

Late twentieth-century trends in tree-community composition in an Amazonian forest

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The rainforests of central Amazonia are some of the most species-rich tree communities on earth. Our analyses suggest that, in recent decades, forests in a central Amazonian landscape have experienced highly non-random changes in dynamics and composition. These analyses are based on a network of 18 permanent plots unaffected by any detectable disturbance. Within these plots, tree mortality, recruitment, and growth have increased over time. Of 115 relatively abundant tree genera, 27 changed significantly ($P \leq 0.01$) in density or basal area—a value nearly 14 times greater than that expected by chance. An independent, 8-yr study in nearby forests corroborates these shifts in composition. Despite increasing tree mortality, pioneer trees did not increase in abundance. However, genera of faster growing trees, including many canopy and emergent species, are increasing in dominance or density, whereas genera of slower growing trees, including many subcanopy species, are declining. Rising atmospheric CO₂ concentrations may explain these changes, although the effects of this and other large-scale environmental alterations have not been fully explored. These compositional changes could potentially have important effects on the carbon storage, dynamics, and biota of Amazonian forests.

Introduction

Are global-change phenomena altering Amazonian forests? Recent studies suggest that undisturbed Amazonian forests have become increasingly dynamic in the past few decades, with higher rates of tree mortality and turnover (Phillips and Gentry 1994; Phillips *et al.* 2004). In addition, carbon storage (Grace *et al.* 1995a; Malhi *et al.* 1998; Phillips *et al.* 1998b; Baker *et al.* 2004b) and productivity (Lewis *et al.* 2004b) in these forests appear to be increasing. Finally, lianas—climbing woody vines that often favour disturbed forest—evidently are increasing in size and abundance (Phillips *et al.*

2002). Possible evidence for such changes comes not only from plot-based studies but also from remote-sensing imagery; an indicator of primary productivity, the normalized difference vegetation index, increased markedly in South American rainforests from 1981–2000 (Paruelo *et al.* 2004).

The causes of these changes are controversial. One prominent suggestion is that the changes arise from increasing plant fertilization caused by rising atmospheric CO₂ concentrations, which is expected to increase forest dynamism and productivity (Reekie and Bazzaz 1989; Phillips and Gentry 1994; Winter and Lovelock 1999; IPCC 2001). However,

other large-scale phenomena, such as alterations in regional temperature (Clark *et al.* 2003), rainfall (Condit *et al.* 1996a; Tian *et al.* 1998), available solar radiation (Wielicki *et al.* 2002), or nutrient deposition (Artaxo *et al.* 2003) might also account for some observations (Lewis *et al.* 2004a). It is also not inconceivable that local or natural phenomena, including past disturbances or sampling artefacts, could contribute to, or even generate at least some of the observed patterns (e.g. Clark 2002a, 2004; Nelson 2005).

Until recently, no studies had assessed whether Amazonian tree communities were changing in taxonomic or functional composition, in concert with observed alterations in productivity and dynamics. We recently conducted the first analysis of this nature, using a long-term (11–18 yr) dataset from permanent plots in a central Amazonian landscape (Laurance *et al.* 2004a). Here we summarize these findings and highlight their potential implications for the ecological functioning of Amazonian forests.

Methods

Study area and field methods

The study area is part of the Biological Dynamics of Forest Fragments Project (BDFFP), a long-term experimental investigation of habitat fragmentation in central Amazonia (Lovejoy *et al.* 1986). A key component of the BDFFP is a network of 66 1-ha forest-dynamics plots in fragmented and intact forest. The present study involves a subset of these plots: 18 discrete plots in lowland *terra firme* forest that span an area of about 300 km², are randomly located with respect to local topography, and are positioned at least 300 m away from any clearing to avoid edge effects (Laurance *et al.* 1997, 1998b, 2000). The plots exhibited no evidence of current or past disturbance from logging, fires, or hunting, although two plots experienced small wet-season floods that caused temporary increases in tree mortality (Laurance *et al.* 2004a).

The 18 plots were established from 1981 to 1987 and recensused at roughly 5-yr intervals for an average of 15.0 yrs (range = 11.4–18.2 yrs), with the final

census of each in 1999 or 2000. Within each plot, all trees (≥ 10 cm d.b.h. [diameter-at-breast-height]) were marked with permanent tags, mapped, measured for trunk diameter (above any buttresses, if present), and identified on the basis of sterile or fertile material. In total, nearly 13,700 trees were recorded (Laurance *et al.* 2004a).

Data analysis

We assessed changes in tree-community composition over time by contrasting data from the first and final censuses of each plot. We assessed changes in the abundance of tree genera, rather than species, for three reasons. First, 88% of tree species in our study area are too rare (<1 individual per hectare) to allow robust analyses of population trends. Second, within a genus of Amazonian trees, species tend to be similar ecologically (Casper *et al.* 1992; ter Steege and Hammond 2001), so analyses at the genus level capture most of the relevant information. Third, 95.3% of study trees were positively identified genus at the level, whereas a smaller percentage was identified at the level of species.

We encountered 244 tree genera in our plots, of which 115 were sufficiently abundant (initially present in at least 8 of the 18 plots) to permit rigorous analysis. For each genus, we used bootstrapping to assess changes in population density and basal area (a strong correlate of tree biomass) between the first and final censuses (see Laurance *et al.* 2004a for further explanation). This analysis makes no assumptions about the underlying statistical distribution of data. Using a conservative 1% significance level in our tests, we expected for each parameter about 1 out of 115 genera to show a significant change by chance alone. Our null hypothesis was that each tree genus exhibited no significant change in population density or basal area, which is appropriate because total density and total basal area of trees did not change significantly during our study (see below). Because this method is unreliable for genera occurring in a small number of plots, we restricted our analyses to genera present in ≥ 8 plots during our initial census (at this frequency, all genera exhibited reasonably stable estimates for recruitment, mortality, and growth).

We also tested whether the observed changes in density and basal area for all 115 tree genera were more similar among our 18 plots than expected by chance, using randomization tests. To do this we selected nine plots at random and determined the mean percentage change in density for each genus in the plots, and then compared these values to the mean percentage change for each genus in the other nine plots, using Pearson correlations. We repeated this 1000 times, using random combinations of plots each time. The mean and standard error for the 1000 correlations was determined, which were then used to calculate a Z statistic ($Z = \text{mean S.E.}^{-1}$). We used a one-tailed Z test to determine whether the mean value of the observed correlations was significantly greater than 0. The same procedure was used to test for changes in basal area.

Ecological traits of tree genera

For most of the 115 genera in this study, data on growth form and successional status were gleaned from published and online data sources as well as personal knowledge of the authors (see Laurance *et al.* 2004a and Supplemental Online Information). Estimates for median and maximum growth rates, mortality and recruitment rates, and mean trunk diameter were derived from demographic data from our long-term study. Distributional data on locally occurring species within each significantly changing genus, with respect to major rainfall zones in Amazonia, were mostly derived from online sources. Finally, an index of drought tolerance for 30 abundant tree species was derived from published and unpublished data from our 18 plots and from other nearby plots in the same study area.

Changes in forest dynamics and growth

Stand-level rates of annual mortality and recruitment, and the annual rate of trunk growth for individual tree genera, were generated for two largely non-overlapping intervals (ca. 1984–91 and 1992–9). For our 18 plots, the first interval averaged 7.6 ± 2.5 yrs in duration, whereas the

second interval averaged 7.4 ± 0.9 yrs in duration; the first interval was more variable in length because the plots were initially established over a 6-yr period, from 1981 to 1987. Annualized mortality and recruitment data for each plot and interval were estimated using logarithmic models.

To calculate annual growth rates for each genus, the mean annual growth of each tree was determined by subtracting its initial d.b.h. from its final d.b.h., and dividing by the number of years. The median growth rate was then determined for all trees within the genus. Maximum growth rate was also calculated for each genus, and to reduce the effects of outliers the upper 10% of the rates was used as an estimate of maximum growth rate. Growth rates were calculated only for genera that had at least 10 live stems in each of the first and second intervals.

Results

Changes in tree density and basal area

A total of 27 genera exhibited significant changes during the study, with 14 genera increasing in basal area and 14 genera declining in density (Table 9.1). One genus, *Couepia*, simultaneously increased in basal area while declining in density (the result of increased tree growth but high mortality of small individuals), whereas three other genera either decreased (*Oenocarpus*) or increased (*Corythophora*, *Eschweilera*) in both density and basal area. Thus, excluding *Couepia*, 13 genera declined in density, and 13 genera increased in basal area, sometimes dramatically (Table 9.1). Most genera that declined in density did not also decline in basal area because of accelerated growth of the surviving trees (see below).

Mortality rates differed between the 13 increasing and 13 decreasing genera. Declining genera had much higher mortality than did increasing genera (1.57 ± 0.90 versus $0.51 \pm 0.31\% \text{ yr}^{-1}$; $t = 4.66$, d.f. = 24, $P = 0.0001$), whereas recruitment rates did not differ between the two (0.50 ± 0.48 versus $0.69 \pm 0.42\% \text{ yr}^{-1}$; $t = 1.06$, d.f. = 24, $P = 0.30$). Recruitment rates of increasing and decreasing genera were both on average lower than the

Table 9.1 Significantly ($P \leq 0.01$) increasing or decreasing tree genera in undisturbed Amazonian rainforests based on population density and basal area data

Genus	Family	Net change (%)
Tree density increases over time		
<i>Corythophora</i>	Lecythidaceae	+9.8
<i>Eschweilera</i>	Lecythidaceae	+4.0
Tree density decreases over time		
<i>Aspidosperma</i>	Apocynaceae	-13.3
<i>Brosimum</i>	Moraceae	-8.1
<i>Couepia</i>	Chrysobalanaceae	-8.9
<i>Croton</i>	Euphorbiaceae	-35.0
<i>Heisteria</i>	Olacaceae	-25.0
<i>Hirtella</i>	Chrysobalanaceae	-13.0
<i>Iryanthera</i>	Myristicaceae	-16.3
<i>Licania</i>	Chrysobalanaceae	-11.0
<i>Naucleopsis</i>	Moraceae	-17.8
<i>Oenocarpus</i>	Arecaceae	-32.3
<i>Quiina</i>	Quiinaceae	-29.0
<i>Tetragastris</i>	Burseraceae	-15.0
<i>Unonopsis</i>	Annonaceae	-15.3
<i>Virola</i>	Myristicaceae	-14.0
Tree basal area increases over time		
<i>Corythophora</i>	Lecythidaceae	+12.0
<i>Couepia</i>	Chrysobalanaceae	+10.8
<i>Couma</i>	Apocynaceae	+14.4
<i>Dipteryx</i>	Leguminosae	+7.2
<i>Ecclinusa</i>	Sapotaceae	+13.8
<i>Eschweilera</i>	Lecythidaceae	+7.0
<i>Licaria</i>	Lauraceae	+17.2
<i>Maquira</i>	Moraceae	+9.9
<i>Parkia</i>	Leguminosae	+22.0
<i>Peltogyne</i>	Leguminosae	+15.9
<i>Sarcaulus</i>	Sapotaceae	+14.4
<i>Sclerolobium</i> (now <i>synonomized as</i> <i>Tachigali</i>)	Leguminosae	+76.6
<i>Sterculia</i>	Sterculiaceae	+23.4
<i>Trattinnickia</i>	Burseraceae	+13.6
Tree basal area decreases over time		
<i>Oenocarpus</i>	Arecaceae	-29.1

stand-level rate ($1.06\% \text{ yr}^{-1}$) because they included few pioneers (which have higher recruitment).

These shifts in tree communities were not driven by large overall changes in tree density or basal area. During the course of our study, average tree density declined by 1.1%, whereas average basal

area rose by 1.9%. Neither change was statistically significant ($P > 0.09$; paired *t*-tests).

Two lines of evidence confirm that these compositional changes reflect underlying biological processes, not sampling errors. First, randomization tests revealed that the observed changes in density ($P = 0.001$) and basal area ($P = 0.002$) for all 115 genera were consistent across the 18 plots. Second, we contrasted our results with those of a separate study (Oliveira and Mori 1999), in which trees in three 1-ha plots were censused in undisturbed forest about 6 km east of our study area, using virtually identical methods. In this study, plots were censused in August 1991 and again in September 1999. A total of 2085 trees were recorded in the plots, of which 97.1% were identified level of genus. To minimize effects of small sample sizes, we included in the analysis the 42 genera with at least 10 individuals in the 3 plots (all of these genera were present in over half of our 18 plots). Changes over time in both density and basal area were significantly and positively correlated between the two studies (Fig. 9.1). Thus, parallel studies conducted by two separate teams of investigators revealed similar patterns of change.

Differences between increasing and declining genera

Do the increasing and declining tree genera differ biologically? We reviewed available literature and Internet resources and used data from our long-term study to quantify key ecological traits for most genera (see Laurance *et al.* 2004a and Supplemental Information). The 13 increasing genera and 13 declining genera differed in growth form: all of the former were canopy or emergent trees, whereas six (46%) of the latter were subcanopy trees (the remainder being canopy or emergent trees), a highly significant difference ($G = 10.15$, d.f. = 1, $P = 0.001$; *G*-test). Similarly, among all 115 genera, there was a clear tendency for large trees to increase in population density (Fig. 9.2) and basal area at the expense of small trees.

Surprisingly, successional status differed little between the 13 increasing and 13 declining genera;

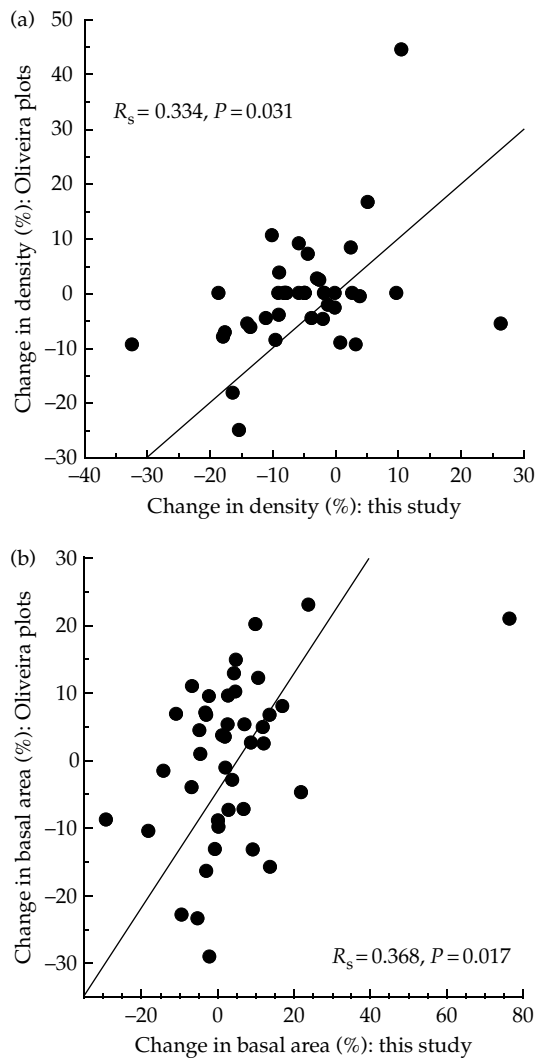


Figure 9.1 Mean percentage changes in (a) population density and (b) basal area of 42 Amazonian tree genera in two different long-term studies (correlation coefficients are for Spearman rank tests). Data are from 18 1-ha plots from the BDFFP and 3 nearby 1-ha plots studied by Oliveira and Mori (1999). The diagonal line in each figure shows $y=x$.

old-growth trees dominated (77%) both groups. In addition, none of the major pioneer genera (*Annona*, *Cecropia*, *Croton*, *Goupia*, *Jacaranda*, *Miconia*, *Pourouma*, *Vismia*) increased significantly in density or basal area, either individually or when pooled. Nevertheless, both median ($t=2.28$, d.f. = 24, $P=0.032$) and maximum ($t=2.07$, d.f. = 24,

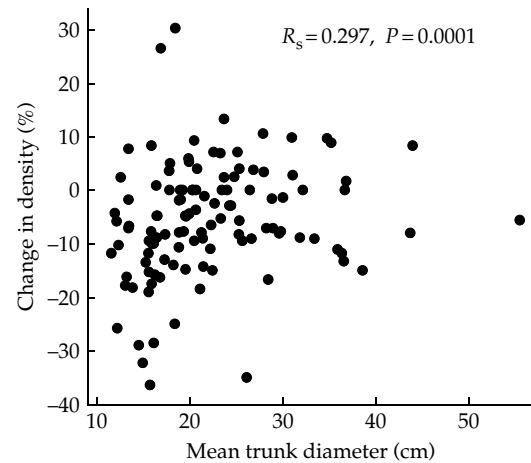


Figure 9.2 Relationship between tree size and long-term population change for Amazonian tree genera (Spearman rank correlation).

$P=0.049$) absolute growth rates were significantly higher in the increasing than declining genera (t -tests with log-transformed data). Similar patterns were evident when all genera that increased and declined in density (not just those that changed significantly) were compared. Collectively, these trends suggest that genera with higher absolute growth rates, including many canopy and emergent trees but not pioneers, are increasing at the expense of slower growing genera, which include many smaller, old-growth subcanopy trees.

In addition, the tree community is changing in taxonomic composition. The increasing genera are dominated (57%) by three families (Leguminosae, Lecythidaceae, Sapotaceae) that are not represented among declining genera, whereas most (64%) declining genera are in families (Arecaceae, Annonaceae, Chrysobalanaceae, Moraceae, Myristicaceae) that are poorly represented among increasing genera (Table 9.1).

Changes in forest dynamics and growth

To help identify the underlying causes of these alterations, we assessed dynamical changes in the tree communities. We divided census data for each plot into two roughly equal intervals (1984–91 and 1992–9) and then contrasted overall rates of tree mortality and recruitment between the two

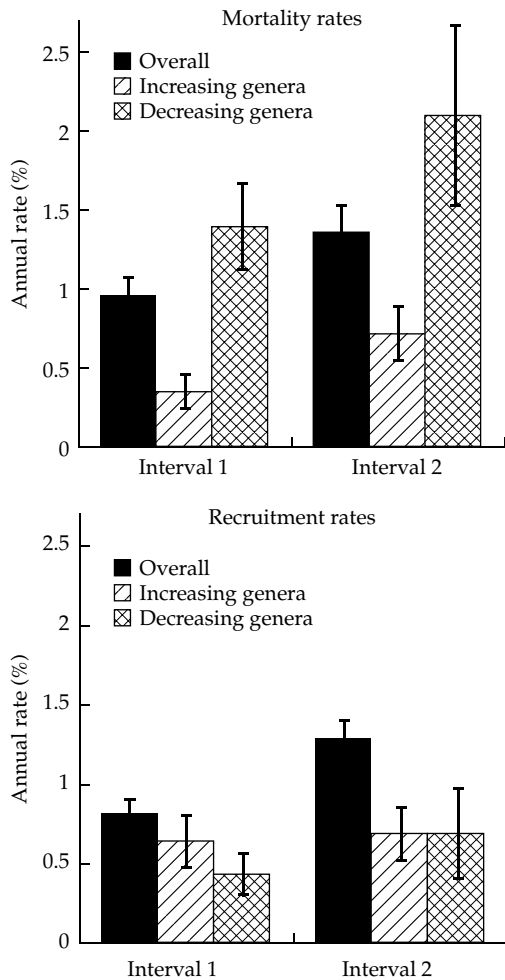


Figure 9.3 Mortality and recruitment rates (± 1 s.d.) for all trees, for 13 genera that increased in basal area, and for 13 genera that declined in density. Overall mortality ($t = -2.38$, d.f. = 17, $P = 0.03$) and recruitment ($t = -4.45$, d.f. = 17, $P = 0.0003$) accelerated from interval 1 (ca. 1984–91) to interval 2 (ca. 1992–9). However, there was no significant change over time ($P > 0.11$) in mortality or recruitment for the increasing and decreasing genera (paired t -tests).

intervals. Both rates rose markedly from interval 1 to interval 2 (Fig. 9.3); thus our forests clearly became more dynamic over time. Mortality and recruitment rates did not rise significantly for the increasing and declining genera, although the latter consistently had higher mortality than recruitment (Fig. 9.3).

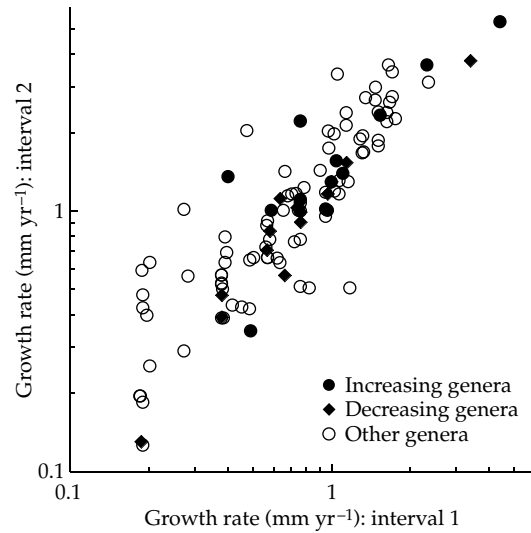


Figure 9.4 Comparison of median growth rates of Amazonian tree genera between interval 1 (ca. 1984–91) and interval 2 (ca. 1992–9). The diagonal line shows $y = x$. Growth rates accelerated markedly over time for all genera ($t = -9.74$, d.f. = 114, $P < 0.00001$; paired t -test), and accelerated significantly more for increasing than decreasing genera ($t = 2.45$, d.f. = 24, $P = 0.022$; t -test for unequal variances).

Moreover, for 87% of genera, rates of trunk growth accelerated between intervals 1 and 2 (Fig. 9.4). This demonstration of enhanced growth across a wide range of tropical tree genera is consistent with stand-level increases in tree growth across South American forests (Lewis *et al.* 2004b). Notably, the average increase in absolute growth rate was higher among increasing genera than declining genera (0.55 ± 0.49 versus 0.19 ± 0.17 mm yr⁻¹); the average for genera showing no significant change was intermediate (0.41 ± 0.50 mm yr⁻¹). This difference did not occur solely because increasing genera were often large in size and decreasing genera often small: in relative terms, growth accelerated much more in increasing (57%) than decreasing (22%) genera.

Discussion

We observed three distinctive trends in this study: (1) there were positively correlated shifts in tree-community composition across geographically well separated plots, with faster growing canopy

and emergent genera (but not pioneers) generally increasing at the expense of slower growing subcanopy genera; (2) for the large majority (87%) of tree genera, incremental trunk growth accelerated from interval 1 (ca. 1984–91) to interval 2 (ca. 1992–9); and (3) tree-community dynamics (mortality and recruitment) also accelerated from interval 1 to interval 2.

There are several plausible explanations for these forest-wide changes in composition and dynamics. We discuss each of these in turn, paying particular attention to local mechanisms or sampling artefacts that could potentially influence our findings (cf. Nelson, in press).

Forest recovery from past disturbance

The forests of our study area might be in a state of disequilibrium because of ongoing recovery from past disturbance, leading to shifts over time in tree composition. The disturbance most likely to operate over such a large spatial scale as our study area (300 km²) is a major forest fire. It is unlikely, however, that past fires could account for the suite of changes we observed. Soil charcoal is found in our study area, but the large majority of charcoal was created at least 1100–1500 yrs ago (Piperno and Becker 1996; Santos *et al.* 1996), and continuous forests have persisted in our study area for at least the last 4500 yrs (Piperno and Becker 1996). Detailed phytolith (plant fragment) studies suggest that the past fires were natural in origin (Piperno and Becker 1996) and, judging from the virtual absence of burnt phytoliths, that they caused relatively little forest damage (D. R. Piperno, personal communication). Moreover, the complex old-growth forest structure (Laurance 2001b), extremely high tree diversity (Oliveira and 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 (Table 9.1), it could not explain accelerating tree growth (Fig. 9.3) and forest dynamics (Fig. 9.4).

Another potentially important cause of disturbance is strong winds, especially from convective thunderstorms (Nelson, in press). Again, these are unlikely to account for the pervasive changes we detected. First, strong winds are 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, pioneer trees, which increase in disturbed forest, were uncommon in our plots (<2.6% of all stems), which would seem unlikely if wind disturbance was pervasive. Third, observed changes in tree communities were not concentrated in one or a few clusters of plots; we found that, for the 115 most abundant tree genera, nearby plots did not show more similar patterns of floristic change during our study than did more-distant plots ($P = 0.92$, Mantel test), as would be expected from convective-storm damage, which is patchy at a landscape scale (Nelson 1994; Nelson *et al.* 1994). Finally, wind disturbance would not cause an acceleration of tree growth, as was observed in our study.

A third possible cause of disturbance is forest flooding and soil saturation (Nelson, in press). Flooding was especially severe in 1989, which had the heaviest wet season recorded in the Manaus area since 1910 (Mori and Becker 1991). However, this is also unlikely to explain observed trends. Wet-season rains in 1989 were indeed heavy (1887 mm), but the pattern is less striking than it might initially seem. From 1968 to 2000, for example, 6 yrs had wet-season rainfall that was >90% of that in 1989, and 14 yrs had >80% of that rainfall (Laurance *et al.* 2005). Thus, many forest microhabitats that flooded in 1989 would also have flooded in preceding years, greatly reducing the likelihood that a single, marginally wetter year would have had exceptional effects on tree communities. Moreover, the tree genera that declined significantly during our study (Table 9.1) did not exhibit larger population declines in plots with flood-prone microhabitats (gullies and plateau depressions) than in plots that lacked flood-prone areas (Laurance *et al.*, in press). Finally, effects of flooding also would not explain accelerated tree growth.

Sampling artefacts

Nelson (in press) suggested that physical damage to trees incurred during the collection of herbarium specimens might increase tree mortality, or render them more vulnerable to disease. Old-growth subcanopy trees, which are strongly energy limited, might be especially vulnerable to such disturbances. If this were the case, this might explain the decline of smaller, slower growing trees observed in our study (e.g. Fig. 9.2).

Notably, however, a previous study (Phillips *et al.* 1998a) 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 increase overall tree mortality (although the authors did not explicitly assess mortality among different size classes of trees). Moreover, our field-sampling methods were less damaging to trees than Nelson (in press) implied: (1) for most trees, only three small leaf samples were collected, usually taken from a single branchlet (flowers or fruits were collected from just 1–2 individuals of each species); (2) slashes on the lower trunks of trees were usually small (<15 cm²) and superficial (<1 cm deep); and (3) 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, and then declined afterwards. In fact, we observed the opposite trend—mortality rates increased over time in our plots (Fig. 9.3), a pattern seen at many other sites in Amazonia (Phillips and 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.

Effects of droughts

Another possibility is that the observed changes in our study might reflect differential vulnerability of

trees to El Niño-related droughts (e.g. Condit *et al.* 1996a,b; Tian *et al.* 1998). Our study area experienced major droughts in 1983 and 1997, and a smaller drought in 1992; such events have increased in frequency this century (Dunbar 2000), possibly because of global warming (Timmerman *et al.* 1999).

We found little direct support for the drought hypothesis. First, we contrasted the geographic distributions of locally occurring species within the increasing and decreasing genera across the Amazon basin. The former did not show stronger associations with drier forest types in the Amazon Basin, as might be expected if the increasing genera were more drought tolerant (Laurance *et al.* 2004a). Second, we tested whether more drought-tolerant tree species had increased in density during our study, in response to the strong droughts in 1983 and 1997. Our index of drought tolerance was generated by dividing the mortality rate of each species during the 1997 drought year, by the baseline mortality rate in years preceding the drought (Williamson *et al.* 2000; Laurance *et al.* 2001c). For the 30 most abundant species in our plots, there was no relationship between the drought-tolerance index and its percentage change in population density during our study (Laurance *et al.* 2004a). Nonetheless, in the only other long-term study of floristic change in mature tropical forest, strong droughts evidently caused a shift in tree-community composition in Panama (Condit *et al.* 1996a,b), so the drought hypothesis requires further examination.

Multi-decadal changes in rainfall

Yet another possibility is that our forests might be responding to multi-decadal changes in rainfall that affect forest productivity and species composition. Drier conditions in rainforests may increase tree growth and reproduction (Clark and Clark 1994; Wright *et al.* 1999), possibly because cloud cover is reduced, increasing available sunlight for light-limited trees.

To test this hypothesis we assessed rainfall data collected near our study area (Manaus, Brazil), contrasting the first (1984–91) and second (1992–9) halves of our study. There was no significant difference between the two intervals for dry-season (June–October) rainfall, wet-season (November–May)

rainfall, total annual rainfall, and the number of dry (<100 mm rain) months per year ($t < 1.5$, d.f. = 14, $P > 0.15$ in all cases; t -tests), nor did any rainfall variable change significantly with calendar year ($r < 0.30$, d.f. = 14, $P > 0.25$; Pearson correlations; Laurance *et al.* 2004a). In addition, a study of tropical climates in the twentieth century (Malhi and Wright 2004) revealed no obvious trend in rainfall at Manaus, with the exception of higher precipitation in the first quarter of the century. Thus, at least in recent decades, it appears unlikely that these forests have been markedly affected by changing rainfall patterns.

Increasing forest productivity

Finally, the observed changes in floristic composition, tree growth, and forest dynamics could be driven by accelerated forest productivity. We believe the most likely cause of higher productivity is rising atmospheric CO₂ levels (cf. Reekie and Bazzaz 1989; Grace *et al.* 1994; Phillips and Gentry 1994; Phillips *et al.* 1998b, 2002, 2004; Winter and Lovelock 1999; Baker *et al.* 2004b; Lewis *et al.* 2004a,b). However, other agents, such as higher airborne nutrient deposition (Artaxo *et al.* 2003) from increasing forest fires, and possible increases in solar radiation from reduced tropical cloudiness (see Wielicki *et al.* 2002; Lewis *et al.* 2004b), are also plausible causes of rising productivity.

Of all the hypothesized factors, rising productivity best explains key observations of this study: (1) that tree growth, mortality, and recruitment have increased markedly, all of which could result from greater productivity (Phillips and Gentry 1994; Lewis *et al.* 2004b; Phillips *et al.* 2004); (2) that many faster growing genera are increasing in basal area, possibly because fast-growing trees show stronger growth enhancement under elevated CO₂ (Reekie and Bazzaz 1989; Körner 1998; Winter and Lovelock 1999); and (3) that forests are experiencing non-random changes in species composition, with fast-growing canopy and emergent genera evidently gaining a competitive advantage over smaller, slower growing genera. That rapidly growing pioneers have not increased in abundance is surprising, but these species usually establish in large treefall gaps, which may be uncommon in our

study area because mortality is greatest among small trees. The group most likely to decline further, we suggest, is old-growth subcanopy species, a highly diverse assemblage that are notable for their slow growth, dense wood, and ability to reproduce in full shade (Thomas 1996; Laurance *et al.* 2004b).

Conclusions and implications

The suite of changes observed in this study appears to be most consistent with those expected from increasing forest productivity, possibly in response to rising atmospheric CO₂ concentrations. This conclusion is bolstered by other studies that also suggest that forest productivity in neotropical forests has generally increased in recent decades (e.g. Phillips and Gentry 1994; Phillips *et al.* 1998b, 2002, 2004; Baker *et al.* 2004b; Lewis *et al.* 2004b; Paruelo *et al.* 2004, Chapter 5 this volume; but see Clark 2002a, 2004 for a different perspective). Regardless of the underlying mechanisms involved, the fact that changes in tree-community composition were positively correlated between two independent studies in central Amazonia (Fig. 9.1) suggests that these trends are real, and not the result of sampling or plant-identification errors.

If Amazonian forests are truly experiencing shifts in tree-community composition and forest dynamics, then these changes could potentially have important consequences. For example, undisturbed Amazonian forests appear to be functioning as a significant carbon sink (Grace *et al.* 1995a; Malhi *et al.* 1998; Phillips *et al.* 1998b; Baker *et al.* 2004b), helping to slow down global warming, but pervasive changes in tree communities could modify this effect (Körner 1998, 2004, Chapter 6). In particular, increases in forest carbon storage might be slowed down by the tendency of canopy and emergent trees to produce wood of reduced density as their size and growth rate increases (Thomas 1996), and by the decline of densely wooded subcanopy species. Forest-wide changes in tree communities, which sustain assemblages of often-specialized pollinators, herbivores, symbiotic fungi, and other species (Bazzaz 1998), may also have serious ecological repercussions for the diverse Amazonian biota. Further studies are urgently needed to determine whether comparably large shifts in tree communities

are occurring throughout the tropics—in concert with widespread increases in forest growth and turnover (Phillips and Gentry 1994; Phillips *et al.* 1998b, 2004; Baker *et al.* 2004b; Lewis *et al.* 2004b)—and to identify the environmental agents driving these changes.

Acknowledgements

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