Unanticipated Effects of Stand Dynamism on Amazonian Tree Diversity

Susan G. W. Laurance[1,2,4], **Ana Andrade**[3], and **William F. Laurance**[1,2]

[1] School of Marine and Tropical Biology, James Cook University, Cairns, Qld. 4878, Australia

[2] Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panama

[3] Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA), C.P. 478, Manaus AM 69011-970, Brazil

ABSTRACT

We assessed a general hypothesis of tropical tree diversity that predicts that species richness will be positively correlated with stand dynamism. Our analysis was based one of the largest and longest-running datasets on Amazonian trees (≥ 10 cm diameter at breast height), with data collected over a 23-yr period within 66 1 ha plots spanning a large (1000 km^2) landscape. Within these plots, maximum tree-species richness (329 species/ha) and Fisher's α values (227.5) were among the highest ever recorded. Contrary to the diversity-dynamism concept, tree species richness in our landscape was significantly and *negatively* associated with stand dynamism (measured as the mean rate of annual tree turnover). Because of this unexpected finding, we critically re-evaluated the relationship between stand dynamism and tree diversity across the Amazon basin and the tropics as a whole. With the inclusion of additional data we found that the relationship between stand dynamism and tree diversity becomes non-significant at larger spatial scales.

Abstract in Portuguese is available at http://www.blackwell-synergy.com/loi/btp

Key words: Amazon; Brazil; forest dynamics; rain forest trees; species richness; tree turnover rates.

TROPICAL RAIN FORESTS SUSTAIN THE RICHEST TREE COMMUNITIES ON EARTH, with up to 329 species (≥ 10 cm diameter at breast height [dbh]) recorded per hectare (this paper). Explanations for this striking diversity have focused on two differing perspectives: evolutionary processes that might facilitate the speciation and persistence of so many species (Terborgh 1973, Ricklefs *et al.* 1999), and contemporary environmental factors that help to maintain current diversity in rain forests (Phillips & Gentry 1994, Pitman *et al.* 2002, Leigh 2008).

In Amazonia, the largest and possibly most species-rich forest in the world, several broad-scale analyses have evaluated environmental and ecological correlates of tree diversity. For example, species richness has been found to peak in areas with: (1) high rainfall and short dry-season length (Gentry 1988, ter Steege *et al.* 2003); (2) high tree-turnover rates (Phillips *et al.* 1994, ter Steege *et al.* 2006); (3) high stem density (Denslow 1995, ter Steege *et al.* 2003); and (4) higher soil fertility (Gentry 1988, Duivenvoorden 1996). Given the vastness of the Amazon, however, these analyses have been based on surprisingly limited data. Even the largest dataset, such as that of ter Steege *et al.* (2003), assessed tree richness across the *ca* 500 million ha of Amazonian forest with just 275 plots, of which most (246) were $\leq$ 1 ha in area.

Here we evaluate a prominent idea about Amazonian tree richness, that diversity is positively associated with stand dynamism (Phillips *et al.* 1994). We focus on a single, intensively studied landscape in central Amazonia, using high-quality tree-community data from 66 1-ha plots collected over a 23-yr period. A key advantage of our study is that, compared with basin-scale studies compli-

cated by an array of varying historical and environmental factors, our landscape is relatively homogeneous in its soils, rainfall, disturbance history, and floristic composition.

Our study has three components. First, we examine the relationship between tree turnover rates and tree diversity, and unexpectedly find it to be negative, rather than positive, in slope. Second, we test three potential explanations for our findings. Finally, we include a random subset of our data with previously published datasets, to critically evaluate the relationship between stand dynamism and tree diversity across the Amazon basin and the tropics as a whole.

METHODS

STUDY SITE.—This study was undertaken as part of the Biological Dynamics of Forest Fragments Project (BDFFP), a long-term experimental study of habitat fragmentation that encompasses a *ca* 1000-km^2 landscape, 80 km north of Manaus, Brazil (2°20′ S, 60°00′ W). The study area supports non-flooded, lowland tropical rain forest, which averages 28–35 m in height with emergents reaching 55 m. The understory is relatively open and dominated by stemless palms. Soils are classified as xanthic ferralsols, which are highly acidic and generally low in nutrients (Chauvel *et al.* 1987). Annual rainfall averages *ca* 2600 mm/yr, with a distinct dry season from July to September.

There is no evidence of major recent disturbances within the intact forests of the BDFFP. Radiocarbon dating of soil charcoal revealed widespread fires from 1300 to 1100 yr BP. More-recent charcoal (550 ± 220 yr BP), however, was found at only 1 of 15 sites, suggesting this was a localized disturbance (Piperno & Becker 1997). An examination of phytoliths found no evidence of domesticated plant species, suggesting the site has no history (over the last

five millennia) of agriculture. However, a community change evidently occurred at 4590 ± 60 yr BP, during which plant species (*e.g.*, Chrysobalanaceae) associated with wetter or inundated sites became less abundant (Piperno & Becker 1997). Past disturbances such as blowdowns (Nelson 1994) are possible, but these tend to be patchy and localized in nature. We have also observed no trends in floristic composition or vegetation structure to suggest that our sites are recovering from any major disturbance (Laurance *et al.* 2005).

Before experimental fragmentation of some forests at the BDFFP, tree communities were studied in 66 1-ha plots scattered across the study area (Laurance *et al.* 1998a, b). Within each plot, all trees (≥ 10 cm dbh) were mapped, measured, and uniquely tagged, with voucher material for nearly all individuals and housed at the BDFFP herbarium. Distances among plots in the study area are 0.1–32.5 km (Bolhman *et al.* 2008).

PLANT-IDENTIFICATION METHODS.—Among our 66 plots, an average of 97.7 percent (range: 95.1–99.7%) of stems were identified to species (or genus and morphospecies) level from the initial census. In total, 1255 species or morphospecies were recorded among 40,352 stems. We used three strategies to minimize the risk of creating unsubstantiated species or morphospecies. First, rather than identifying species on a plot-by-plot basis, we pooled vouchers from all plots into families, and then morphotyped and identified presumptive species within each family. This allowed us to observe the range of morphological variability within species, and thereby limit erroneously subdividing single species into two or more different morphospecies. Second, the long-term nature of our study allowed us to recollect numerous singletons and rare morphotypes, and to collect fertile material whenever possible, and thereby confirm the status of many species. Finally, the BDFFP herbarium and taxonomic keys were established with the assistance of many world-leading plant taxonomists (Pennington 1990, Nee 1995), and this has also increased confidence in our identifications.

DATA ANALYSIS.—We used simple and multiple linear regressions to test the effects of turnover rate and stem density on tree species richness. Species richness data did not deviate significantly from normality ($P > 0.05$; Wilk–Shapiro test) and so were not transformed. Data from the initial census of 66 plots were used to test the relationship between stem density and tree richness. To test effects of turnover on tree diversity, a subset of 27 forest-interior plots were used, because the remaining plots were part of a large-scale experiment on forest fragmentation and were substantially altered by edge and matrix effects (Laurance *et al.* 1998a, b, 2006).

We estimated stand dynamics by calculating tree turnover rates, using data from five consecutive censuses during 1981–2003 (Laurance *et al.* 2009). For each census, turnover was the average of annualized tree mortality and recruitment rates; where mortality = $(\log[N1] - \log[N2])/(\text{time2} - \text{time1})$, $N1$ is the number of individuals alive in the first census, $N2$ is the number of live individuals (excluding new recruits) in the following census, and time2 and time1 are the respective census dates (in year); and where recruitment = $(\log[N2] - \log[N1])/(\text{time2} - \text{time1})$, $N2$ is the number of live individuals (including new recruits) in the second

census, and the other parameters are as defined above. Mortality and recruitment rates were calculated with the statistical package R 2.21 (http://www.R-project.org), using modified functions from the Center for Tropical Forest Studies (http://ctfs.si.edu) and (Condit *et al.* 2006). Census intervals were 3.5–7.9 yr, and to minimize bias associated with varying interval length we used a correction factor when calculating mortality and recruitment: $\lambda_{\text{corr}} = \lambda t^{0.08}$, where λ is the rate and t is the census interval in years (Lewis *et al.* 2004). When testing effects of turnover on tree diversity, we used mean values (averaged across the five censuses, and weighted by census-interval length) for each plot.

For each plot, temporal variability in turnover rates was examined by testing the relationship between mean turnover and the coefficient of variation (CV) of turnover among the four census intervals. We also assessed the effect of turnover on the number and species richness of 'pioneer' trees in our plots, averaged across censuses, using data on 52 species in the key early-successional genera (*Annona*, *Bellucia*, *Cecropia*, *Croton*, *Goupia*, *Jacaranda*, *Miconia*, *Pourouma*, *Vismia*) in our study area (Laurance *et al.* 2006).

Finally, in addition to our central-Amazonian landscape, we extended our analysis of turnover effects on tree species richness to include data from other Amazonian and tropical sites, using data in Phillips *et al.* (1994); we eliminated one anomalous, low-diversity Amazonian plot dataset that occurred in a waterlogged swamp; all the remaining plots were in *terra firme* forest. For all plots, we calculated tree species richness using a standard sample of 500 randomly selected stems, and we also corrected all turnover estimates to account for varying census-interval lengths (Lewis *et al.* 2004). We incorporated 10 of our plots into this analysis, selected by stratified random sampling (by dividing our study area into 10 blocks and then randomly selecting one plot from each block).

RESULTS

DIVERSITY AND TURNOVER.—Stem density across all 66 plots averaged 611 ± 54 (mean $\pm$ SD) stems/ha (range: 521–750 stems/ha), whereas mean species richness was 263 ± 19 species/ha (range: 226–329). The plot with 329 species is, to our knowledge, the highest tree diversity recorded anywhere (for stems ≥ 10 cm dbh). Fisher's α values, which are little influenced by sample size, averaged 177 ± 25 (range: 114–228) for the 66 plots. Stem density was a positive predictor of tree-species richness ($F_{1,64} = 7.17$, $R^2 = 10.1\%$, $P = 0.009$; linear regression), although there was considerable scatter around the fitted regression line, especially for plots with higher stem numbers (Fig. 1).

Among the 27 forest-interior plots, tree turnover rates averaged 1.27 ± 0.30 percent/yr (range: 0.71–1.81%/yr). For each plot, the mean turnover rate was a strong predictor of mean species richness ($F_{1,25} = 9.10$, $R^2 = 26.7\%$, $P = 0.006$; linear regression). However, the slope of the relationship was unexpectedly negative, rather than positive (Fig. 2).

ALTERNATIVE HYPOTHESES.—Because the negative relationship between turnover and species richness (Fig. 2) was opposite to that observed elsewhere (Phillips *et al.* 1994, ter Steege *et al.* 2006), we
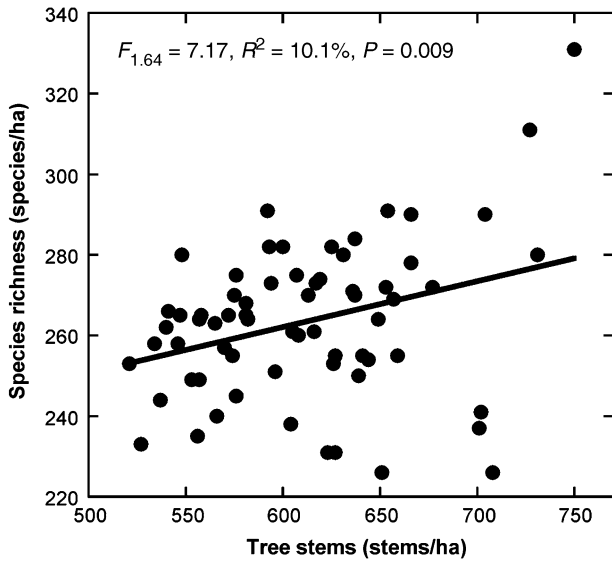
FIGURE 1. Relationship between stem density and species richness across 66 1-ha plots in central Amazonian rain forest.

evaluated three possible explanations for the pattern. First, might plots with high turnover have lower species richness simply because they have fewer stems? Turnover had no significant effect on mean stem density per plot ($F_{1,25} = 0.76$, $R^2 = 2.9\%$, $P = 0.39$; linear regression). Moreover, stem density was not significant ($P = 0.37$) when included along with turnover as a potential predictor of species richness in a multiple-regression model, nor was it significantly correlated with richness when effects of variation in turnover were removed with a partial correlation analysis ($r = -0.183$, df = 24,

$P = 0.36$). The reverse, however, was not true: when effects of variation in stem number were removed with a partial correlation, turnover remained a strong and negative correlate of tree species richness ($r = -0.537$, df = 24, $P = 0.004$). Thus, the negative relationship between turnover and species richness did not occur because plots with high turnover had fewer stems.

Second, high turnover might depress species richness if occasional, intense tree-mortality events (such as those from windstorms of local floods) drive local species losses. If this were occurring, we reasoned, then plots with high average turnover should exhibit elevated variability in turnover among different census intervals as a consequence of major pulses of mortality and recruitment. Turnover, however, did not appear to be temporally more variable in plots with high turnover rates: among the 27 plots, there was no significant relationship between mean turnover and the CV of turnover rates ($F_{1,25} = 0.58$, $R^2 = 2.2\%$, $P = 0.45$; linear regression).

Finally, high turnover might depress species richness if it: (1) leads to an increase in pioneer trees at the expense of non-pioneers; and (2) pioneers are species poor, relative to the non-pioneer trees they replace. Plots with higher turnover did have more pioneer stems ($F_{1,25} = 6.70$, $R^2 = 21.1\%$, $P = 0.016$) and species ($F_{1,25} = 3.18$, $R^2 = 11.3\%$, $P = 0.087$), and clearly had fewer non-pioneer species ($F_{1,25} = 10.8$, $R^2 = 30.1\%$, $P = 0.003$); however, there was no clear tradeoff in the abundances of pioneer vs. non-pioneer stems ($F_{1,25} = 1.27$, $R^2 = 4.8\%$, $P = 0.27$; linear regressions), suggesting that pioneers (which comprised just 0.2–8.3% of all stems per plot) did not depress the abundance of non-pioneers. Furthermore, across all 27 plots, pioneers had a significantly ($P < 0.0001$; Mann–Whitney U test) higher species-richness-to-stem ratio (0.65 ± 0.18) than did non-pioneers (0.43 ± 0.4), indicating that, at least at the low abundances at which they occurred in our plots, pioneers were not species poor relative to non-pioneers. Hence, modest increases in pioneers with increasing turnover did not explain the negative turnover–tree diversity relationship, and, if anything, would have tended to counteract this relationship slightly.

TURNOVER AND DIVERSITY AT LARGER SPATIAL SCALES.—We reexamined the relationships between tree turnover and species richness across Amazonia (Fig. 3A) and the tropics as a whole (Fig. 3B), by adding a stratified-random sample of 10 of our plots to the original analysis of Phillips *et al.* (1994). Using these augmented datasets, we found no significant relationship between tree turnover and species richness for either Amazonia ($F_{1,19} = 1.96$, $R^2 = 9.3\%$, $P = 0.18$) or the tropics as a whole ($F_{1,32} = 0.01$, $R^2 = 0.0\%$, $P = 0.92$; linear regressions).

DISCUSSION

PATTERNS IN CENTRAL AMAZONIA.—Despite its nutrient-impoverished soils, central Amazonia sustains some of the most species-rich tree communities on earth. An earlier analysis of three 1 ha plots in our study area revealed an average of 285 tree species/ha (≥ 10 cm dbh; Oliveira & Mori 1999). With a larger sample size (66 1 ha plots) spanning a considerably larger area (Bolhman *et al.* 2008), we
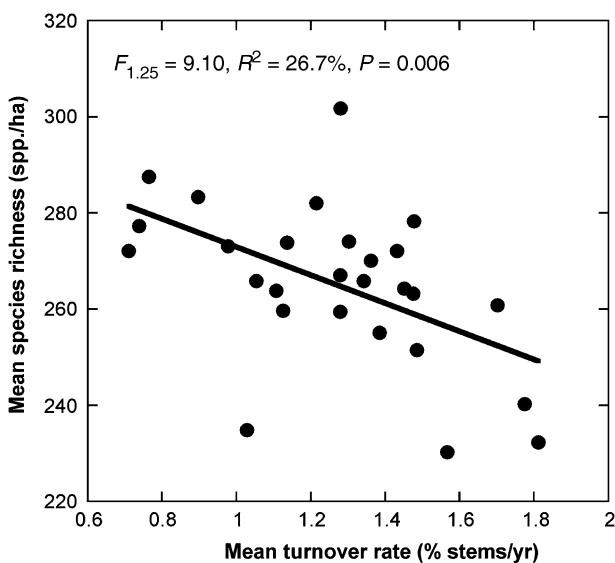

FIGURE 2. Relationship between stand dynamism (mean tree-turnover rate from five censuses from 1979 to 2003, adjusted for census-interval length) and mean tree-species richness for 27 forest-interior plots in central Amazonia.
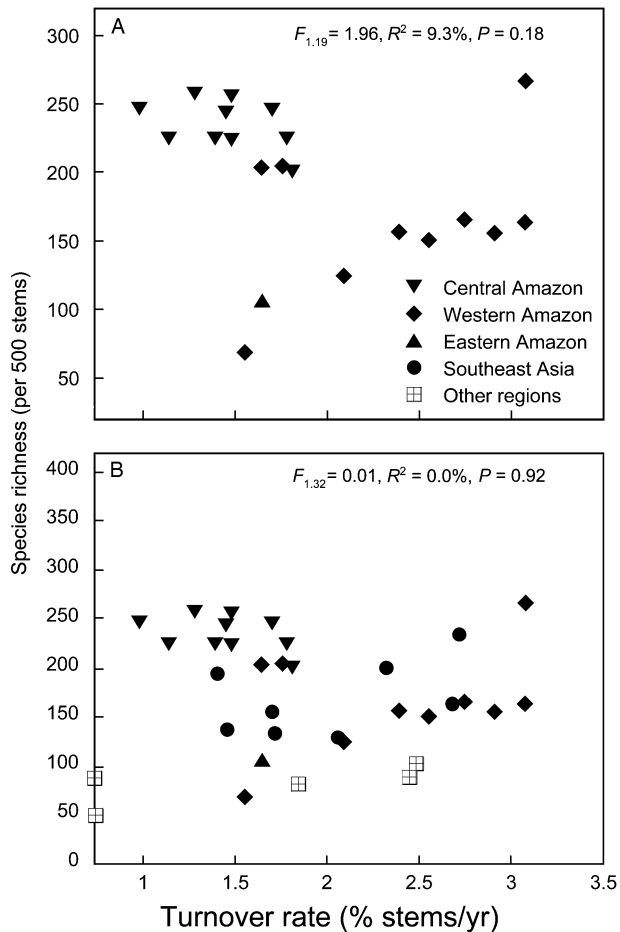
FIGURE 3. Relationship between stand dynamism (tree turnover rate) and species richness per 500 stems for (A) Amazon sites and (B) tropical forest sites globally. Data are from Phillips *et al.* (1994), with the exception of 10 randomly selected plots from our study in central Amazonia. Turnover rates were adjusted to compensate for varying census-interval lengths.

detected slightly lower species richness on average (263 species/ha), but found that richness varied considerably among plots (226–329 species/ha). To pack so many species into a 1 ha plot, rarity becomes the norm, with singletons constituting 56 percent of the species on average in each plot. Thus, in our study area, tree communities are exceptionally diverse but somewhat variable in species richness and dominated by locally rare species.

In general, tree turnover in terra firme forests of central Amazonia is quite low (averaging just 1.27%/yr) compared with sites elsewhere in the tropics (*e.g.*, > 2% in western Amazonia and Central America; Phillips *et al.* 1994, 2004; Condit *et al.* 1999, Laurance *et al.* 2009). This seems largely attributable to low soil fertility and relatively infrequent disturbances from wind and other factors, which promote slow growth, reduced competition, and generally high longevity of tree species in our study area (Laurance *et al.* 2004). Primary forests in central Amazonia sustain many old trees, with maximum longevities for some species exceeding a millennium (Chambers *et al.* 1998, Laurance *et al.* 2004, Vieira *et al.*

2005). Under such apparently stable conditions, canopy gaps are quite rare and most species are shade-tolerant and adapted for low rates of forest disturbance.

During our 23-yr study, turnover rates explained a relatively high proportion (27%) of the variability in tree species richness but unexpectedly had a negative, rather than positive, slope (Fig. 2). We found no support for three plausible explanations for this pattern. First, there was no evidence that plots with higher turnover had fewer species simply because they had fewer tree stems. In fact, turnover did not influence stem number significantly, although plots with more stems did tend to support more tree species (Fig. 1).

Second, we found no compelling evidence that tree diversity was being reduced by major, short-term pulses of tree mortality. In Amazonian forests, small-scale flooding (Mori & Becker 1991) and downbursts from convectional thunderstorms (Nelson *et al.* 1994) can cause heavy but highly localized tree mortality, and such events could lead to elevated tree turnover and, potentially, a loss of local tree diversity. Intense mortality events, however, would lead to strong spikes in tree mortality and recruitment, as observed in some fragmented forests in our study area (Laurance *et al.* 1998a, b). Such spikes would cause plots with high mean turnover to exhibit high temporal variability in turnover among different censuses of the plot (Laurance *et al.* 2009). The fact that we observed no such pattern (the mean and CV of turnover in each plot were not significantly correlated) militates against such an interpretation.

Finally, elevated turnover could potentially affect tree diversity by shifting community composition toward successional and canopy species that require treefall gaps for germination and/or growth into larger size-classes, and against shade-tolerant subcanopy species that decline as forest disturbance increases (Laurance *et al.* 2006). In communities in which old growth species are competitively dominant, some level of disturbance could help to promote local diversity, by allowing pioneers to persist (Connell 1978). However, species richness would likely decline with rising turnover if successional trees are species poor and tend to replace more-diverse assemblages of old growth species (Pitman *et al.* 2002). We found little support for this latter proposition under the relatively low rates of turnover observed in our study area. Under these circumstances pioneer trees were generally rare (just 2.5% of all stems on average) and a small increase in pioneers tended, if anything, to increase local tree diversity slightly.

PATTERNS ACROSS AMAZONIA AND THE TROPICS.—Whatever the reason for the negative relationship between tree turnover and diversity (Fig. 2), it clearly contrasts with some earlier tropical studies, where the highest-diversity forests were detected at sites with high net productivity and turnover (Phillips *et al.* 1994, Givnish 1999, ter Steege & Hammond 2001). Moreover, when we added data from a random subset of our plots to those evaluated by Phillips *et al.* (1994), we found no significant relationship between tree turnover and species richness for either Amazonian forests (Fig. 3A) or tropical forests globally (Fig. 3B).

Our findings suggest it is premature to conclude that increasing turnover generally enhances tropical forest diversity. When

making broad comparisons across different studies and locales, the relationship between turnover and tree diversity could be complicated by factors such as limited or inadequate sampling, varying spatial scales of analysis, varying census-interval lengths, and differing measures of disturbance used by different investigators (Phillips *et al.* 1994, Mackay & Currie 2001, Lewis *et al.* 2004). At large spatial scales, confounding factors such as environmental heterogeneity and varying sizes of the local or regional species pool might also complicate the relationship between turnover and species richness. Furthermore, studies that assess the effects of turnover on tree diversity do so based on forest-dynamics data collected over just a few decades. Given that some trees live for many centuries, one must implicitly assume that conditions observed during the course of the study reasonably mirror long-term trends at each site. If this assumption is violated, then the relationship between tree diversity and turnover could be altered.

These various complications seem to underlie in part the widely varying effects of disturbance on species diversity seen in different studies (Mackay & Currie 2001, Shea *et al.* 2004), and might explain why the negative turnover–diversity relationship apparent in our central-Amazonian landscape (Fig. 2) became nonsignificant at Amazon-wide and pantropical scales (Fig. 3). In our study, which encompassed a single, relatively homogeneous study area, one can at least assume that major climatic events, such as past droughts, would have affected trees in all plots quite similarly, and that other potentially confounding factors, such as the size of the regional tree-species pool, were minimal.

In our view, a combination of factors, such as the vast Amazonian species pool that enhances local diversity (Terborgh 1973, Ricklefs 2004), possible mid-domain effects (Colwell & Lees 2000), and a mixing of different regional floras (Oliveira & Daly 1999), collectively underlay the very high local diversity of central Amazonian forests. Across our landscape, some of the among-plot variability in tree diversity we encountered can be explained by local soil and topographic features, with higher diversity occurring on more-fertile, better-drained soils (Laurance *et al.* in press). At this spatial scale we found no support for the idea that increasing turnover enhances local tree diversity, and some evidence to the contrary (Fig. 2). We believe that further comparative studies are needed—especially those that factor out potentially confounding environmental and historical factors—before we can infer a general relationship between forest dynamism and tropical tree diversity.

ACKNOWLEDGMENTS

LITERATURE CITED

BOLHMAN, S. A., W. F. LAURANCE, S. G. W. LAURANCE, H. E. M. NASCIMENTO, P. M. FEARNSIDE, AND A. ANDRADE. 2008. Importance of soil, topography, and geographic distance in structuring central Amazonian tree communities. J. Veg. Sci. 19: 863–874.

CHAMBERS, J. Q., N. HIGUCHI, AND J. P. SCHIMEL. 1998. Ancient trees in Amazonia. Nature 391: 135–136.

CHAUVEL, A., Y. LUCAS, AND R. BOULET. 1987. One the genesis of the soil mantle of the region of Manaus, central Amazonia, Brazil. Experientia 43: 234–240.

COLWELL, R. K., AND D. C. LEES. 2000. The mid-domain effect: Geometric constraints on the geography of species richness. Trends Ecol. Evol. 15: 70–76.

CONDIT, R., P. ASHTON, S. BUNYAVEJCHEWIN, H. DATTARAJA, S. DAVIES, S. ESUFALI, C. EWANGO, R. FOSTER, U. GUNATILLEKE, C. GUNATILLEKE, P. HALL, K. HARMS, T. HART, C. HERNANDEZ, S. P. HUBBELL, A. ITOH, S. KIRATIPRAYOON, J. LAFRANKIE, S. LAO, J. MAKANA, M. NOOR, A. KASSIM, S. RUSSO, R. SUKUMAR, C. SAMPER, H. SURESH, S. TAN, S. THOMAS, R. VALENCIA, M. VALLEJO, G. VILLA, AND T. ZILLIO. 2006. The importance of demography niches to tree diversity. Science 313: 98–101.

CONDIT, R., P. ASHTON, N. MANOKARAN, J. LAFRANKIE, S. P. HUBBELL, AND R. B. FOSTER. 1999. Dynamics of the forest communities at Pasoh and Barro Colorado: Comparing two 50 ha plots. Philos. Trans. R Soci. Lond. B 82: 865–872.

CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1309.

DENSLOW, J. S. 1995. Disturbance and diversity in tropical rain forests: The density effect. Ecol. Appl. 5: 962–968.

DUIVENVOORDEN, J. 1996. Patterns of tree species richness in rain forests of the middle Caqueta area, Colombia. Biotropica 28: 142–158.

GENTRY, A. H. 1988. Tree species richness of upper Amazonian forests. Proc. Nat. Acad. Sci. U.S.A. 85: 156–159.

GIVNISH, T. J. 1999. On the causes of gradients in tropical tree diversity. J. Ecol. 87: 193–210.

LAURANCE, S. G., W. F. LAURANCE, H. E. M. NASCIMENTO, A. ANDRADE, P. M. FEARNSIDE, E. REBELLO, AND R. CONDIT. 2009. Long-term variation in Amazon forest dynamics. J. Veg. Sci. 20: 323–333.

LAURANCE, S. G. W., W. F. LAURANCE, A. ANDRADE, P. M. FEARNSIDE, K. HARMS, A. VINCENTINI, AND R. C. C. LUIZAO. In press. Influence of soils and topography on Amazonian tree diversity: A landscape-scale study. J. Veg. Sci.

LAURANCE, W. F., L. V. FERREIRA, J. M. RANKIN-DE MERONA, AND S. G. LAURANCE. 1998a. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology 79: 2032–2040.

LAURANCE, W. F., L. V. FERREIRA, J. M. RANKIN-DE MERONA, S. G. LAURANCE, R. W. HUTCHINGS, AND T. E. LOVEJOY. 1998b. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. Conserv. Biol. 12: 460–464.

LAURANCE, W. F., H. NASCIMENTO, S. G. LAURANCE, A. ANDRADE, J. RIBEIRO, J. GIRALDO, T. E. LOVEJOY, R. CONDIT, J. CHAVE, AND S. D'ANGELO. 2006. Rapid decay of tree-community composition in Amazonian forest fragments. Proc. Nat. Acad. Sci. U.S.A. 103: 19010–19014.

LAURANCE, W. F., H. NASCIMENTO, S. G. LAURANCE, R. CONDIT, S. D'ANGELO, AND A. ANDRADE. 2004. Inferred longevity of Amazonian rain forest trees based on a long-term demographic study. For. Ecol. Manag. 190: 131–143.

LAURANCE, W. F., A. A. OLIVEIRA, S. G. W. LAURANCE, R. CONDIT, C. W. DICK, A. ANDRADE, H. E. M. NASCIMENTO, T. E. LOVEJOY, AND J. E. RIBEIRO. 2005. Altered tree communities in undisturbed Amazonian forests: A consequence of global change? Biotropica 37: 160–162.

LEIGH, E. G. 2008. Tropical forest ecology: Sterile or virgin for theoreticians? *In* W. P. Carson and S. Snitzer (Eds.). Tropical rain forest community ecology, pp: 121–142. Wiley-Blackwell, Oxford, UK.

Lewis, S. L., O. L. Phillips, D. Sheil, B. Vincenti, T. R. Baker, S. Brown, A. W. Graham, N. Higuchi, D. W. Hilbert, W. F. Laurance, J. Lejoly, Y. Malhi, A. Monteagudo, V. P. Nunez, B. Sonke, M. N. Nur Supardi, J. W. Terborgh, and V. R. Martinez. 2004. Tropical forest tree mortality, recruitment and turnover rates: Calculation, interpretation and comparison when census intervals vary. J. Ecol. 92: 929–944.

Mackay, R. L., and D. J. Currie. 2001. The diversity-disturbance relationship: Is it generally strong and peaked? Ecology 82: 3479–3492.

Mori, S. A., and P. Becker. 1991. Flooding affects survival of Leythidaceae in terra firme forest near Manaus, Brazil. Biotropica 23: 87–90.

Nee, M. 1995. Flora Preliminar do Projeto Dinâmica Biológica de Fragmentos Florestais (PDBFF). New York Botanical Gardens and INPA/SI.

Nelson, B. W. 1994. Natural forest disturbance and change in Brazilian Amazon. Remote Sens. Rev. 10: 105–125.

Nelson, B. W., V. Kapos, J. B. Adams, W. J. Oliviera, O. P. G. Braun, and I. L. Do Amaral. 1994. Forest disturbance by large blow downs in the Brazilian Amazon. Ecology 75: 853–858.

Oliveira, A. A., and D. C. Daly. 1999. Geographic distribution of tree species occurring in the region of Manaus, Brazil: Implications for regional diversity and conservation. Biodiv. Conserv. 8: 1245–1259.

Oliveira, A. A., and S. Mori. 1999. A central Amazonian terra firme forest I. High tree species richness on poor soils. Biodiv. Conserv. 8: 1219–1244.

Pennington, T. D. 1990 Sapotaceae. Flora Neotropical Monograph 52.

Phillips, O. L., T. R. Baker, L. Arroyo, N. Higuchi, T. J. Killeen, W. F. Laurance, S. L. Lewis, J. Lloyd, Y. Malhi, A. Monteagudo, D. A. Neill, P. N. Vargas, J. N. M. Silva, J. Terborgh, R. V. Martinez, M. Alexiades, S. Almeida, S. Brown, J. Chave, J. A. Comiskey, C. I. Czimczik, A. Di Fiore, T. Erwin, C. Kuebler, S. G. Laurance, H. E. M. Nascimento, J. Olivier, W. Palacios, S. Patiño, N. C. A. Pitman, C. A. Quesada, M. Saldias, A. Torres Lezama, and B. Vinceti. 2004. Pattern and process in Amazon tree turnover, 1976–2001. Phil. Trans. R. Soc. Lond. B 359: 381–407.

Phillips, O. L., and A. H. Gentry. 1994. Increasing turnover through time in tropical forests. Science 263: 954–958.

Phillips, O. L., P. Hall, A. H. Gentry, A. S. Sawyer, and R. Vasquez. 1994. Dynamics and species richness of tropical rain forests. Proc. Nat. Acad. Sci. U.S.A. 91: 2805–2809.

Piperno, D. R., and P. Becker. 1997. A vegetational history of a site in the central Amazon basin derived from phytolith and charcoal records from natural soils. Quartern. Res. 45: 202–209.

Pitman, N., J. Terborgh, M. Silman, V. P. Nunez, D. A. Neill, C. Ceron, W. Palacios, and M. Aulestia. 2002. A comparison of tree species diversity in two upper Amazonian forests. Ecology 83: 3210–3224.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecol. Lett. 7: 1–15.

Ricklefs, R. E., R. E. Latham, and H. Qian. 1999. Global patterns of tree species richness in moist forests: Distinguishing ecological influences and historical contingency. Oikos 86: 369–373.

Shea, K., S. H. Roxburgh, and E. S. J. Rauschert. 2004. Moving from pattern to process: Coexistence mechanisms under intermediate disturbance regimes. Ecol. Lett. 7: 491–508.

ter Steege, H., and H. S. Hammond. 2001. Character convergence, diversity and disturbance in tropical rain forest in Guyana. Ecology 82: 3197–3212.

ter Steege, H., N. Pitman, O. Phillips, J. Chave, D. Sabatier, A. Duque, J.-F. Molion, M.-F. Prevost, R. Spichiger, H. Castellanos, P. von Hildebrand, and R. Vasquez. 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. Nature 443: 444–447.

ter Steege, H., N. Pitman, D. Sabatier, H. Castellanos, P. Van der Hout, D. C. Daly, M. Silveira, O. Phillips, R. Vasquez, T. Van Andel, J. Duivenvoorden, A. A. Oliveira, R. Ek, R. Lilwah, R. Thomas, J. Van Essen, C. Baider, P. Maas, S. Mori, J. W. Terborgh, V. P. Nunez, H. Mogollon, and W. Morawetz. 2003. A spatial model of tree α-diversity and tree density for the Amazon. Biodiv. Conserv. 12: 2255–2277.

Terborgh, J. 1973. On the notion of favorableness in plant ecology. Am. Nat. 107: 481–501.

Vieira, S., S. Trumbore, P. B. Camargo, D. Selhorst, J. Q. Chambers, N. Higuchi, and L. A. Martinellis. 2005. Slow growth rates of Amazonian trees: Consequences for carbon cycling. Proc. Nat. Acad. Sci. U.S.A. 102: 18502–18507.