment

Information about obtaining reprints of this article or about obtaining permission to reproduce this article in whole or in part can be found at:
http://www.sciencemag.org/about/permissions.dtl
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 Yasuni 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 could 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 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 Yasuni 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 intraspecific variation should be considered. We heartily agree that greater sampling and study of intraspecific variation in forests like Yasuni would be valuable, but we are doubtful that the effect of such variation in a properly specified null model analysis of Yasuni 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 across species 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 variation in adult wood density, 360-fold variation in adult wood density, 20-fold variation in adult wood density, and 20-fold variation in adult wood density.

There are additional points to consider. In our model including species from multiple habitats, we detected an effect of habitat filtering on SLA. We agree that greater sampling and study of intraspecific variation in forests like Yasuni would be valuable, but we are doubtful that the effect of such variation in a properly specified null model analysis of Yasuni would be as dramatic as they envision.

In our analyses (2), we addressed the interaction between habitat filtering and niche differentiation with a restricted 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 intraspecific variation should be considered. We heartily agree that greater sampling and study of intraspecific variation in forests like Yasuni would be valuable, but we are doubtful that the effect of such variation in a properly specified null model analysis of Yasuni 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 across species 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 variation in adult wood density, 360-fold variation in adult wood density, 20-fold variation in adult wood density, and 20-fold variation in adult wood density.

There are additional points to consider. In our model including species from multiple habitats, we detected an effect of habitat filtering on SLA. We agree that greater sampling and study of intraspecific variation in forests like Yasuni would be valuable, but we are doubtful that the effect of such variation in a properly specified null model analysis of Yasuni would be as dramatic as they envision.

In our analyses (2), we addressed the interaction between habitat filtering and niche differentiation with a restricted 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 intraspecific variation should be considered. We heartily agree that greater sampling and study of intraspecific variation in forests like Yasuni would be valuable, but we are doubtful that the effect of such variation in a properly specified null model analysis of Yasuni 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 across species 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 variation in adult wood density, 360-fold variation in adult wood density, 20-fold variation in adult wood density, and 20-fold variation in adult wood density.

There are additional points to consider. In our model including species from multiple habitats, we detected an effect of habitat filtering on SLA. We agree that greater sampling and study of intraspecific variation in forests like Yasuni would be valuable, but we are doubtful that the effect of such variation in a properly specified null model analysis of Yasuni would be as dramatic as they envision.

In our analyses (2), we addressed the interaction between habitat filtering and niche differentiation with a restricted 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.
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 related 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
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.

9 January 2009; accepted 29 April 2009
10.1126/science.1169885