

COMMENTARY

Altered Tree Communities in Undisturbed Amazonian Forests: A Consequence of Global Change?¹**William F. Laurance²**

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NELSON (2005) HAS PROVIDED A THOUGHT-PROVOKING CHALLENGE to our recent suggestion that pervasive changes in central Amazonian tree communities were most likely caused by global- or regional-scale drivers, such as increasing atmospheric CO₂ concentrations (Laurance *et al.* 2004a). We are pleased to participate in this exchange of views because we believe it is of general relevance for those attempting to understand the causes and consequences of long-term changes in tropical forest communities.

In our recent paper, we described three distinctive alterations in apparently undisturbed tree communities in central Amazonia: (1) positively correlated shifts in tree community composition across 18 one-hectare plots spanning an area of about 300 km², with faster-growing canopy and emergent genera (but not pioneers) generally increasing at the expense of slower-growing subcanopy genera; (2) accelerated growth in the 1990s relative to the 1980s for the large majority (87%) of tree genera in our plots; and (3) accelerated tree community dynamics (mortality and recruitment) in the 1990s relative to the 1980s (Laurance *et al.* 2004a,b).

We interpreted these changes as being consistent with an ecological “signature” expected from increasing forest productivity (cf., Phillips & Gentry 1994, Lewis *et al.* 2004a,b, Phillips *et al.* 2004). Further, we suggested that global or regional scale changes, such as increased plant fertilization driven by rising atmospheric CO₂ levels, elevated nutrient deposition from ash produced by regional forest fires, and/or reduced tropical cloudiness, were the most plausible causes (Laurance

et al. 2004a). Nelson (2005), however, suggests that natural or local mechanisms might better explain the pervasive changes we detected. Although not implausible, the mechanisms he describes, we believe, are unlikely to account for the three distinctive trends we observed.

It is highly unlikely that past forest fires could account for the suite of observed changes. Nelson is correct that soil charcoal is relatively common in our study area, as we have previously emphasized (Laurance 2001, Laurance *et al.* 2004b), but both of the studies he cited (Piperno & Becker 1996, Santos *et al.* 2000) concluded that the large majority of charcoal was created at least 1100–1500 yr ago (minus the age of burned trees, which have a mean carbon residence time of 80 yr in our forests; Chambers *et al.* 1998). Detailed phytolith (plant fragment) studies suggest that these past fires were natural in origin (Piperno & Becker 1996) and, judging from the virtual absence of burnt phytoliths, that they caused relatively little forest damage (D. R. Piperno, pers. comm.). Moreover, the complex old-growth forest structure (Laurance 2001), extremely high tree diversity (Oliveira & Mori 1999), and, especially, the high incidence of old (500–1000 yr-old) trees in our study plots (Laurance *et al.* 2004b), all suggest that fires during the past millennium had only patchy, limited effects on forest structure and composition. Finally, although recovery from past fires might plausibly promote shifts in tree community composition (trend 1), it could not explain accelerating tree growth (trend 2) and community dynamics (trend 3).

Nelson also suggests that collecting herbarium specimens might increase mortality among old-growth subcanopy trees, which are strongly energy limited. Notably, a previous study concluded that collecting vouchers in tropical forests (including tree climbing with spiked ascenders that can cause >400 small wounds to the tree trunk) did not

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increase overall tree mortality (although the authors did not explicitly assess mortality among different size classes of trees; Phillips *et al.* 1998). Moreover, our field-sampling methods were usually far less damaging to trees than Nelson implies: (1) for most trees, leaf samples were collected from a single branchlet (flowers or fruits were collected from just one to two individuals of each species); (2) only a limited subset of all trees (<20%) were slashed on the lower trunks to examine bark features, with slashes typically being small (<15 cm²) and superficial (<1 cm deep); and (3) ascended trees were climbed only with cloth ankle bands and rubber-soled shoes, not with spiked ascenders.

If botanical collecting had a significant impact on tree composition, then tree mortality rates should have peaked soon after the initial census of each plot, then declined afterward. In fact, we observed the opposite trend—mortality rates increased over time in our plots (trend 3), a pattern seen at many other sites in Amazonia (Phillips & Gentry 1994, Phillips *et al.* 2004). In fact, old-growth subcanopy trees, which generally have dense, strong wood to withstand recurring damage from litterfall (Thomas 1996, Laurance *et al.* 2004b), may actually be relatively robust to minor physical damage. If they are not, then the enhanced mortality effect that Nelson proposes should plague many permanent-plot studies, not just ours. We are aware of no evidence to this effect.

Forest flooding and soil saturation in 1989 are also unlikely to explain the trends we observed, despite the fact that such floods clearly can cause localized tree mortality (Mori & Becker 1991). First, flood-prone microhabitats (gully bottoms and plateau depressions) are very limited in extent in our 18 study plots, constituting <5 percent of the total area (W. F. Laurance *et al.*, unpublished data). Second, wet-season rains in 1989 were indeed heavy (1887 mm), but the pattern is less striking than Nelson suggests (based on Instituto Nacional de Meteorologia records for Manaus). For example, from 1968 to 2000, 6 yr had wet-season rainfall that was >90 percent of that in 1989, and

14 yr had >80 percent of that rainfall (Fig. 1). Moreover, while it is true that May of 1989 was an exceptionally wet month (555 mm of rain, three standard deviations above the mean for the 1910–2000 interval), even wetter months (also over three standard deviations above the norm) were recorded in March of 1968 (633 mm), February of 1993 (619 mm), and January of 1996 (570 mm). Collectively, these data suggest that most forest microhabitats that flooded in 1989 would also have flooded in preceding and subsequent years, greatly reducing the likelihood that a single, marginally wetter year would have had exceptional effects on tree communities. In addition, flooding could not explain the strongly accelerated tree growth observed in our study.

Finally, although our study area receives occasional windbursts from convective storms, we doubt that wind damage caused the observed trends. First, strong winds are probably more likely to cause population declines of canopy and emergent trees than of subcanopy trees (Laurance *et al.* 2000)—the opposite of the pattern we observed. Second, disturbance-adapted pioneer trees were uncommon in our plots (<2.6% of all stems of ≥10 cm diameter at breast height), which seems unlikely if wind disturbance was pervasive. Third, observed changes in tree communities were not concentrated in one or a few clusters of plots, as would be expected from convective storm damage, which is patchy at a landscape scale (Nelson 1994, Nelson *et al.* 1994). This is illustrated by the fact that, for the 115 tree genera considered in our original analysis (Laurance *et al.* 2004a), nearby plots in our study area did not show more similar patterns of floristic change over time (*i.e.*, stronger positive correlations between changes in densities of the 115 genera) than did more distant plots ($P = 0.92$, Mantel test). In addition to poorly accounting for the observed population trends, wind disturbance would not cause the strongly accelerated tree growth that we observed.

Although we disagree with his assertions, Nelson’s insightful challenge has stimulated a useful scientific discourse about the mechanisms underlying apparently rapid, forest-wide changes in Amazonian tree communities. Unfortunately, current efforts to assess the potential effects of rapidly rising atmospheric CO₂ levels and other global change phenomena on tropical forests are being conducted at two enormously different spatial scales. On the one hand are small-scale lab or open-top chamber studies that experimentally manipulate CO₂ concentrations, but that necessarily focus on tree seedlings or saplings, rather than mature trees, and on just one or a few species (*e.g.*, Reekie & Bazzaz 1989, Norby *et al.* 1999, Winter & Lovelock 1999). On the other hand are permanent-plot studies (*e.g.*, Phillips & Gentry 1994, Laurance *et al.* 2004a, Lewis *et al.* 2004b, Phillips *et al.* 2004), which assess changes in complex, mature forests at much larger spatial scales, but which lack any form of control over ambient environmental or climatic conditions.

Between these two extremes lies an enormous gulf. An important link, we believe, would be to implement a replicated Free Air Carbon dioxide Enrichment (FACE) experiment (*e.g.*, Allen *et al.* 2000) to manipulate CO₂ concentrations in mature tropical forests. To date, there is not a single FACE experiment in a natural tropical forest. Although expensive and logistically challenging, a replicated FACE experiment may provide the only direct means to evaluate the effects of elevated CO₂ on tropical forest composition, growth, and dynamics, separately from the confounding effects of other environmental changes. FACE experiments are not a panacea, and suffer from some important limitations (*e.g.*, Schulze & Mooney 1994). However, without such an experimental approach, the results of permanent-plot studies—with their many

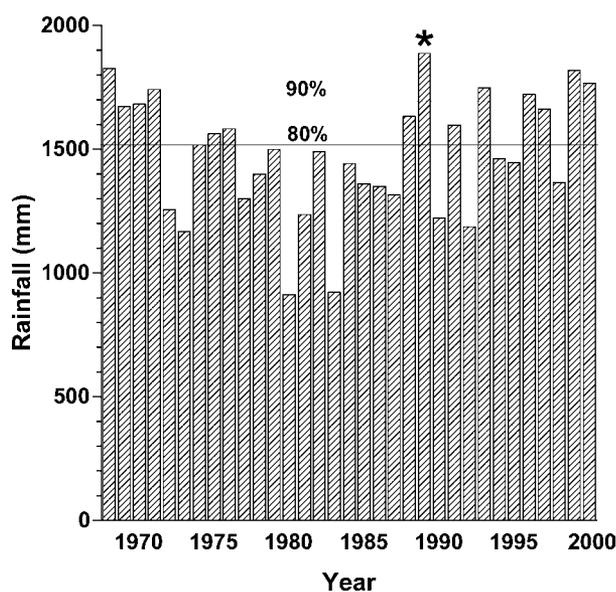


FIGURE 1. Peak wet-season rainfall (first 5 mo of each year) at Manaus, Brazil from 1968 to 2000. The asterisk indicates 1989, an unusually wet year, whereas the horizontal lines show 90 percent and 80 percent of the 1989 rainfall.

uncontrolled environmental factors—will inevitably be the subject of debate.

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