

Response to Comment on “Ecosystem Properties and Forest Decline in Contrasting Long-Term Chronosequences”

Kitayama (1) correctly recognizes that the six forested chronosequences we studied (2) do not include any of the hyperdiverse forests commonly found in the tropics. We welcome others to test whether the patterns we found for our six sites also occur in other systems and also recognize that there are plausible reasons as to why these patterns may or may not occur. However, we believe that the way Kitayama has attempted to test the validity of our ideas with regard to hyperdiverse tropical rainforests has substantial limitations.

First, Kitayama pools data from six studies spanning the continental tropics and suggests that nitrogen to phosphorus (N:P) ratios and aboveground biomass are not negatively related. However, this analysis involves individual sites that span very large spatial scales, across which a range of other driving factors (notably macroclimate, geology, and disturbance regime) would vary considerably and could well override effects of soil fertility. It is well recognized that macroclimate is the key driver of biogeochemical processes and ecosystem functioning at large spatial scales, whereas variables related to resource quality are more important at local spatial scales, where variations in climate are more likely to be minor (3, 4). Kitayama's demonstration that N:P ratios are unimportant as drivers of tree biomass at large spatial scales therefore does not preclude these ratios from being important drivers at local spatial scales such as at the within-chronosequence scale that we studied (2). His analysis is therefore not relevant to the question that we have addressed. Kitayama's own work in Borneo (5) is more relevant, but is based on only three sites that have formed on different geological substrates rather than by pedogenesis along a single substrate, as in our work. Whether his findings are characteristic of hyperdiverse tropical forests at large remains to be

tested, and we maintain that this question could best be tested by using long-term chronosequence data.

Second, we have particular concerns about the mechanistic basis that Kitayama proposes to explain why hyperdiverse tropical rainforests apparently do not decline drastically with increasing P limitation, i.e., that the additional diversity that these forests have over less diverse ones confers benefits for forest stand nutrient efficiency. We note that our chronosequences are not “extremely low” and “impoverished” in diversity, as claimed by Kitayama; the Franz Josef and Cooloola sequences in particular have more than 30 tree species that occur with some abundance. More important, Kitayama's proposed diversity mechanism requires that increasing tree diversity from tens of species (our study sites) to hundreds of species (hyperdiverse tropical rainforests) has beneficial effects on ecosystem functions (in this case, the ability of forest stands to resist decline by P limitation). This mechanism assumes that ecosystem functioning (i.e., the rate of ecosystem-level processes) increases monotonically with increasing diversity at levels of plant species richness well beyond 100 species. However, several studies have found little effect of plant diversity on ecosystem functioning except at very low levels of diversity (6, 7). Even those studies that have been the most generous in ascribing positive roles of biodiversity to ecosystem functioning (8, 9) have suggested an asymptotic relation between diversity and function, which effectively saturates at a diversity of around 10 species. This relation is also supported by theoretical predictions (10). The mechanistic basis that Kitayama proposes therefore has no support from literature on the diversity-function issue, whether theoretical, experimental, or empirical.

Finally, Kitayama claims that our use of basal area to show biomass decline during

retrogression is not justified. However, this basal-area decline is matched by published measured declines of tree height and/or tree biomass for most of these chronosequences (11–14). It is indisputable that tree biomass drops sharply during retrogression for each of our chronosequences, and this is apparent from visual inspection of the stands that we considered, including photographs of them [see figure S1 in (2)].

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References and Notes

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