

Long-term variation in Amazon forest dynamics

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Abstract

Questions: Have forest dynamics changed significantly in intact Amazon rainforests since the early 1980s? If so, what environmental drivers might potentially be responsible?

Location: Central Amazonia, north of Manaus, Brazil.

Methods: Within 20 1-ha plots scattered over ~300 km², all trees (≥ 10 cm diameter at breast height) were marked, identified, and measured five times between 1981 and 2003. We estimated stand-level dynamics (mortality, recruitment, and growth) for each census interval and evaluated weather parameters over the study period.

Results: We observed a widespread, significant increase in tree mortality across our plots. Tree recruitment also rose significantly over time but lagged behind mortality. Tree growth generally accelerated but varied considerably among census intervals, and was lowest when mortality was highest. Tree basal area rose 4% overall, but stem number exhibited no clear trend. In terms of climate variation, annual maximum and minimum temperatures increased significantly during our study. Rainfall anomalies were strongly and positively associated with ENSO events.

Conclusions: The increasing forest dynamics, growth, and basal area observed are broadly consistent with the CO₂ fertilization hypothesis. However, pronounced shorter-term variability in stand dynamics might be associated with climatic vicissitudes. Tree mortality peaked, and tree recruitment and growth declined during atypically wet periods. Tree growth was fastest during dry periods, when reduced cloudiness might have increased available solar radiation. Inferences about causality are tenuous because tree data were collected only at multi-year intervals. Mean temperatures and rainfall seasonality have both increased over time in central Amazonia, and these could potentially have long-term effects on forest dynamics and carbon storage.

Keywords: Amazon, Climatic trends, El Niño, Forest dynamics, Permanent plots, Rainforest, Tree growth, Tree mortality, Tree recruitment, Tropical forests, Weather variation.

Abbreviations: BDFFP = Biological Dynamics of Forest Fragments Project; ENSO = El Niño–Southern Oscillation.

Introduction

Old-growth tropical forests were once widely thought to be in long-term equilibrium, but some now believe that they are being altered by global-scale drivers (Fearnside 1995; Lewis et al. 2004a; Wright 2005; Clark 2007). Two lines of evidence support this view. First, anthropogenic carbon emissions are rapidly altering the composition of Earth's atmosphere, and few now doubt that this underlies recent global warming and certain other potentially important shifts in climate (Houghton et al. 1996). Such large-scale changes might also be affecting certain biological processes in terrestrial vegetation, such as carbon storage and cycling, which, in turn, could have important feedbacks on the global atmosphere (Houghton et al. 2001; Anon. 2002, 2007).

Second, fundamental ecological processes such as forest dynamics have seemingly changed across the tropics since the 1950s (Phillips & Gentry 1994), and in Amazonia since the 1970s (Phillips et al. 2004). Amazon forest productivity and biomass have apparently increased at many sites (Baker et al. 2004) and the species composition of tree (Laurance et al. 2004) and liana communities (Phillips et al. 2002) has shifted, at least in certain areas. However, such trends are not apparent in all tropical regions.

For example, rates of tree growth have evidently declined in recent decades at study plots in Costa Rica (Clark et al., 2003), Panama, and Malaysia (Feeley et al. 2007), whereas other tropical sites show inconsistent shifts in tree community composition (Chave et al. 2008).

Explanations for such alterations in forest processes are varied (see Lewis et al. 2004a) and often controversial (Nelson 2005; Wright 2005; Clark 2007). One view is that forest dynamics are being altered by large-scale changes in atmospheric composition or temperature. Since the mid-1970s, atmospheric CO₂ concentrations have increased by 14%, whereas temperatures have risen by $0.26 \pm 0.5^\circ\text{C}$ per decade (Malhi & Wright 2004). If plant growth is not limited by other nutrients, then rising CO₂ levels might lead to higher primary productivity and plant growth (Winter & Lovelock 1999), and also to increasing tree mortality and turnover as a consequence of elevated competition among individuals. Higher productivity, in turn, could potentially increase forest carbon storage (Phillips et al. 1998) and cause shifts in floristic composition and plant functional attributes (Körner 2004; Laurance et al. 2004). Rising temperatures, however, might have different and possibly opposing effects to those of rising CO₂ levels. Clark et al. (2003) have suggested that rising tropical temperatures may markedly increase plant respiration rates and thereby lower forest productivity. If their hypothesis is correct, then tropical forests might become a significant carbon source to the atmosphere, rather than a carbon sink, and hence help to accelerate global warming.

Other researchers are unconvinced that global-scale drivers are altering forest dynamics. One view is that many forests are simply recovering from past disturbances, such as fires, droughts, floods, or major blow downs (Whitmore 1984; Nelson et al. 1994), which lead to shifts in forest dynamics and composition over time (Whitmore & Burslem 1998; Chazdon 2003; Clark 2007). A second idea is that changing forest dynamics are the result of recent environmental fluctuations. For example, tropical rainforests are strongly influenced by dry season length (Richards 1996), with abnormally long dry seasons causing widespread tree mortality (Leighton & Wirawan 1986; Condit et al. 1995). Intense rainfall can also increase tree mortality via flooding, although such events are often confined to gullies and sites with poor drainage (Mori & Becker 1991). Some environmental fluctuations are entirely natural, whereas others could be affected by global change phenomena. For example, some global cir-

culational models suggest that the frequency and amplitude of ENSO events may increase in response to global warming (McPhaden 2002).

Given their importance in the global carbon cycle, understanding the long-term dynamics of tropical forests is an obvious scientific priority. However, documenting such dynamics on large enough spatial and temporal scales, and discerning their proximate and ultimate drivers, is a major challenge (Clark 2007). Here, we contribute to these efforts by evaluating long-term changes across 20 permanent study plots scattered across an expansive central Amazonian landscape. We assess stand-level changes in forest dynamics (tree mortality, recruitment, and growth) from 1981 to 2003, and consider the roles that local weather variation and larger-scale drivers might potentially be playing in our study area.

Methods

Study area

The study was conducted in central Amazonia, at the Biological Dynamics of Forest Fragments Project (BDFFP), a 1000-km² experimental landscape that includes primary rainforest, forest fragments, and a matrix of grassland and regenerating forest, 80 km north of Manaus, Brazil (60°00'W, 2°20'S) (Lovejoy et al. 1986; Laurance et al. 2002). Intact forest in this area has a canopy height of 28–35 m, with emergent trees reaching 55 m. The understory is relatively open and dominated by stemless palms. Soils are yellow latosols, which are nutrient poor and highly acidic (Chauvel et al. 1987). Rainfall averages ~ 2600 mm yr⁻¹ with a moderately strong dry season from June to August.

There is no evidence of recent fires in intact forests at the BDFFP. Radiocarbon dating of soil charcoal revealed widespread fires from 1300 to 1100 BP. More recent charcoal (550 ± 220 BP) was found at only one of 15 sites, suggesting 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 5 millennia) of swidden agriculture. However, a community change evidently occurred at 4590 ± 60 BP, during which plant species commonly associated with wetter or inundated sites became less abundant (Piperno & Becker 1997). Past disturbances, such as blow downs (Nelson 1994), are possible, but these tend to be patchy and localized in nature. We have observed no trends in

floristic diversity or vegetation structure to suggest that our sites are recovering from any major disturbance (Laurance et al. 2005).

Forest dynamics

We estimated forest dynamics from 21 667 stems recorded in 20 permanent 1-ha plots, all located in intact, unlogged, terra firme rainforest that were initially established from 1981 to 1983. The plots span $\sim 300 \text{ km}^2$ and are positioned independent of local topography using a system of grids. All plots are located at least 200 m from the nearest forest edge to minimize edge effects (cf. Laurance et al. 1998, 2002). Within each plot, all trees [$\geq 10 \text{ cm}$ diameter at breast height (dbh)] were mapped, measured, and fitted with numbered tags, with fertile or sterile botanical material collected for species identification. All plots were sampled five times during the study, at roughly similar intervals.

Five standard metrics were used to assess stand-level forest dynamics in this study: (1) annualized tree mortality = $[\log(N1) - \log(N2)] / [\text{time2} - \text{time1}]$, where 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 years); (2) annualized tree recruitment rate = $[\log(N2) - \log(N1)] / [\text{time2} - \text{time1}]$, where N2 is the number of live individuals (including new recruits) in the second census, and the other parameters are as defined above; (3) annual tree turnover = $[\text{mortality rate} + \text{recruitment rate}] / 2$; (4) mean annual tree growth, where growth of each tree = $[\log(\text{dbh}(\text{census2}) - \log(\text{dbh}(\text{census1})))] / [\text{time2} - \text{time1}]$ and data for each plot were averaged; and (5) basal area (in m^2) = $\pi(\text{dbh}/2000)^2$.

Forest dynamic measures were calculated with the statistical package R 2.21 (<http://www.R-project.org>), using modified functions provided by the Center for Tropical Forest Studies (<http://ctfs.si.edu>) and Condit et al. (2006). Census intervals ranged from 3.5 to 7.9 years; to minimize potential bias associated with varying interval length, we used a correction factor when calculating mortality, recruitment, and turnover rates: $\lambda_{\text{corr}} = \lambda t^{0.08}$ where λ is the rate and t is the time between censuses in years (Lewis et al. 2004c). We corrected for measurement errors by excluding any growth rates of $> 75 \text{ mm year}^{-1}$.

Climate parameters

We considered possible effects on forests of long-term climate variation. Data on monthly rain-

fall were recorded by one of us (PMF) from Manaus, and mean annual daily maximum and minimum temperatures were provided by the Brazilian National Meteorological Institute (INMET) weather station ($59^{\circ}57'W$, $3^{\circ}07'S$) in Manaus. This station is adjacent to the Rio Negro and probably experiences slightly drier and warmer conditions than our study area 80 km northward (Laurance 2001), but should provide a reasonable basis for assessing inter-annual trends. Monthly rainfall data were pooled to yield annual and seasonal totals for different years. We also tested for effects on forests of the multivariate ENSO Index (<http://www.cdc.noaa.gov/people/klauswolter/MEI/mei.html#ElNino>), which is strongly associated with certain Amazonian rainfall and temperature variables (Malhi & Wright 2004).

Statistical analysis

For our 20 plots, we tested for stand-level changes in forest dynamics across five roughly equal census intervals spanning ~ 23 years (1981–2003), using repeated measures analysis of variance (ANOVA) in the GLM module of Systat 11 (Systat 2004). Response variables were log-transformed to improve normality. For significant ANOVAs, paired t -tests were used to contrast sample means; all pairwise differences reported below are significant at the $P \leq 0.05$ level. We examined forest dynamics across tree size classes (10–19.9, 20–29.9, 30–49.99, $\geq 50 \text{ cm}$ dbh) over the study, using repeated measures multivariate analysis of variance (MANOVA), with pairwise comparisons calculated using Hotelling's T^2 statistic (Systat 2004). Changes in stand basal area and stem number were examined with repeated measures ANOVA over the five censuses.

We used one-way ANOVAs to examine changes in weather variables (total rainfall, annual rainfall anomaly, wet season and dry season rainfall, annual maximum and minimum daily temperatures) over the four census intervals. Pearson correlations were used to test for associations among monthly rainfall, rainfall anomaly, and ENSO values and to search for possible associations among weather trends and forest dynamics.

Results

Stand-level forest dynamics

During our 23-year study, tree mortality rates increased significantly in our 20 plots (Fig. 1a)

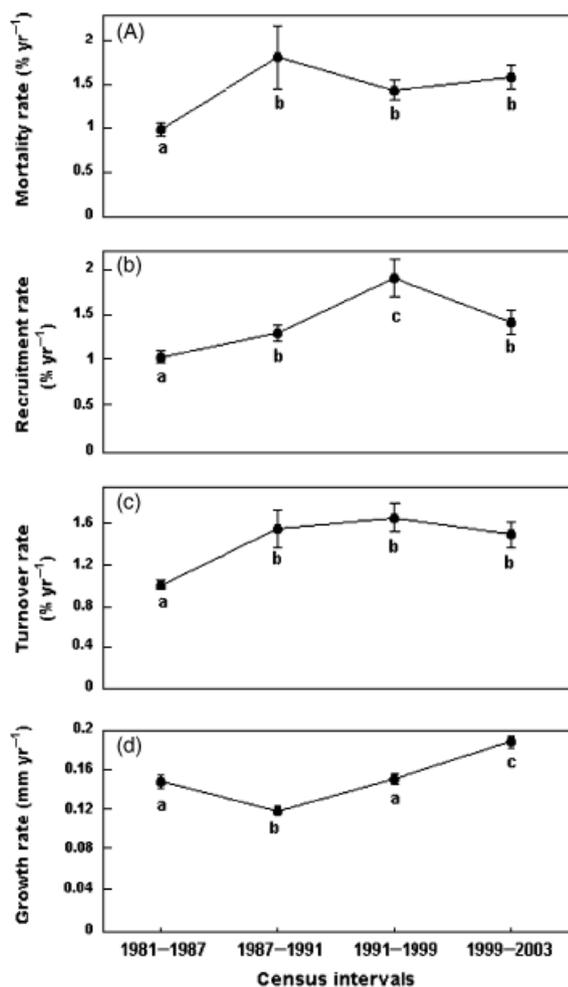


Fig. 1. Average rates (+SE) of (a) tree mortality (b) recruitment (c) turnover, and (d) growth from 20 1-ha plots in intact central Amazon forests, calculated during five censuses from 1981 to 2003. Rates were corrected to account for varying census intervals.

($F_{3,57} = 10.30$, $P < 0.0001$), with mean mortality being significantly higher during the latter three census intervals (1987–2003) than the first interval (1981–1987). Mortality peaked in the second interval (1987–1991, Fig. 1a), in part because a local flooding event caused mortality in one plot to increase by $> 500\%$ (Fig. A1). However, when the flooded plot was removed the overall pattern remained the same ($F_{3,54} = 9.82$, $P < 0.0001$), with mean mortality again being significantly higher in the latter three intervals than the first interval (repeated measures ANOVAs). This overall increase was not merely driven by changes in a few plots; rather, mortality rose over time in most (17/20) of the plots.

Tree recruitment also increased significantly over time (Fig. 1b) ($F_{3,57} = 10.66$, $P < 0.0001$;

repeated measures ANOVA), with a strong peak in the third census interval (1991–1999). In pairwise comparisons, recruitment was significantly higher in the latter three intervals (1991–2003) than the first interval (1981–1987), and was also higher in the third than second or fourth intervals. Like mortality, recruitment rates rose over time in most (18/20) plots.

Tree recruitment evidently rose following pulses of tree mortality, creating a time lag between mortality and subsequent recruitment. For individual plots, this is shown by a highly significant relationship ($F_{1,18} = 28.07$, $R^2 = 60.9\%$, $P < 0.0001$) between recruitment rates in the third census interval, when recruitment peaked strongly, and mortality rates in the preceding interval (Fig. 1a and b). The relationship between recruitment and mortality during the same interval was always weaker ($R^2 < 41\%$ in all cases) and was significant only for the third and fourth intervals (linear regressions with log-transformed data). Because mortality and recruitment peaked at different times, the ratio of overall mortality to overall recruitment differed markedly among census intervals. Mortality exceeded recruitment in intervals 1, 2, and 4, but was much lower than recruitment in interval 3 (Fig. 1a and b).

Tree turnover (Fig. 1c) accelerated during the study ($F_{3,57} = 18.07$, $P < 0.0001$), being significantly higher in the latter three intervals than the first, and also higher in the third than fourth interval (repeated measures ANOVA). On average, turnover was 55% higher in the latter three intervals than the first interval. Turnover increased over time in all 20 plots, although the magnitude varied markedly: four plots increased by $< 10\%$, six by 10–50%, eight by 50–100%, and two by $> 100\%$ (Fig. A1).

Overall tree growth (Fig. 1d) also accelerated significantly during our study ($F_{3,57} = 28.53$, $P < 0.0001$; repeated measures ANOVA), but also varied considerably among census intervals. Relative to the first interval, growth declined significantly in the second interval, rose in the third, and then rose much further in the fourth. These differences reflect broad trends: most (18/20) plots had higher growth in the last than the first interval (Fig. A1).

Forest dynamics and tree size

Tree mortality rates (Fig. 2a) did not differ significantly ($F_{3,76} = 0.62$, $P = 0.61$) among the four tree size classes (10–19.9, 20–29.9, 30–49.9, and ≥ 50 cm dbh). However, tree recruitment (Fig. 2b)

did vary significantly among the size classes ($F_{3,76} = 7.15$, $P < 0.0001$; repeated measures MANOVAs), with the larger (≥ 50 cm dbh) trees having significantly higher recruitment than the smaller size classes, especially during the latter two census intervals. Recruitment into the smallest size class peaked in the third interval, following heavy mortality in the preceding interval.

As expected, absolute growth rates (Fig. 2c) also varied among size classes ($F_{3,76} = 31.23$, $P < 0.0001$), with the smallest trees (10–19.9 cm) having significantly lower rates than the three larger size classes, and medium-sized trees (20–29.9 and 30–49.9 cm dbh) having significantly lower rates than the largest size class. Thus, tree mortality was similar among tree size classes, whereas recruitment and growth varied markedly across size classes.

Basal area and stem number

Tree basal area (Fig. 3) varied significantly among the five censuses ($F_{4,76} = 5.10$, $P = 0.001$; repeated measures ANOVA), increasing over time, except for a temporary decline in the third census. Basal area was significantly higher in the second, fourth, and fifth censuses than in the first census, and also higher in the fourth and fifth censuses than the third census. By the end of the study, average basal area had risen by 4% over its initial value, from 27.7 ± 0.5 to 28.8 ± 0.6 $m^2 ha^{-1}$ (Fig. 3).

The density of stems per plot varied significantly among censuses ($F_{4,76} = 2.64$, $P = 0.04$; repeated measures ANOVA), but there was no strong trend over time. Average stem number per plot declined temporarily in the third census and then recovered in the fourth and fifth censuses ($t_1 = 605.9$, $t_2 = 605.5$, $t_3 = 594.9$, $t_4 = 613.0$, $t_5 = 609.2$ stems).

Climate variation

Climate in central Amazonia varies considerably over time, and we therefore tested for possible effects of multi-year weather trends on forest dynamics. Temperatures in central Amazonia appear to be increasing over time (Fig. 5), with both daily mean minimum ($r_s = 0.259$, $P = 0.066$) and maximum ($r_s = 0.313$, $P = 0.021$) temperatures rising over the past half-century (Spearman rank correlations). Mean minimum ($F_{3,16} = 3.77$, $P = 0.032$) and maximum ($F_{3,19} = 6.70$, $P = 0.003$) temperatures also varied significantly during our study (one-way ANOVAs); in both cases being significantly higher in the final census interval than in the first three intervals.

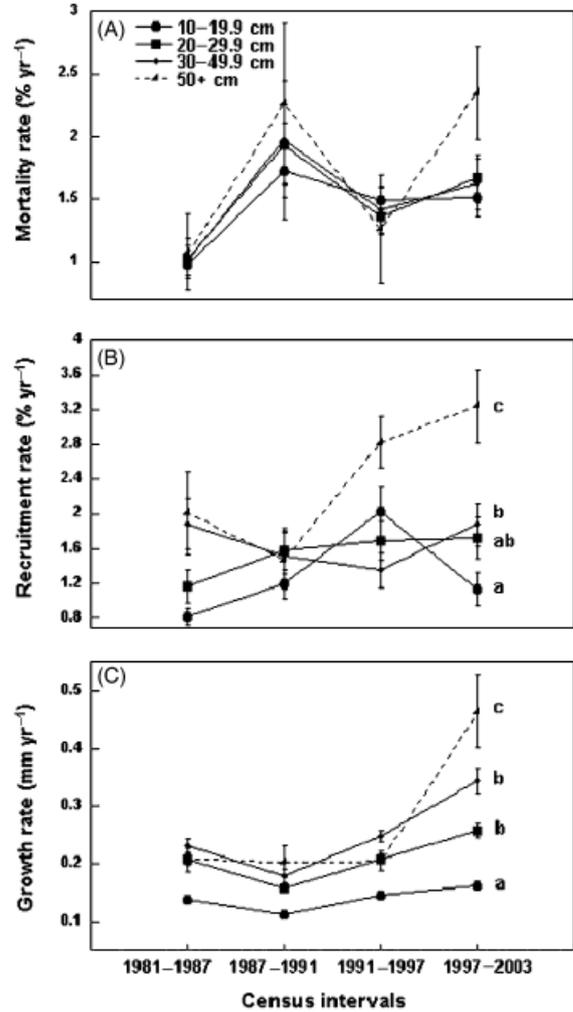


Fig. 2. Comparison of annual mortality (a), recruitment (b), and growth (c) rates (mean + SE) among four diameter classes (10–19.9, 20–29.9, 30–49.9, and ≥ 50 cm dbh) of central Amazonian trees.

Manaus area rainfall is clearly influenced by ENSO. During our study (1981–2003), the multivariate ENSO index was negatively correlated with monthly total rainfall ($r = -0.162$, $df = 274$, $P = 0.007$). Moreover, it was a strong predictor of monthly rainfall anomalies, being positively correlated ($r = 0.273$, $df = 274$, $P < 0.0001$; Pearson correlations) with the standard normal deviate of monthly rainfall (i.e. the deviation of each month from the long-term monthly mean, divided by the monthly SD).

We found no difference in annual rainfall ($F_{3,19} = 0.20$, $P = 0.89$), dry season (July–November) rainfall ($F_{3,19} = 1.47$, $P = 0.25$), or wet season (December–June) rainfall ($F_{3,19} = 0.42$, $P = 0.74$) among the four census intervals in our study (1981–1986, 1987–1990, 1991–1996, 1997–

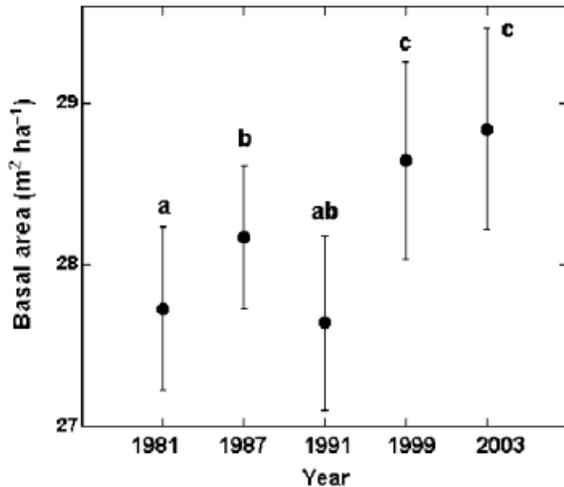


Fig. 3. Average stand-level basal area for 20 1-ha Amazon forest plots, across five census intervals from 1981 to 2003.

2003). However, rainfall anomalies (the standard normal deviate of annual rainfall) varied strongly among the intervals ($F_{3,19} = 7.44$, $P = 0.0017$; all one-way ANOVAs). The second interval, with two of the driest and two of the wettest years in our study (Fig. 4), was more atypical than the others ($P < 0.01$; Tukey's test).

As a hypothesis-generating exercise, we examined correlations between annual weather variables (dry and wet season rainfall, annual rainfall anomalies, maximum and minimum daily temperatures) and forest dynamics parameters (tree mortality, recruitment, turnover, and growth), averaged across our four census periods (Table 1). Although analyses were highly conservative because of small sample sizes, two correlations were statistically significant ($P < 0.037$): tree recruitment was negatively correlated with dry season rainfall, and tree growth was positively correlated with maximum daily temperatures. However, none of the 20 correlations would be significant if a Bonferroni-corrected alpha value ($P = 0.0075$) were used.

Discussion

In a central Amazonian landscape, forest dynamics changed markedly over a 23-year period and in at least two distinctive ways. First, despite some inter-census variability, rates of tree mortality, recruitment, turnover, and growth all generally rose during the course of our study (Fig. 1). These increases were substantial; for example, average mortality and turnover rates rose by 68% and 55%, respectively, between the initial and subsequent

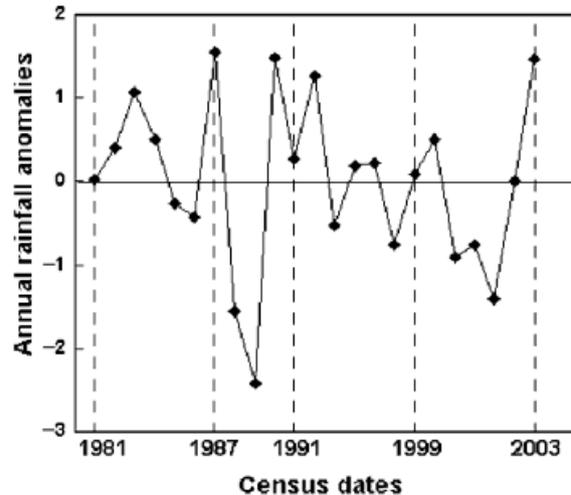


Fig. 4. Annual rainfall anomalies in Manaus, Brazil during the study period (1981–2003).

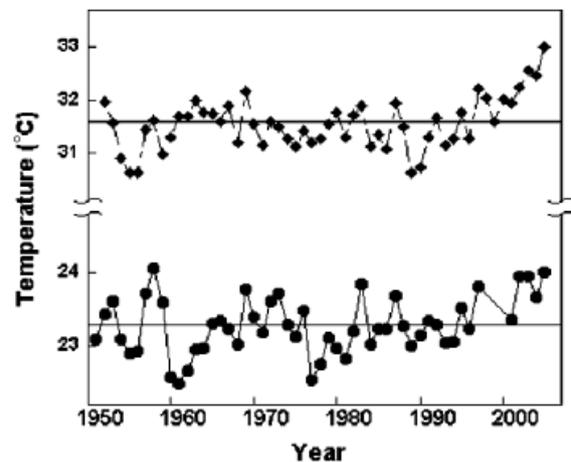


Fig. 5. Mean annual temperature minima and maxima for Manaus, Brazil, from 1952 to 2005 (data for 1998–2000 were excluded because rounding errors were made during data collection).

census intervals. Forest biomass also increased over time, with the basal area of trees in our plots, which correlate strongly with tree biomass (Phillips et al. 1998), rising by 4% on average (Fig. 3). These trends were relatively consistent among different plots in our study area, with mortality, recruitment, turnover, and basal area each increasing over time in 85, 90, 100, and 80% of our plots, respectively.

The suite of changes we observed—accelerating tree growth and forest dynamism, and rising biomass—largely accords with findings from other long-term, comparative studies of forest dynamics across the Amazon Basin (e.g. Phillips & Gentry 1994; Phillips et al. 1998, 2004; Baker et al. 2004; Laurance

Table 1. Pearson correlations (P -values) of forest dynamic parameters and annual climate variables averaged over four census periods. Values in bold are significant at $P < 0.05$.

Weather	Mortality	Recruitment	Turnover	Growth
Temperature				
Mean daily max.	0.074 (0.926)	0.111 (0.888)	0.086 (0.914)	0.964 (0.036)
Mean daily min.	0.349 (0.650)	0.096 (0.904)	0.244 (0.756)	0.828 (0.172)
Rainfall				
Dry season	-0.639 (0.360)	-0.976 (0.023)	-0.929 (0.071)	-0.225 (0.775)
Wet season	0.894 (0.106)	0.603 (0.396)	0.866 (0.134)	0.333 (0.667)
Annual anomaly	0.743 (0.257)	-0.103 (0.897)	0.397 (0.603)	-0.682 (0.318)

et al. 2004; Lewis et al. 2004b). One of the most frequent explanations for such findings is that forest productivity is rising, possibly in response to increasing CO₂ fertilization or some other regional or global driver(s) (Phillips & Gentry 1994; Lewis et al. 2004a), such as increasing irradiance (Wielicki et al. 2002) or rainfall variability (Gu et al. 2007; Lau & Wu 2007). Such changes are hypothesized to cause increased tree growth, which, in turn, would lead to increased competition among individual trees for light or other limiting resources. This, in turn, would presumably result in higher tree mortality, which then directly promotes increased tree recruitment and turnover. This hypothesis is controversial, however, with others advancing alternative explanations (e.g. Nelson 2005; Wright 2005; Clark 2007) and emphasizing that trends observed in Amazonia are not universal elsewhere in the tropics (Clark et al. 2003; Feeley et al. 2007; Chave et al. 2008). It goes beyond the scope of our study to delve into this controversy, other than to note that our findings seem broadly consistent with the rising productivity hypothesis, while acknowledging that alternative explanations are certainly plausible.

The second major trend observed is that forest dynamics fluctuated markedly over time. These fluctuations did not obviate the long-term trends detected, but they certainly complicated them. The most conspicuous change occurred during the second census interval (1987–1991), when tree mortality peaked while tree growth declined (Fig. 1a and d), possibly in response to some environmental stressor. Tree recruitment also fluctuated over time (Fig. 1b) but peaked in the third, rather than second, census interval. This arose, we believe, because pulses of recruitment closely followed pulses of mortality in time; for instance, among our 20 plots, tree recruitment in the third census interval was strongly predicted ($R^2 > 60\%$; linear regression) by tree mortality in the preceding interval. Heavy tree mortality in a plot would create canopy gaps that increase the availability of light and other limiting

resources, thereby increasing local recruitment of young trees (Hartshorn 1978). The strong pulse of tree mortality in the second census interval was also likely responsible for temporary declines in tree stem density and basal area (Fig. 3), although both recovered subsequently.

Hence, a marked pulse of tree mortality and conspicuous slowing of tree growth in the second census interval had important, subsequent impacts on forest dynamics. What might account for these changes? Localized events, such as a pathogen outbreak or windstorm damage, seem unlikely explanations because high mortality and low growth affected most of our plots, which were scattered over an expanse of ~ 300 km² (Laurance et al. 2005). The most likely driver, we believe, is atypical weather, although we must exercise considerable caution because of the coarse temporal scale of our multi-annual tree censuses.

The second census interval had the most anomalous rainfall, with two of the wettest and two of the driest years in our study (Fig. 4). During the wettest year, local flooding caused tree mortality in one of our plots to rise by $> 500\%$ (Fig. A1), a pattern observed in other low-lying microsites in our study area (Mori & Becker 1991). Atypically dry conditions also tend to elevate tree mortality and, unlike flooding, are not confined to any particular topographic setting. During a strong ENSO drought in 1997, for instance, tree mortality in our forest interior plots rose from 1.13% to 1.91% yr⁻¹ on average (Williamson et al. 2000). In simple correlations using mean values for each census interval, tree mortality was positively associated with wet season rainfall ($r = 0.894$), suggesting that flooding or waterlogging increased mortality; and was negatively associated with dry season rainfall ($r = -0.639$), suggesting that dry conditions increased mortality, presumably via drought stress (Table 1). These correlations are based on small sample sizes with temporally coarse tree census data, but they are at least consistent with a view that atypical weather

involving unusually wet and/or dry years created poor conditions for Amazonian tree survival and growth.

Unlike tree mortality, tree growth rates appeared most strongly correlated with temperature trends, with growth increasing significantly with daytime maximum temperatures (Table 1). Although this correlation was based on just a few multi-annual censuses, the broad trend does not appear consistent with the idea that rising tropical temperatures might reduce plant growth as a result of increasing plant respiration rates (Clark et al. 2003). A differing explanation—that plant growth may be most strongly limited by solar radiation, which increases on warm, cloudless days (Myneni et al. 2007)—seems more consistent with our findings, because it would account for a positive relationship between plant growth and daytime temperature. In Amazonian forests, dry season increases in solar radiation have been positively correlated with increasing plant leaf area (Myneni et al. 2007), carbon dioxide gains (Saleska et al. 2003), stem growth (Schultz, 1960; Vieira et al. 2005), and higher modeled photosynthesis and transpiration rates (Lee et al. 2005).

An obvious limitation of our study—and of most other long-term studies of tropical forest dynamics—is that our plots were censused relatively infrequently, at a nominal interval of roughly 5 years (see Sheil et al. 1995; Sheil & May 1996 for discussion). This greatly constrained our ability to test effects of annual or seasonal climate variation on forest dynamics. The logistical and financial challenges of conducting more frequent censuses are considerable; in our study area, two three-person field teams require 1.5–2 years to fully census all of our 1-ha plots. Yet efforts to discern the effects of climate variables on forest dynamics (e.g. Clark et al. 2003; Chazdon et al. 2005) will be frustrated unless more frequent census protocols are established (Clark 2007). Even with annual censuses, complicating factors such as time lags, legacy effects, and the potential for ephemeral climate events (e.g. storms or low-temperature anomalies) to have lasting effects, will hinder efforts to link forest dynamics confidently to climate phenomena.

In summary, our large-scale, long-term study appears to illustrate two contrasting patterns: (1) long-term trends in which tree mortality, recruitment, turnover, and basal area are progressively increasing over time in most (80–100%) of our study plots; and (2) shorter-term fluctuations in which strong pulses of tree mortality and poor growth have more transitory impacts on forest dynamics.

The former trend is consistent with hypotheses that invoke rising forest productivity, whereas the latter might be related to varying climate conditions. Such explanations must remain tentative, however, because of the coarse temporal scale of our multi-annual tree censuses.

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References

- Anon. (IPCC) 2002. *Climate Change 2001: The scientific basis*. Cambridge University Press, Cambridge, GB.
- Anon. (IPCC) 2007. Summary for policymakers. In Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J. & Hanson, C.E. (eds.) *Climate change 2007: Impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, pp. 7–22. Cambridge University Press, Cambridge, GB.
- Anon (Systat) 2004. *Systat for Windows, version 11*. Systat Inc., Evanston, IL, US.
- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Vargas Nunez, P., Pitman, N.C.A.N. & Vasquez Martinez, R. 2004. Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London B* 359: 353–365.
- Chauvel, A., Lucas, Y. & Boulet, R. 1987. On the genesis of the soil mantle of the region of Manaus, central Amazonia, Brazil. *Experientia* 43: 234–240.
- Chave, J., Condit, R., Muller-Landau, H., Thomas, S., Ashton, P., Bunyavejchewin, S., Co, L., Dattaraja, H., Davies, S., Esufali, S., Ewango, C., Feeley, K., Foster, R., Gunatilleke, N., Gunatilleke, S., Hall, P., Hart, T., Hernandez, C., Hubbell, S., Itoh, A., Kiratiprayoon, S., LaFrankie, J., Lao, S., Makana, J., Noor, M., Rahman Kassim, A., Samper, C., Sukumar, R., Suresh, H., Tan, S., Thompson, J., Tongco, M., Valencia, R., Vallejo, M., Villa, G., Yamakura, T., Zimmerman, J. & Losos, E. 2008. Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biology* 6: e45, doi: 10.1371/journal.pbio.0060045.
- Chazdon, R.L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 51–71.
- Chazdon, R.L., Bienes, A.R. & Alvarado, B.V. 2005. Effects of climate and stand age on annual tree

- dynamics in tropical second-growth rain forests. *Ecology* 86: 1808–1815.
- Clark, D.A. 2007. Detecting tropical forests' response to global climatic and atmospheric change: current challenges and a way forward. *Biotropica* 39: 4–19.
- Clark, D.A., Piper, S.C., Keeling, C.D. & Clark, D.B. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences of the United States of America* 100: 5852–5857.
- Condit, R., Hubbell, S.P. & Foster, R.B. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65: 419–439.
- Condit, R., Ashton, P., Bunyavechewin, S., Dattaraja, H., Davies, S., Esufali, S., Ewango, C., Foster, R., Gunatilleke, U., Gunatilleke, C., Hall, P., Harmes, K., Hart, T., Hernandez, C., Hubbell, S.P., Itoh, A., Kiratiprayoon, S., LaFrankie, J., Lao, S., Makana, J., Noor, M., Kassim, A., Russo, S., Sukumar, R., Samper, C., Suresh, H., Tan, S., Thomas, S., Valencia, R., Vallejo, M., Villa, G. & Zillio, T. 2006. The importance of demography niches to tree diversity. *Science* 313: 98–101.
- Fearnside, P.M. 1995. Potential impacts of climatic change on natural forests and forestry in Brazilian Amazonia. *Forest Ecology and Management* 78: 51–70.
- Feeley, K.J., Wright, S.J., Supardi, M.N., Kassim, A.R. & Davies, S.J. 2007. Decelerating growth in tropical forest trees. *Ecology Letters* 10: 461–469.
- Gu, G., Adler, R.F., Huffman, G.J. & Curtis, S. 2007. Tropical rainfall variability on interannual-to-interdecadal and longer time scales derived from the GPCP monthly product. *Journal of Climate* 20: 4033–4046.
- Hartshorn, G. 1978. Tree falls and tropical forest dynamics. In Tomlinson, P.B. & Zimmerman, M.H. (eds.) *Tropical Trees as Living Systems*, pp. 617–638. Cambridge University Press, London, GB.
- Houghton, J.T., Meira Filho, L.G., Callender, B.A., Harris, N., Kattenberg, A. & Maskell, K. 1996. *The Science of Climate Change*. Cambridge University Press, Cambridge, GB.
- Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K. & Johnson, C.A. (eds.) 2001. *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, GB.
- Körner, C. 2004. Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Philosophical Transactions of the Royal Society of London B* 359: 493–498.
- Lau, K.-M. & Wu, H.-T. 2007. Detecting trends in tropical rainfall characteristics 1979–2003. *International Journal of Climatology* 27: 979–988.
- Laurance, W.F. 2001. The hyper-diverse flora of the central Amazon. In Bierregaard, R.O., Gascon, C., Lovejoy, T. & Mesquita, R.C. (eds.) *Lessons from Amazonia: The ecology and conservation of fragmented forest*, pp. 47–53. Yale University Press, New Haven, CT, US.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G.W. & Sampaio, E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16: 605–618.
- Laurance, W.F., Oliveira, A.A., Laurance, S.G., Condit, R., Nascimento, H.E.M., Sanchez-Thorin, A.C., Lovejoy, T.E., Andrade, A., D'Angelo, S., Ribeiro, J.E. & Dick, C.W. 2004. Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* 428: 171–175.
- Laurance, W.F., Oliveira, A.A., Laurance, S.G.W., Condit, R., Dick, C.W., Andrade, A., Nascimento, H.E.M., Lovejoy, T.E. & Ribeiro, J.E. 2005. Altered tree communities in undisturbed Amazonian forests: a consequence of global change? *Biotropica* 37: 160–162.
- Lee, J.E., Oliveira, R.S., Dawson, T.E. & Fung, I. 2005. Root functioning modifies seasonal climate. *Proceedings of the National Academy of Sciences USA* 102: 17576–177581.
- Leighton, M. & Wirawan, N. 1986. Catastrophic drought and fire in tropical rain forest associated with the 1982–1983 El Niño–Southern Oscillation event. In Prance, G.T. (Ed.) *Tropical rain forests and the world atmosphere symposium*. Vol. 10, 75–102. American Association for the Advancement of Science, Washington, DC, US.
- Lewis, S.L., Malhi, Y. & Phillips, O.L. 2004a. Fingerprinting agents of global change in tropical forests. *Philosophical Transactions of the Royal Society of London B* 359: 437–462.
- Lewis, S.L., Phillips, O.L., Baker, T., Lloyd, L., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W., Neill, D., Silva, N., Terborgh, J., Lezama, A., Brown, S., Vasquez, R., Chave, J., Kuebler, C., Nuñez, P. & Vinceti, B. 2004b. Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical Transactions of the Royal Society B* 359: 421–436.
- Lewis, S.L., Phillips, O.L., Sheil, D., Vincenti, B., Baker, T.R., Brown, S., Graham, A.W., Higuchi, N., Hilbert, D.W., Laurance, W.F., Lejoly, J., Malhi, Y., Monteagudo, A., Nunez, V.P., Sonke, B.N.S., Terborgh, J.W. & Martinez V, R. 2004c. Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary. *Journal of Ecology* 92: 929–944.
- Lovejoy, T.E., Bierregaard, R.O.J., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown, K.S.J., Powell, A.H., Powell, G.V.N., Schubart, H.O.R. & Hays, M.B. (1986). Edge and other effects of isolation on Amazon forest fragments. In: Soulé, M.E. (ed.) *Conservation biology: the science of scarcity*

- and diversity. pp. 257–285. Sinauer Associates, Sunderland, MA, US.
- Malhi, Y. & Wright, J. 2004. Spatial patterns and recent trends in the climate of tropical forest regions. *Philosophical Transactions of the Royal Society of London B* 359: 311–329.
- McPhaden, M.J. 2002. El Niño and La Niña: causes and global consequences. In: MacCracken, M.C. & Perry, J.S. (eds.) *Encyclopedia of Global Environmental Change. The earth system: physical and chemical dimensions of global environment change*, pp. 353–370. John Wiley and Sons, Chichester, GB.
- Mori, S.A. & Becker, P. 1991. Flooding affects survival of *Leythidaceae* in terra firme forest near Manaus, Brazil. *Biotropica* 23: 87–90.
- Myneni, R.B., Yang, W., Nenmani, R., Huete, A., Dickinson, R., Knyazikhin, Y., Didan, K., Fu, R., Negron Juarez, R., Saatchi, S., Hashimoto, H., Ichii, K., Shabanov, N., Tan, B., Ratana, P., Privette, J., Morisette, J., Vermote, E., Roy, D., Wolfe, R., Friedl, M., Running, S., Votava, P., El-Saleous, N., Devadiga, S., Su, Y. & Salomonson, V. 2007. Large seasonal swings in leaf area of Amazon rainforests. *Proceedings of the National Academy of Sciences USA* 104: 4820–4823.
- Nelson, B.W. 1994. Natural forest disturbance and change in Brazilian Amazon. *Remote Sensing Reviews* 10: 105–125.
- Nelson, B.W. 2005. Commentary: pervasive alteration of tree communities in undisturbed Amazonian forests. *Biotropica* 37: 158–159.
- Nelson, B.W., Kapos, V., Adams, J.B., Oliveira, W.J., Braun, O.P.G. & Do Amaral, I.L. 1994. Forest disturbance by large blow downs in the Brazilian Amazon. *Ecology* 75: 853–858.
- Phillips, O.L. & Gentry, A.H. 1994. Increasing turnover through time in tropical forests. *Science* 263: 954–958.
- Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Nunez, P.V., Vasquez, R.M., Laurance, S.G., Ferreira, L.V., Stern, M., Brown, S. & Grace, J. 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* 282: 439–442.
- Phillips, O.L., Vasquez Martinez, R., Arroyo, L., Baker, T.R., Killeen, T.J., Lewis, S.L., Malhi, Y., Monteagudo, A., Neill, D.A., Nunez Vargas, P., Alexiades, M., Ceron, C., Di Fiore, A., Erwin, T., Jardim, A., Palacios, W., Saldias, M. & Vinceti, B. 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* 418: 770–774.
- Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D.A., Vargas, P.N., Silva, J.N.M., Terborgh, J., Martinez, R.V., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patiño, S., Pitman, N.C.A., Quesada, C.A., Saldias, M., Torres Lezama, A. & Vinceti, B. 2004. Pattern and process in Amazon tree turnover, 1976–2001. *Philosophical Transactions of the Royal Society of London B* 359: 381–407.
- Piperno, D.R. & Becker, P. 1997. A vegetational history of a site in the central Amazon basin derived from phytolith and charcoal records from natural soils. *Quaternary Research* 45: 202–209.
- Richards, P.W. 1996. *The tropical rain forest*. 2nd ed. Cambridge University Press, Cambridge, GB.
- Saleska, S., Miller, S., Matross, D.M., Goulden, M.L., Wofsy, S.C., Rocha, H.R., Camargo, P.B., Crill, P., Daube, B.C., Freitas, H.C., Hutyrá, L., Keller, M., Kirchloff, V., Menton, M., Munger, J.W., Hammon Pyle, E., Rice, A. & Silva, H. 2003. Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. *Science* 302: 1554–1557.
- Schultz, J.P. 1960. *Ecological studies in northern Surinam*. North-Holland, Amsterdam, NL.
- Sheil, D. & May, R.M. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* 84: 91–100.
- Sheil, D., Burslem, D. & Alder, D. 1995. The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology* 83: 331–333.
- Vieira, S., Trumbore, S., Camargo, P.B., Selhorst, D., Chambers, J.Q., Higuchi, N. & Martinellis, L.A. 2005. Slow growth rates of Amazonian trees: consequences for carbon cycling. *Proceedings of the National Academy of Sciences of the United States of America* 102: 18502–18507.
- Whitmore, T.C. 1984. *Tropical rain forests of the Far East*. 2nd ed. Clarendon Press, Oxford, GB.
- Whitmore, T.C. & Burslem, D.F.R. 1998. Major disturbances in tropical rainforests. In: Newbery, D.M., Prins, H.H.T. & Brown, N.D. (eds.) *Dynamics of tropical communities*. pp. 549–565. Blackwell Science, Oxford, GB.
- Wielicki, B.A., Wong, T., Allan, R.P., Slingo, A., Kiehl, J.T., Soden, B.J., Gordon, C.T., Miller, A.J., Yang, S.-K., Randall, D.A., Robertson, F., Susskind, J. & Jacobowitz, H. 2002. Evidence for large decadal variability in the tropical mean radiative energy budget. *Science* 295: 841–844.
- Williamson, G.B., Laurance, W.F., Oliveira, A., Delamonica, P., Gascon, C., Lovejoy, T. & Pohl, L. 2000. Amazonian wet forest resistance to the 1997–98 El Niño drought. *Conservation Biology* 14: 1538–1542.
- Winter, K. & Lovelock, C.E. 1999. Growth responses of seedlings of early and late successional tropical forest trees to elevated atmospheric CO₂. *Flora* 195: 289–302.
- Wright, S.J. 2005. Tropical forests in a changing environment. *Trends In Ecology & Evolution* 20: 553–560.

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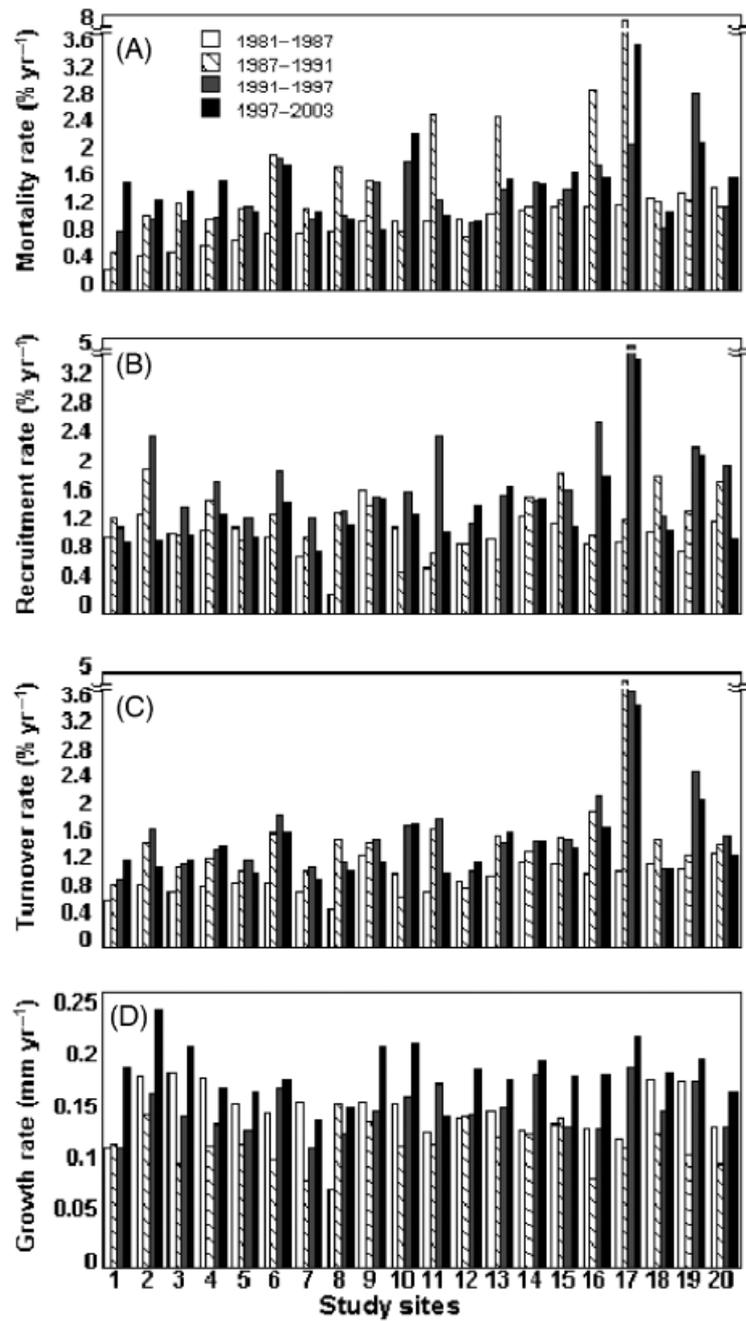


Fig. A1. Individual rates of tree (a) mortality, (b) recruitment, (c) turnover, and (d) growth in 20 1-ha forest plots in central Amazonia, calculated during five censuses from 1981 to 2003. Rates were corrected to account for varying census intervals.