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Rapid change in Amazonian forest dynamics: effects of climate change?

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Running title: Amazon forest dynamics and climate

1 **Abstract**

2 Recent studies suggest that the dynamics of tropical forests are changing, with
3 potentially important implications for ecosystem functioning, carbon storage, and
4 biodiversity. We examined stand-level changes in Amazon forest dynamics over a 23-year
5 period (1981-2003), based on five repeated censuses of trees (≥ 10 cm diameter-at-breast-
6 height) within 20 1-ha plots in intact forest. We observed a widespread, significant increase
7 in tree mortality across our plots. Tree recruitment also rose significantly over time but
8 lagged behind mortality, suggesting that mortality increases led to subsequent increases in tree
9 recruitment and turnover. Tree growth generally increased during our study but varied
10 considerably among census intervals, and was lowest when mortality was highest. Tree basal
11 area also rose over time, increasing by 4% overall, but stem numbers exhibited no clear
12 directional change. Increasing forest dynamics, growth, and basal area in our plots are
13 consistent with the expected effects of rising atmospheric CO₂ concentrations, but climatic
14 vicissitudes may underlie marked short-term variability in stand dynamics. In particular, tree
15 mortality appears to have peaked, and tree recruitment and growth declined, during periods of
16 atypically wet weather, whereas tree growth was fastest during dry periods, when reduced
17 cloudiness probably increased available solar radiation. Temperature and rainfall seasonality
18 has increased in central Amazonia over the past 50 years, in concert with stronger ENSO
19 events, and this could potentially have long-term effects on forest dynamics and carbon
20 storage.

1 1. Introduction

2
3 Anthropogenic carbon emissions are rapidly altering the composition of earth's
4 atmosphere, and few now doubt that this underlies recent global warming and certain other
5 potentially important shifts in climate (Houghton *et al.*, 1996). A growing concern is that
6 such large-scale changes are also affecting biological processes that influence carbon sources
7 and sinks in terrestrial vegetation. These alterations, in turn, could have important feedbacks
8 on the global atmosphere and on various ecosystem processes (Houghton *et al.*, 2001; IPCC,
9 2002).

10 Many now believe that tropical forests are being altered by global-scale drivers (cf.
11 Wright, 2005; Clark, 2007). Fundamental ecological processes such as forest dynamics have
12 seemingly changed across the tropics since the 1950s (Phillips and Gentry, 1994) and in
13 Amazonia since the 1970s (Phillips *et al.*, 2004). In the Amazon, forest productivity and
14 biomass have apparently increased at many sites (Baker *et al.*, 2004) and the species
15 composition of tree (Hubbell, 2004; Laurance *et al.*, 2004) and liana communities (Phillips *et*
16 *al.*, 2002) has changed, at least in certain areas. However, such trends are not apparent in all
17 tropical regions; rates of tree growth, for example, have evidently declined at study sites in
18 Costa Rica (Clark *et al.*, 2003), Panama, and Malaysia (Feeley *et al.*, 2007) in recent decades.

19 Explanations for such basic alterations in forest processes are varied and controversial.
20 One theory is that many forests are simply recovering from natural past disturbances, such as
21 fires, droughts, floods, or major blowdowns (Whitmore, 1984; Nelson *et al.*, 1994), which
22 lead to shifts in forest dynamics and composition over time (Whitmore and Burslem, 1998;
23 Chazdon, 2003; Clark, 2007). Various forest parameters could be used to test this hypothesis
24 (Ferreira and Prance, 1999). For example, tree diversity is generally lower in sites that have
25 been disturbed more recently (Sanford *et al.*, 1985). Progressive changes in floristic
26 composition and wood density are expected in recovering forests, with a decline in
27 recruitment of light-demanding species with lower wood density, and an increase in
28 recruitment of shade-tolerant species with higher wood density (Swaine and Whitmore, 1988).
29 Recovering forests may also be characterized by even-aged stands and an absence of large,
30 old trees. Further, recovering stands will tend to self-thin, with recruitment rates, stem
31 density, and mortality declining over time, and basal area and biomass progressively
32 increasing (Whitmore and Burslem, 1998).

33 A second explanation is that changing forest dynamics result from recent
34 environmental fluctuations. For example, tropical rainforests are strongly influenced by dry-
35 season length (Richards, 1996), and abnormally long dry seasons can cause widespread tree
36 mortality (Leighton and Wirawan, 1986). Intense rainfall can also increase tree mortality via
37 flooding, although such events are often confined to gullies and sites with poor drainage
38 (Mori and Becker, 1991). Some environmental fluctuations are entirely natural, whereas
39 others may be affected by global-change phenomena. For example, El Niño-Southern
40 Oscillation (ENSO) events have increased in intensity throughout the 20th century,
41 culminating with the powerful 1982-83 and 1997-98 El Niños that caused strong droughts
42 across much of the tropics; some global circulation models suggest that ENSO frequency and
43 amplitude may be increasing in response to recent global warming (McPhaden, 2002).

44 A third possible driver of forest dynamics is recent changes in atmospheric
45 composition or temperature. Since the mid-1970s, atmospheric CO₂ concentrations have
46 increased by 14%, whereas temperatures have risen by 0.26±0.5° C per decade (Malhi and
47 Wright, 2004). If plant growth is not limited by other nutrients, then rising CO₂ levels could
48 potentially lead to higher primary productivity and plant growth (Winter and Lovelock, 1999),

1 and increasing tree mortality and turnover as a consequence of elevated competition. Higher
2 productivity could potentially increase forest carbon storage (Phillips *et al.*, 1998) and cause
3 shifts in floristic composition and plant functional attributes (Körner, 2004). Rising
4 temperatures, however, might have different and possibly opposing effects to those of rising
5 CO₂ levels. Clark *et al.* (2003) have suggested that rising tropical temperatures may markedly
6 increase plant respiration and, at times, lower forest productivity. If their hypothesis is
7 correct, then tropical forests might become a significant carbon source to the atmosphere,
8 rather than a carbon sink, thereby accelerating global warming.

9 Given their importance in the global carbon cycle, understanding the long-term
10 dynamics of tropical forests is an obvious priority. However, documenting these dynamics,
11 and disentangling the effects of their many potential proximate and ultimate drivers, is a
12 major challenge (Clark, 2007). Here we describe changes in forest dynamics in central
13 Amazonia, based on one of the largest and longest-term datasets available in this region. We
14 describe both shorter-term fluctuations and longer-term trends in rates of tree mortality,
15 recruitment, turnover, growth, and basal area. We also conduct a preliminary test of weather
16 variables that might have influenced forest dynamics, and hypothesize about the possible
17 effects of local and global-scale drivers in our study area.

18 19 **2. Methods**

20 21 *2.1 Study area*

22
23 The study was conducted in central Amazonia at the Biological Dynamics of Forest
24 Fragments Project (BDFFP), a 1000-km² experimental landscape that includes primary
25 rainforest, forest fragments, and a matrix of grassland and regenerating forest, 80 km north of
26 Manaus, Brazil (60°00'W, 2°20'S) (Lovejoy *et al.*, 1986; Laurance *et al.*, 2002). Intact forest
27 in this area has a canopy height of 28-35 m with emergent trees reaching 55 m. The
28 understory is relatively open and dominated by stemless palms. Soils are yellow latosols,
29 which are nutrient poor and highly acidic (Chauvel *et al.*, 1987). Rainfall averages 2600 mm
30 yr⁻¹ with a moderately strong dry season from June to August.

31 There is no evidence of recent fires in intact forests at the BDFFP. Radiocarbon
32 dating of soil charcoal revealed widespread fires from 1300 to 1100 yr B.P. More-recent
33 charcoal of 550 ± 220 yr B.P. was found at only 1 of 15 sites, suggesting a localized
34 disturbance (Piperno and Becker, 1997). An examination of phytoliths found no evidence of
35 domesticated plant species, suggesting the site has no history (over the last 5 millennia) of
36 swidden agriculture. However, a community change evidently occurred at ca. 4590 ± 60 yr
37 B.P., during which plant species commonly associated with wetter or inundated sites became
38 less abundant (Piperno and Becker, 1997). Past disturbances such as blowdowns (Nelson,
39 1994) are possible, but these tend to be patchy and localized in nature. We have observed no
40 trends in floristic diversity or vegetation structure to suggest that our sites are recovering from
41 any major disturbance (Laurance *et al.*, 2005).

42 43 *2.2 Forest dynamics*

44
45 We used forest-dynamics data from 20 permanent 1-ha plots, all located in intact
46 rainforest, that were initially established from 1981-1983. The plots spanned an area of ca.
47 400 km² and were positioned randomly with respect to local topography. All plots were
48 located at least 200 m from the nearest forest edge in order to minimize any edge effects (cf.

1 Laurance et al., 1998, 2002). Within each plot, all trees (≥ 10 cm diameter-at-breast-height
2 [dbh]) were mapped, measured, and fitted with numbered tags, with fertile or sterile botanical
3 material collected for species identification. All plots were sampled five times at roughly
4 similar intervals.

5 Five standard metrics were used to assess stand-level forest dynamics in this study: (1)
6 annualized tree mortality = $[\log(N1) - \log(N2)] / [\text{time2} - \text{time1}]$, where N1 is the number of
7 individuals alive in the first census, N2 is the number of live individuals (excluding new
8 recruits) in the following census, and time2 and time1 are the respective census dates (in
9 years); (2) annualized tree recruitment rate = $[\log(N2) - \log(N1)] / [\text{time2} - \text{time1}]$, where N2 is
10 the number of live individuals (including new recruits) in the second census, and the other
11 parameters are as defined above; (3) annual tree turnover = $[\text{mortality rate} + \text{recruitment}$
12 $\text{rate}] / 2$; (4) average annual tree growth, where growth of each tree = $[\log(\text{dbh}(\text{census2}) -$
13 $\log(\text{dbh}(\text{census1}))] / [\text{time2} - \text{time1}]$ and data for each plot were averaged; and (5) basal area (in
14 m^2) = $\pi (\text{dbh}/2000)^2$.

15 Forest-dynamic measures were calculated with the statistical package R 2.21
16 (<http://www.R-project.org>), using modified functions provided by the Center for Tropical
17 Forest Studies (<http://ctfs.si.edu>) and (Condit *et al.*, 2006). Census intervals ranged from 3.5
18 – 7.9 years, and to avoid any bias associated with varying interval length we used a correction
19 factor when calculating mortality, recruitment, and turnover rates: $\lambda_{\text{corr}} = \lambda t^{0.08}$ where λ is the
20 rate and t is the time between censuses in years (Lewis *et al.*, 2004). We corrected for
21 measurement errors by excluding any growth rates of $> 75 \text{mm year}^{-1}$.

22 2.3 Weather parameters

23 We tested for possible effects of long-term weather variation on forests in our study area.
24 Data on monthly rainfall data and mean annual daily maximum and minimum temperatures
25 were provided by the Brazilian National Meteorological Institute (INMET) weather station
26 ($60^{\circ}01'W$, $3^{\circ}08'S$) in Manaus. This station is adjacent to the Rio Negro and probably
27 experiences slightly drier and warmer conditions than our study area 80 km northward
28 (Laurance 2001), but should provide a reasonable basis for assessing inter-annual trends.
29 Monthly rainfall data were pooled to yield annual and seasonal rainfall totals for different
30 years. We also tested for effects on forests of the multivariate ENSO (El Niño-Southern
31 Oscillation) Index, which is strongly associated with certain rainfall and temperature variables
32 in the Amazon (Malhi and Wright, 2004). The ENSO index was downloaded from the U.S.
33 National Oceanic and Atmospheric Administration website ([http://www.cdc.noaa.gov/people/](http://www.cdc.noaa.gov/people/klauswolter/MEI/mei.html#ElNino)
34 [klauswolter/MEI/mei.html#ElNino](http://www.cdc.noaa.gov/people/klauswolter/MEI/mei.html#ElNino)).
35
36

37 2.4 Statistical analysis

38 For our 20 study plots, we tested for stand-level changes in forest-dynamic parameters
39 across five approximately equal census intervals spanning a period of up to 23 years (1981-
40 2003), using repeated-measures analysis of variance (ANOVA) in the GLM module of Systat
41 11 (Systat, 2004). Explanatory variables were log-transformed for normality. For significant
42 ANOVAs, paired t -tests were used to contrast sample means; all pairwise differences reported
43 below are significant at the $P \leq 0.05$ level. We examined forest dynamics across tree
44 size classes (10-19.9, 20-29.9, 30-49.99, 50+ cm dbh) over the study period, using
45 repeated-measures multivariate analysis (MANOVA) with pairwise comparisons calculated
46 using Hotelling's T^2 statistic (Systat, 2004). Changes in stand basal area and stem number
47
48

1 were examined with repeated measures ANOVA over the 5 censuses. We used one-way
 2 ANOVA's to examine changes in weather variables (total rainfall, annual rainfall anomaly,
 3 wet season and dry season rainfall, annual maximum and minimum daily temperatures) over
 4 the 4 census intervals and Pearson's correlations to assess possible relationships between
 5 forest-dynamic parameters and weather variables.

7 3. Results

9 3.1 Stand-level forest dynamics

11 During our 23-year study, tree mortality rates increased significantly in our 20 plots
 12 (Fig. 1A) ($F_{3,57}=10.302$, $P<0.0001$), with mean mortality being significantly higher during the
 13 latter three census intervals (1987-2003) than the first interval (1981-1987). Mortality peaked
 14 in the second interval (1987-1991, Fig. 1A), in part because of a local flooding event that
 15 cause mortality in one plot to increase by $>500\%$ (Appendix 1). When the flooded plot was
 16 removed the overall pattern remained the same ($F_{3,54}=9.822$, $P<0.0001$), with mean mortality
 17 again being significantly higher in the latter three intervals than the first interval (repeated-
 18 measures ANOVAs). This overall increase was not merely driven by changes in a few plots;
 19 rather, mortality rates rose over time in the large majority (17/20) of plots.

20 Tree recruitment also increased significantly over time (Fig. 1B) ($F_{3,57}=10.66$,
 21 $P<0.0001$; repeated-measures ANOVA), with a strong peak in the third census interval (1991-
 22 1999). In pairwise comparisons, recruitment was significantly higher in the latter three census
 23 intervals (1991-2003) than in the first interval (1981-1987), and was also higher in the third
 24 interval than in the second and fourth intervals. Like mortality, recruitment rates rose over
 25 time in the large majority (18/20) of plots.

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

37 Tree turnover (Fig. 1C) accelerated during the study ($F_{3,57}=18.07$, $P<0.0001$), being
 38 significantly higher in the latter three intervals than in the first, and also higher in the third
 39 than fourth interval (repeated-measures ANOVA). On average, turnover was 55% higher in
 40 the latter three intervals than in the first interval. Although turnover increased over time in all
 41 20 plots, the magnitude of the increase varied greatly: four plots increased by $<10\%$, six by
 42 10-50%, eight by 50-100%, and two by $>100\%$ (Appendix A).

43 Overall tree growth (Fig. 1D) also generally accelerated during our study ($F_{3,57}=28.53$,
 44 $P<0.0001$; repeated-measures ANOVA), but varied considerably among census intervals.
 45 Relative to the first interval, growth fell significantly in the second interval, returned to a
 46 similar rate in the third, and then increased markedly in the fourth, with this final interval
 47 being significantly higher than all preceding intervals. These differences reflect broad trends

1 across most plots; the large majority (18/20) of plots had higher growth in the last than first
2 interval (Appendix A).

3 3.2 *Forest dynamics and tree size*

4
5
6 Tree mortality rates (Fig. 2A) did not differ significantly ($F_{3,76}=0.615$, $P=0.607$)
7 among trees of four different size-classes (10-19.9, 20-29.9, 30-49.9, and ≥ 50 cm dbh). Tree
8 recruitment (Fig. 2B), however, did vary significantly among the size classes ($F_{3,76}=7.15$,
9 $P<0.0001$), with the larger (≥ 50 cm dbh) trees having significantly higher recruitment than
10 the three smaller size-classes, especially during the last two census intervals. Recruitment
11 into the smallest size-class peaked significantly in the third interval, following heavy tree
12 mortality in the preceding interval. As expected, absolute growth rates (Fig. 2C) also varied
13 among size-classes ($F_{3,76}=31.23$, $P<0.0001$; all repeated-measures MANOVAs), with the
14 smallest trees (10-19.9 cm) having significantly lower rates than the three larger size classes,
15 and medium-sized trees (20-29.9 and 30-49.9 cm dbh) having significantly lower rates than
16 the largest size-classes. Thus, tree mortality was similar among different size-classes,
17 whereas recruitment and growth varied markedly across size-classes.

18 19 3.3 *Basal area and stem number*

20
21 Basal area (Fig. 3) varied significantly among the five censuses ($F_{4,76}=5.10$, $P=0.001$),
22 increasing over time except for a temporary decline in the third census. Basal area was
23 significantly higher in the second, fourth, and fifth censuses than in the first census, and also
24 higher in the fourth and fifth censuses than the third census. By the end of the study, basal
25 area had risen by 4% over its initial value, from 27.7 ± 0.5 to 28.8 ± 0.6 m² ha⁻¹ (Fig. 3). The
26 average number of stems per plot fluctuated during the study, beginning with moderate values
27 in the first two censuses (605.9 and 606.5 stems ha⁻¹), declining in the third census (594.9
28 stems ha⁻¹), and then rebounding in the fourth and fifth (613.0 and 609.2 stems ha⁻¹).
29 Although stem number was significantly higher in the final two censuses than in the third
30 census, it showed no overall trend with time ($F_{4,76}=2.64$, $P=0.04$; repeated-measures
31 ANOVAs).

32 33 3.3 *Weather variation*

34
35 Does weather affect forest dynamics in our study area? We initially tested for
36 differences in rainfall parameters among our four study intervals (1981-1986, 1987-1990,
37 1991-1996, 1997-2003). We found no difference in annual rainfall ($F_{3,19}=0.20$, $P=0.89$), dry-
38 season (July-November) rainfall ($F_{3,19}=1.47$, $P=0.25$), or wet-season (December-June) rainfall
39 ($F_{3,19}=0.42$, $P=0.74$) among the four intervals. However, rainfall anomalies (measured as the
40 absolute value of the standard normal deviate of annual rainfall) varied strongly among census
41 intervals ($F_{3,19}=7.44$, $P=0.0017$; all one-way ANOVAs), with the second interval having
42 much more atypical rainfall than other intervals ($P<0.01$; Tukey's test). The second interval
43 had two of the driest and two of the wettest years in our study (Fig. 4). Although we did not
44 detect a significant difference in seasonality in annual, dry and wet season rainfall over our
45 four census intervals, dry-season rainfall shows a significant declining trend over the 23 years
46 of the study ($y=-0.011(\log\text{dryseason})+2.45$; $r^2=0.253$, d.f.=21, $P<0.01$). Wet season rainfall
47 shows an increasing trend but is not significant.

1 Manaus-area rainfall is correlated with the multivariate ENSO index. During our
 2 study (1981-2003), the ENSO index was weakly but negatively correlated with monthly
 3 rainfall ($r = -0.162$, d.f.=274, $P = 0.007$). It was more strongly correlated with the standard
 4 normal deviate of monthly rainfall (i.e. the deviation of each month from the long-term
 5 monthly mean, divided by the monthly SD), indicating that the ENSO index helps to predict
 6 monthly rainfall anomalies ($r = 0.273$, d.f.=274, $P < 0.0001$; Pearson correlations).

7 Temperatures in central Amazonia (Manaus, Brazil) appear to be increasing over time.
 8 Both daily mean minimum and maximum temperatures rose over a recent 50-year period (Fig.
 9 5). Mean minimum ($F_{3,16} = 3.77$, $P = 0.032$) and maximum ($F_{3,19} = 6.70$, $P = 0.003$; one-way
 10 ANOVAs) temperatures varied significantly during our study, in both cases being
 11 significantly higher in the final census interval than in the first three intervals.

12 We examined the correlations of weather (dry and wet season rainfall, annual rainfall
 13 anomaly, and maximum and minimum daily temperatures) and forest-dynamic (tree mortality,
 14 recruitment, turnover and growth) parameters, all averaged over the corresponding census
 15 periods (Table 1). Tree recruitment was negatively correlated with dry season rainfall
 16 ($P = 0.023$) whereas tree growth was positively correlated with maximum daily temperatures
 17 ($P = 0.036$). Although based on only four data points (each representing 20 individual plots),
 18 these associations suggest some possible trends that could be tested in subsequent studies.

20 4. Discussion

22 4.1. Forest dynamics and growth

23 In central Amazonia, forest dynamics changed significantly over a 23-year period
 24 (Fig. 1). Tree mortality seemed to be a fundamental driver of these changes, increasing
 25 markedly during the study but clearly spiking in the second census interval (1987-1991).
 26 Recruitment of small (<19.9cm dbh) and large (>50cm) trees also rose significantly over time
 27 but appeared to lag behind mortality, with >30% of the variation in among-plot recruitment
 28 being predicted by mortality in the preceding census interval. In addition, tree turnover rose
 29 significantly over time, increasing by two-thirds on average between the first and subsequent
 30 censuses.

31 In general, our findings support the contention by Phillips and colleagues (Phillips
 32 and Gentry, 1994; Phillips *et al.*, 2004) that Amazon tree turnover rates are accelerating; at
 33 the least, they rose substantially following an initially low value in the initial census (Fig. 1C).
 34 If tree turnover rates were to become chronically elevated, this could potentially have wide-
 35 ranging impacts on forest composition and carbon storage. In an earlier study, we
 36 demonstrated seemingly concerted changes in tree-community composition within these same
 37 plots during the first three census intervals (Laurance *et al.*, 2004). A number of faster-
 38 growing canopy and emergent taxa in our plots increased in density or basal area, whereas
 39 slow-growing subcanopy taxa have declined. Such compositional changes could have at least
 40 two, potentially opposing effects on forest carbon stocks: carbon storage could rise if tree
 41 stands become larger or more densely packed and thereby contain more live biomass (Phillips
 42 *et al.*, 1998; Chambers *et al.*, 2001), or alternatively they could diminish if accelerating
 43 growth and turnover favor faster-growing, lightly-wooded tree and liana species that store less
 44 carbon than do the slower-growing species they replace (Körner, 2005). Both of these
 45 processes may be occurring in our plots. That average basal area rose by 4% during our study
 46 (Fig. 3) suggests that these plots might currently be functioning as a carbon sink (cf. Phillips
 47 *et al.*, 1998), but this conclusion remains tenuous without detailed data on wood densities of
 48 trees in our study area.

1 Another important finding is that tree-growth rates varied markedly over time.
2 Stand-level growth rates declined sharply in the second census interval (1987-1991) at the
3 same time that tree-mortality rates peaked (Fig. 1), suggesting a period of marked
4 environmental stress. By the third census growth rates had recovered in the majority (13/20)
5 of plots and they rose further, by 25% on average, by the final census. These stand-level
6 trends are generally mirrored by changes in the growth rates of individual tree taxa. In these
7 same plots, the large majority (87%) of 115 relatively abundant tree genera exhibited
8 increasing growth, when comparing the 1984-1991 and 1992-1999 intervals (Laurance *et al.*,
9 2004).

10 11 4.2. Potential drivers

12 What might be driving these short- and longer-term changes in forest dynamics and
13 growth? We explored potential associations with weather and global-change phenomena in
14 an initial effort to identify potential trends (Table 1) that could be evaluated further in
15 subsequent studies. Although we had only five census intervals during our 23-year study, our
16 large number of widespread, replicate plots gives us increased confidence in the generality of
17 the main trends we discerned.

18 Perhaps the most striking trend we identified was a major spike in tree mortality, and
19 decline in stand-level tree growth, during our second census interval (1987-1991). Factors
20 such as drought, intense flooding, prolonged cloud cover (which can reduce sunlight and
21 thereby limit tree growth; Wright *et al.*, 1999), or some combination of these could potentially
22 be responsible. Annual rainfall did not differ significantly among our census intervals, but
23 rainfall anomalies did, with the second census interval exhibiting two of the driest and two of
24 the wettest years in our study. Droughts or strong rainfall deficits can lead to markedly
25 elevated tree mortality, as previously documented in both intact (Williamson *et al.*, 2000) and
26 fragmented (Laurance *et al.*, 2001) forests in our study area. Intense rainfall can also elevate
27 tree mortality via localized flooding, as observed in at least one of our study sites (Mori and
28 Becker, 1991). Rainfall anomalies were strongly and positively associated with the
29 multivariate ENSO index, suggesting that the El Niño-Southern Oscillation may be helping to
30 drive ecologically important weather extremes in central Amazonia.

31 Notably, we found no evidence of a decline in tree growth rates or a negative
32 correlation of growth with minimum daily temperatures, as has been reported elsewhere in the
33 tropics (Clark *et al.*, 2003; Feeley *et al.*, 2007). We did, however, detect a significant positive
34 correlation between tree growth and daytime maximum temperatures (Table 1). We suspect
35 this relationship might have arisen indirectly: temperatures often peak during dry, sunny
36 periods when cloud cover is minimal, and this is also when sunlight, which can be limiting for
37 tropical tree growth (Wright *et al.*, 1999; Myneni *et al.*, 2007), is most available. The
38 observed decline in dry season rainfall could result in increased solar radiation and may be
39 related to the long-term decline in intermediate rainfall that was recently detected in
40 Amazonia (Lau and Wu, 2007). In Amazon forests dry season increases in solar radiation
41 have been correlated with leaf area increases of ca. 25% (Myneni *et al.*, 2007), carbon dioxide
42 gains (Saleska *et al.*, 2003), faster photosynthesis and transpiration rates in models (Lee *et al.*,
43 2005) and increased stem growth (Schultz, 1960; Vieira *et al.*, 2005).

44 Several long-term changes observed in Amazon forests, such as increasing forest
45 dynamics (Phillips and Gentry, 1994; Phillips *et al.*, 2004) and biomass (Phillips *et al.*, 1998)
46 and shifts in forest composition (Phillips *et al.*, 2002; Laurance *et al.*, 2004), seem consistent
47 with the expected effects of rising forest productivity that, in turn, could potentially result
48 from rising levels of atmospheric carbon dioxide (Lewis *et al.*, 2004). However, these

1 hypothesized changes and their drivers are controversial (e.g. Wright, 2005; Clark, 2007).
 2 The recent discovery of long-term trends in tropical irradiation (Wielicki *et al.*, 2002),
 3 temperature (Gu *et al.*, 2007; Fig. 5), and rainfall (Lau and Wu, 2007) may complicate the
 4 picture, and highlight a general need to focus on potential mechanisms and drivers of global
 5 change (Lewis *et al.*, 2004). Our 23-year study suggests that any long-term trends in central
 6 Amazonian forest dynamics are punctuated by important, short-term fluctuations, and our
 7 preliminary analyses suggest that these might be related to inter-annual weather variation.

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10
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27

1 Table 1. Pearson correlations (with *P*-values) of forest-dynamic parameters and annual
 2 weather variables, averaged over four census periods^A.

3

Weather	Mortality	Recruitment	Turnover	Growth
Temperature				
Daily maximum	0.074 (0.926)	0.111 (0.888)	0.086 (0.914)	0.964 (0.036)
Daily minimum	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)

4 ^AValues in bold are significant at the $P < 0.05$ level. A Bonferroni correction was not applied
 5 because these correlations are merely being used to identify possible trends that could be
 6 assessed in subsequent studies.

7

Figure captions

1

2

3 **Fig. 1.** Mean rates (\pm SE) of tree mortality (A), recruitment (B), turnover (C), and growth (D)
4 from 20 1-ha plots in intact central-Amazon forests, calculated during five censuses from
5 1981-2003. Rates were corrected to account for varying census intervals.

6

7 **Fig. 2.** Comparison of annual mortality (A), recruitment (B), and growth (C) rates (mean \pm
8 SE) among four diameter classes (10-19.9, 20-29.9, 30-49.9, and \geq 50 cm dbh) of central-
9 Amazonian trees.

10

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

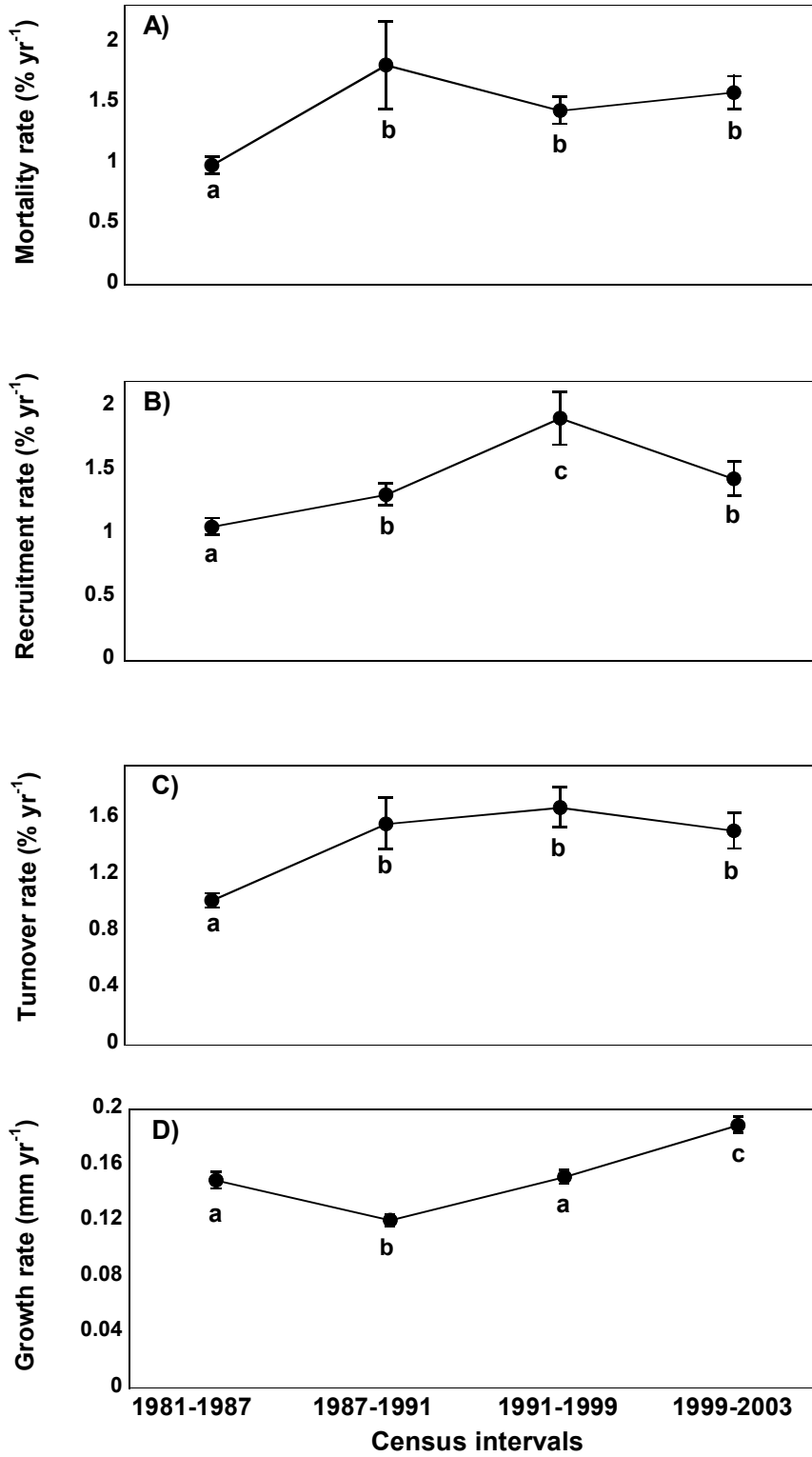
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14 **Fig. 4.** Annual rainfall anomalies in Manaus, Brazil during the study (1981-2003).

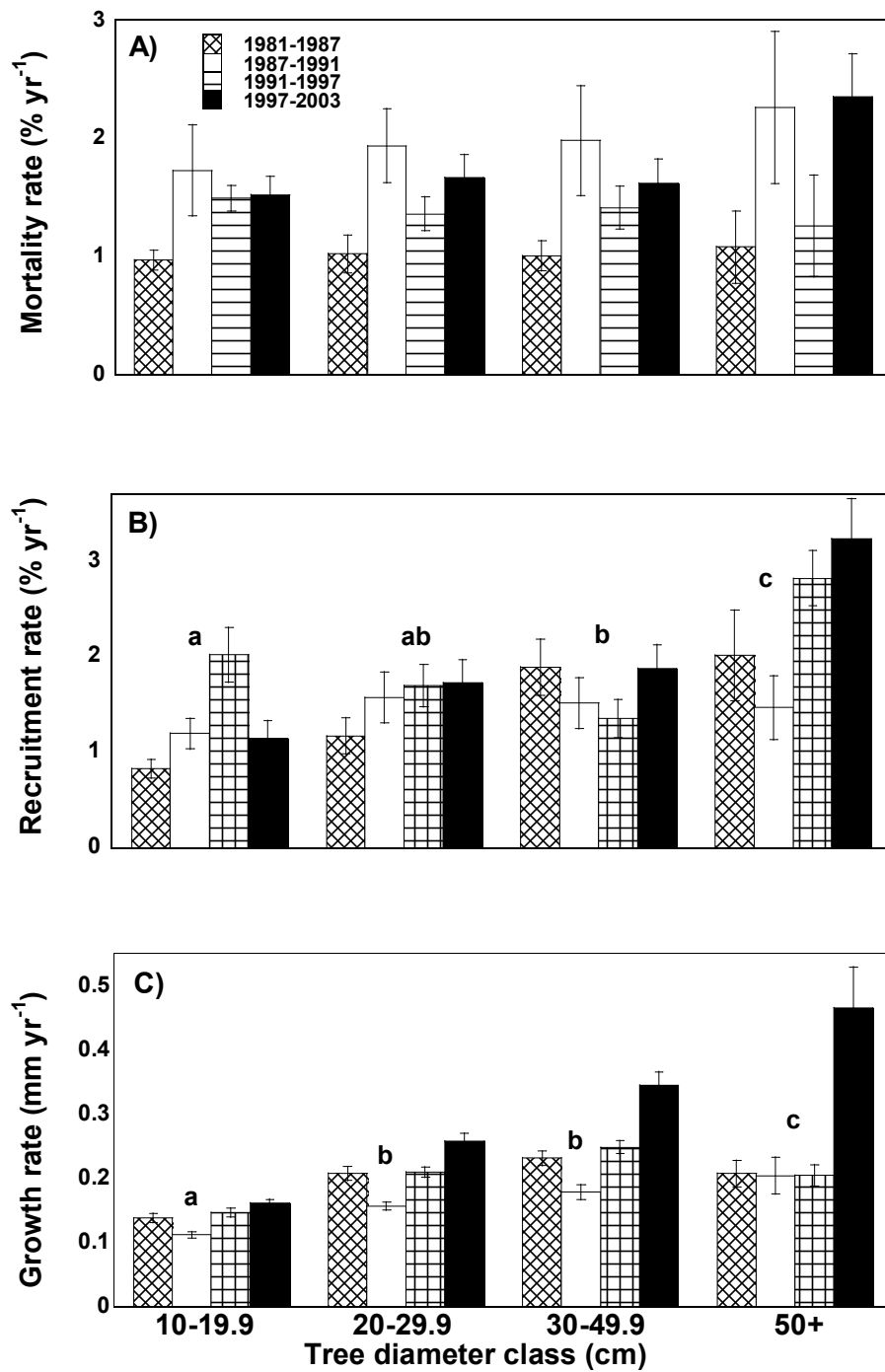
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16 **Fig. 5.** Mean annual temperature minima (circles) and maxima (diamonds) for Manaus,
17 Brazil, from 1950-2003.

1 Fig. 1

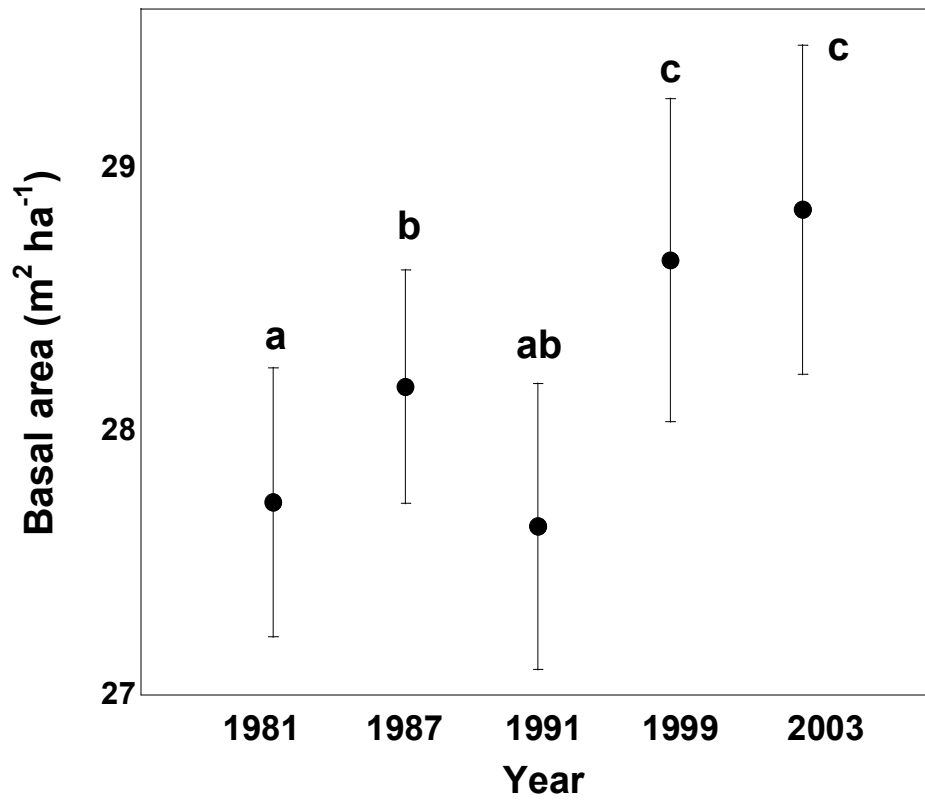


1
2 Fig. 2

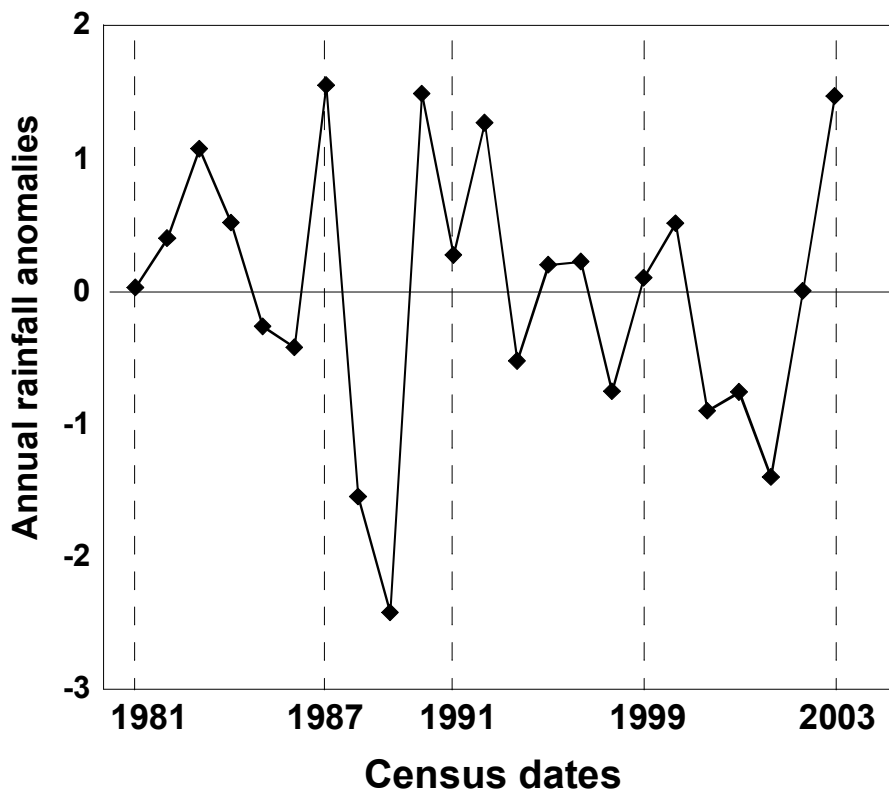


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1 Fig. 3

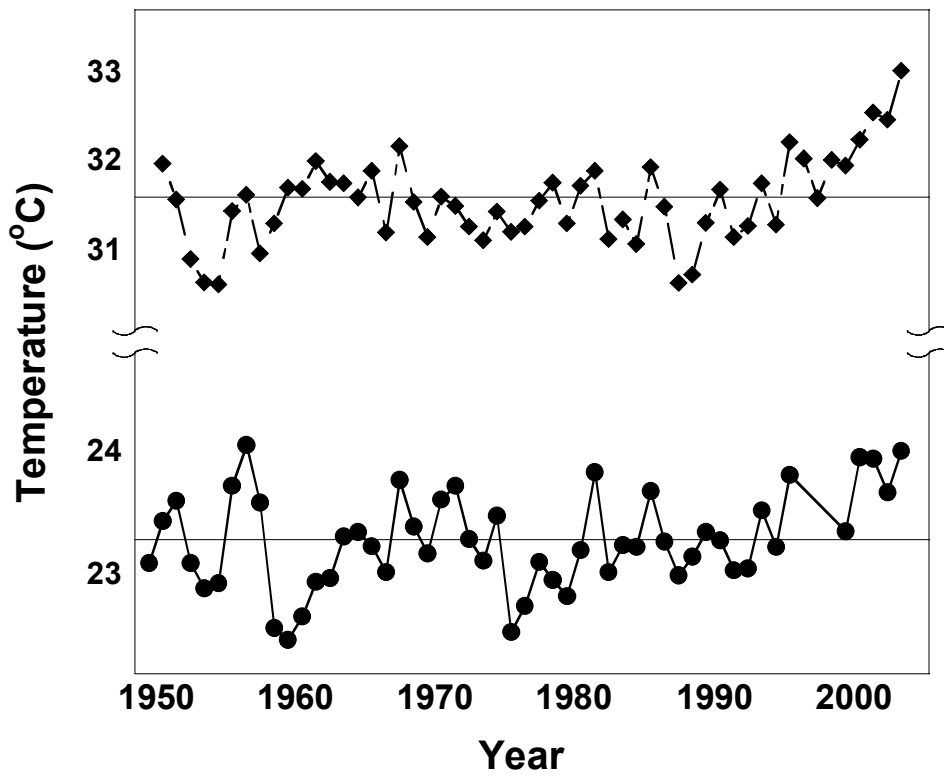
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1 Fig. 4
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1 Fig. 5
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3

- 1 Appendix A. Individual rates of tree mortality (A), recruitment (B), turnover (C) and
 2 growth (D) of 20 1-ha plots in intact central-Amazon forests, calculated during five
 3 censuses from 1981-2003. Rates were corrected to account for varying census intervals.

