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Pattern and process in Amazon tree turnover, 1976–2001

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Previous work has shown that tree turnover, tree biomass and large liana densities have increased in mature tropical forest plots in the late twentieth century. These results point to a concerted shift in forest ecological processes that may already be having significant impacts on terrestrial carbon stocks, fluxes and biodiversity. However, the findings have proved controversial, partly because a rather limited number of permanent plots have been monitored for rather short periods. The aim of this paper is to characterize regional-scale patterns of 'tree turnover' (the rate with which trees die and recruit into a population) by using improved datasets now available for Amazonia that span the past 25 years. Specifically, we assess whether concerted changes in turnover are occurring, and if so whether they are general throughout the Amazon or restricted to one region or environmental zone. In addition, we ask whether they are driven

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by changes in recruitment, mortality or both. We find that: (i) trees 10 cm or more in diameter recruit and die twice as fast on the richer soils of southern and western Amazonia than on the poorer soils of eastern and central Amazonia; (ii) turnover rates have increased throughout Amazonia over the past two decades; (iii) mortality and recruitment rates have both increased significantly in every region and environmental zone, with the exception of mortality in eastern Amazonia; (iv) recruitment rates have consistently exceeded mortality rates; (v) absolute increases in recruitment and mortality rates are greatest in western Amazonian sites; and (vi) mortality appears to be lagging recruitment at regional scales. These spatial patterns and temporal trends are not caused by obvious artefacts in the data or the analyses. The trends cannot be directly driven by a mortality driver (such as increased drought or fragmentation-related death) because the biomass in these forests has simultaneously increased. Our findings therefore indicate that long-acting and widespread environmental changes are stimulating the growth and productivity of Amazon forests.

Keywords: recruitment; mortality; tree turnover; dynamics; Amazonia; forest

1. INTRODUCTION

Ecosystems worldwide are changing as a result of myriad anthropogenic processes. Some processes are physically obvious (e.g. deforestation), others may be less so but also affect biodiversity (e.g. fragmentation, hunting). Atmospheric changes such as increasing CO_2 concentrations, increasing temperatures and altered rates of nitrogen deposition are changing the environment of even remote regions. Anthropogenic atmospheric change will certainly become more significant through the century, as atmospheric CO_2 concentrations will reach values unprecedented for at least 20 or even 60 million years (Retallack 2001; Royer *et al.* 2001). Nitrogen-deposition rates and climates are predicted to move far beyond Quaternary envelopes (Prentice *et al.* 2001; Galloway & Cowling 2002).

Although we are able to measure most of these physical and chemical drivers with reasonable accuracy and precision, quantifying possible ecological responses to atmospheric change is an extremely difficult task. The task is particularly urgent in the tropical forests, as a high proportion of the Earth's biodiversity, plant carbon stocks and forest productivity is centred within this biome (Malhi & Grace 2000). The principal means of monitoring ecological processes within mature forests is with permanent sample plots, but the network of assessment and monitoring sites has traditionally been sparse, spatially aggregated and poorly integrated at regional scales. Over the past decade we have sought to overcome these limitations by developing collaborative networks of researchers: recognizing that by pooling local efforts and small-scale datasets we can start to answer large-scale questions. In particular the Amazon Forest Inventory Network (RAINFOR, see http://www.geog.leeds.ac.uk/projects/rainfor/), which was established in 2000, seeks to document and understand patterns and changes in mature Amazon forests on both spatial and temporal scales (Malhi *et al.* 2002).

Earlier large-scale analyses have suggested that significant changes occurred in the structure and function of mature tropical forests by the close of the twentieth century. For example, turnover rates of trees in mature tropical forest plots increased throughout the 1980s and early 1990s (Phillips & Gentry 1994; Phillips 1996). This trend was demonstrated separately for both the neotropics and the palaeotropics, with the changes appearing to be generally immune to concerns such as the effect of individual ENSO cycles (Phillips 1995; cf. Sheil 1995*a*), bias towards high-biomass 'majestic forest' when plots are established (Condit 1997; Phillips *et al.* 1997), damage caused by botanical collecting (Phillips *et al.* 1998*a*; cf. Sheil 1995*b*) and census-interval artefacts (Lewis *et al.* 2004*c*; cf. Sheil 1995*a*). In a set of forest plots in Amazonia that largely overlaps with that used in the neotropical turnover dataset, we have also shown that the structure and composition of mature non-fragmented forests are changing, with an increase in the biomass of trees (Phillips *et al.* 1998*b*; Baker *et al.* 2004*b*; but see Clark 2002; Phillips *et al.* 2002*a*) and in the density and relative dominance of large lianas (Phillips *et al.* 2002*b*). Taken together, these results imply that changes in structure, composition and dynamics are common manifestations reflecting a profound shift in the overall ecology of tropical forests. However, to fully test the proposition that ecological processes in mature tropical forests are changing systematically, additional evidence needs to be evaluated against two sets of criteria.

(i) Are the changes observed so far concerted across space and time? Are they geographically coincident (occurring together in the same forest region and sites), geographically widespread (occurring across spatial and environmental gradients) and temporally robust (occurring over protracted periods of time and relatively insensitive to short-term climatic fluctuations)?

(ii) Can the phenomena be explained in terms of underlying ecological processes, such as growth, mortality and recruitment? Specifically, is the increase in turnover driven by changes in recruitment or mortality, or both? Is the increase in above-ground biomass driven by greater basal area growth or reduced basal area death? Are these ecological processes consistent with one another and with possible mechanistic drivers?

In this paper, we provide a much fuller description of the patterns of tree turnover than has been possible so far, concentrating on Amazonia which comprises more than half the world's remaining area of humid tropical forest and where changes in tree and liana biomass have previously been demonstrated. We explore aspects of the two sets of criteria described above, and show results before and after accounting for potentially important artefactual sources of error. Companion papers (Lewis *et al.* 2004*a*,*b*) develop a conceptual framework that links plausible

physical and chemical mechanistic drivers to predicted changes and present tests for the phenomena that complement the approach taken here. We define 'turnover' as the rate with which trees move through a population (the flux) in relation to the number of trees in the population (the pool), and estimate this flux by the mean rate with which they recruit and die.

In this paper our specific aims are to determine the following.

(i) The extent to which turnover rates have changed (or not) throughout the Amazon Basin. (Note that the turnover increase has so far only been shown for the neotropics and palaeotropics as a whole).
(ii) If there are consistent patterns in the changes in turnover rates across the different climatic, edaphic and geographical regions within Amazonia. (Amazon forests vary greatly, so it is important to know if the patterns of change vary too.)
(iii) Whether these changes are driven by recruitment rate changes, mortality rate changes or both. (Turnover changes in neotropics and palaeotropics have only been shown so far in aggregate, and have not been deconstructed into component processes.)

Addressing these questions first requires careful consideration of possible sources of error, and correcting for these where possible. Potential sources of error stem from the differing census intervals with which plots are monitored, the timing of censuses, the possible tendency of foresters and ecologists to select good-looking, high-biomass, mature-phase patches for plots ('majestic forest'), and changes through time in the spatial and environmental distribution of available datasets ('site-switching'). In § 2 we describe how we have attempted to address these problems, but first we briefly review these concerns.

Turnover rates are sensitive to the length of interval over which they are measured and the actual timing of censuses in at least four ways. First, individual stem death and recruitment are discrete events. This means that over progressively shorter intervals, estimates of rates depart disproportionately from long-term trends as a function of when census dates fall in relation to individual tree deaths and the local forest gap-phase cycles: short intervals therefore introduce more random noise (Hall *et al.* 1998). Second, detecting new recruits and deaths is not always straightforward. Over shorter intervals the error associated with determining recruitment increases because a larger proportion of ingrowing stems are close to the minimum size threshold of 10 cm, which increases the relative impact of stem hydration fluctuations or measurement error on recruitment estimates (Sheil 1995*b*). Similarly, measurement errors of mortality rates may increase because proportionally greater fractions of apparently dead trees will be 'barely alive' or 'just dead'. However, over longer time intervals the precision of recruitment and mortality estimates declines as more trees will have recruited and died undetected in the interval. Third, seasonality and regional and global-scale climate fluctuations such as ENSO events generate intra-annual and supra-annual fluctuations in stem hydration (e.g. Baker *et al.* 2002), growth rates and mortality probabilities (e.g. Nakagawa *et al.* 2000), so the timing of the census can affect the rates measured in each interval. Finally, the cohort of stems dying over short intervals is represented disproportionately by intrinsically short-lived trees, so shorter census intervals are biased to record higher turnover rates than longer intervals. Sheil & May (1996) provide a theoretical discussion of this effect. Lewis *et al.* (2004*c*) developed an empirical quantification of its significance but found that it probably cannot account for published findings of increased turnover.

Additional methodological issues that have been suggested to account for increased turnover include possible biases in the way that plots are selected on local, regional and global scales. Locally, some sites could be affected by a 'majestic forest' artefact, if ecologists preferentially select mature-stage forest when establishing plots (Phillips & Sheil 1997; Phillips *et al.* 1997, 2002*a*). Such plots would subsequently undergo locally accelerated dynamics as large trees die, killing smaller trees and improving the light environment for new recruits. On much larger scales, regionally and globally aggregated turnover results could be biased by unequal sampling of forest types across time ('site-switching'). In large multi-site datasets, site-switching is inevitable because plots are monitored at different times for different lengths in different environments and different parts of the world. For example, in the dataset used in Phillips (1996) the average monitoring date for palaeotropical forest plots was 1971, whereas for neotropical plots it was 1982 (Lewis *et al.* 2004*c*). If the nature of the site-switching is such that inherently more dynamic forests have been monitored more recently than less dynamic forests, then simply correlating turnover rates with time may lead to type I error: the erroneous conclusion that forests as a whole are becoming more dynamic when in fact they are not (Condit 1997).

A final concern that has been raised is that the stochastic nature of forest dynamics makes it very difficult to use small plots to detect signals of change (e.g. Hall *et al.* 1998). This is undoubtedly true. However, we have shown before that our approach of looking for aggregate effects across many plots can overcome this difficulty (e.g. Phillips & Gentry 1994; Phillips 1996). We wish to emphasize that the null hypothesis being tested here is not that 'tree turnover rates have not increased *within a specific, individual site*'. Rather, it is that 'tree turnover rates have not systematically increased *across all sites in a region*'.

2. METHODS

(a) *Site selection*

The region considered is the Amazon river basin and contiguous forested areas, including all mature forest except for that which has experienced obvious anthropogenic disturbances (logging, fragmentation and fires) and excluding small forest patches in forest–savannah mosaic landscapes. Data were obtained from published sources where available, but most data analysed are from unpublished permanent monitoring plots maintained by the authors, across sites in Bolivia, Brazil, Ecuador, French Guiana, Peru and Venezuela. Together, these forests constitute a substantial proportion of the RAINFOR Amazon forest inventory network (Malhi *et al.* 2002). The criteria used for selecting appropriate tree turnover data include a minimum initial population of 200 or more trees, 10 cm or greater diameter, a minimum area of 0.25 hectares (ha, where 1 ha = 10^4 m^2) and a minimum monitoring period of 2 years. Most reported data are much more substantial than these values

might suggest: among the plot data analysed, the mean (and median) values of the initial population are 954 (572) trees, the area monitored averages 1.7 (1.0) ha and the monitoring period averages 10.1 (9.6) years. These plots are mostly replicates from within different landscapes across Amazonia, with each plot separated from others in the same landscape by between a few hundred metres and a few kilometres.

(b) *Turnover rate calculations*

Annual mortality and recruitment rates were separately estimated using standard procedures that use logarithmic models which assume a constant probability of mortality and recruitment through each inventory period (Swaine *et al.* 1987; Phillips *et al.* 1994). To reduce noise, turnover rates for each period were represented by the mean of recruitment and mortality (91 sites), or as mortality rates alone when recruitment data were not available (four sites) (table 1).

(c) *Analytical approach*

Change in a rate process can be evaluated in many ways, depending on the exact hypothesis being tested and the quality of the data (Phillips 1996). Some sites have only one measurement interval, whereas others have turnover rates reported for multiple intervals. To use the greatest information content possible, we have used several different approaches here and in a companion paper (Lewis *et al.* 2004*a*).

The core approach used in this paper involves calculating mortality and recruitment rates for each site for each year in which it was monitored, and plotting these rates as a function of calendar year. (In the companion paper we focus on evaluating changes within plots.) We test for change by comparing measured rates in the last year in which at least 10 sites were monitored with rates in the first year in which at least 10 sites were monitored. With our current dataset this typically allows comparisons across two decades from the early 1980s to 2001.

The method described here has the advantages of using all the available turnover data and of being able to show graphically the statistical range of site values within each calendar year and across all calendar years. However, a concern is that the results may be skewed by using short or varying census intervals through time as it is not possible to coordinate censuses at the Amazonian scale, nor is it even possible to select censuses retrospectively so that they are simultaneous and equally frequent at all sites. We take a pragmatic approach to minimize the impact of this concern. Thus, all rates are calculated for each site over intervals of as close to 5 years as practical, so that short intervals are collapsed together where possible (see electronic Appendix A). Adjacent intervals less than 5 years are combined when the difference between the combined period and 5 years is less than the summed difference between each of the constituent intervals and 5 years. To account for any residual census interval effect, we also present key results with and without an empirical correction for the census interval effect derived from 10 long-term sites from Latin America, Africa, Asia and Australia (Lewis *et al.* 2004*c*).

We also needed to identify those plots potentially affected by a 'majestic forest' bias, as a gradual or sudden breakdown of mature phase forest will lead to locally accelerated dynamics. We can rule out the possibility that a majestic forest effect could be artificially accelerating dynamics in most plots, based on either the sample unit shape and size, or the site selection procedures used, or the fact that the stand has gained basal area through the monitoring period as their rate processes are unlikely to be driven by locally accelerated dynamics resulting from death of large trees (table 2). The remaining seven plots potentially most susceptible to majestic forest bias were excluded from these analyses. Out of these, four (BDF-04, BDF-08, CRP-01 and JAS-02) have more than one interval, and the impact of leaving these forests out is evaluated in the results.

A further concern with our analytical approach is that a calendar year signal confounds within-site change with among-site change, so aggregated results could be influenced by biases that could arise through unequal sampling of forest types across time ('site-switching'). Therefore we also present results in a way that eliminates site-switching, to show only the aggregate of *within-site* changes. This is achieved by 'stretching' all multi-interval data backwards and forwards. We do this by applying the rate actually recorded in the first interval rate for each year before the first census back to 1976 (for each site initiated after 1976), and applying the rate actually recorded in the last interval forwards to 2001 (for each site last censused before 2001). This should be a conservative procedure with respect to the null hypothesis because we are assuming no change in rates for all years in which a site was not monitored. Most plots have been monitored for less than 25 years and so stretching always flattens the average gradient of any trend in rates. The main analyses—correcting for site-switching, census-interval and majestic-forest effects—are shown graphically and in table 3. Results using the raw uncorrected data are shown principally in tabular form. To explore the sensitivity of the main results to the exclusion of the four potential majestic forest sites, a supplementary set of census-interval and site-switching corrected analyses was run using these data, and results compared with the main analyses that corrected for all possible effects.

To be able to test whether patterns are widespread or simply driven by change in one region or another, we arbitrarily divided Amazonia into two roughly equal areas with as equal sample sizes as possible: western and southern Amazonia, which we call 'west and south', and eastern and central Amazonia, which we call 'east and central' (figure 1). Most east and central Amazon forests are on the actively weathering Guyanan or Brazilian shield or associated Cretaceous and Tertiary planation surfaces, whereas most west and south Amazon forests are located on Quaternary or Holocene Andean sediment (Irion 1978; Sombroek 1984; Richter & Babbar 1991; but see also Lips & Duivenvoorden 1996). Our geographical division is also consistent with what we know about the floristic make-up of Amazon forests, lying roughly perpendicular to the main southwest–northeast gradient in composition (Terborgh & Andresen 1998). In separate disaggregations we divided Amazonia in a climatic sense ('aseasonal' versus 'seasonal', using the criterion of one month or more receiving less than 100 mm rain to define seasonality), and in an edaphic sense (poor soil versus richer soils, with oxisols, oligotrophic histosols, and spodosols and other white sands defined as 'poor', and alfisols, eutrophic histosols, ultisols, clay-rich entisols, and alluvial and basaltic inceptisols defined as 'richer'). Climate data come from local meteorological stations where possible, and otherwise from a twentieth century climatology developed to characterize baseline climates for the International Panel on Climate Change (see http://ipcc-ddc.cru.uea.ac.uk). Soil classifications come from published profiles where possible, and otherwise are based on our own preliminary analyses (C. A. Quesada, C. I. Czimczik and J. Lloyd, unpublished data). These categories represent an advance on previous approaches that lumped the neotropics into a single category (e.g. Phillips 1996) and allow us to maintain reasonable sample sizes in each through the late twentieth century.

Table 1. Site-by-site descriptions, all sites.
(Data are the best available to the lead author at the time of final analyses, but are subject to future revision as a result of additional censuses and continued error-checking. Date of final analyses for this paper, *ca*. 1 March 2003.)

site name	site code	country	latitude	longitude	altitude (m)	region	forest type[a]	rainfall (mm)	soil order	soil (0 = poor, 1 = richer)	seasonality (0 = aseasonal, 1 = seasonal)	area (ha)	max. plot dimension (m)	min. plot dimension (m)	principal investigator	institution/ publication	monitoring period (years)	census interval 1 (years)	census interval 2 (years)
Cerro Pelao 1	CRP-01	Bolivia	14°32′ S	61°30′ W	350	W + S	terra firme	1500	inceptisol	1	1	1	100	100	T.K.	Museo Noel Kempff	7.25	N/A	N/A
Cerro Pelao 2	CRP-02	Bolivia	14°32′ S	61°30′ W	350	W + S	terra firme	1500	inceptisol	1	1	1	100	100	T.K.	Museo Noel Kempff	7.19	N/A	N/A
Chore 1	CHO-01	Bolivia	14°21′ S	61°10′ W	170	W + S	terra firme, liana forest	1500	oxisol	0	1	1	500	20	T.K.	Museo Noel Kempff	4.91	N/A	N/A
Huanchaca Dos, plot 1	HCC-21	Bolivia	14°35′ S	60°45′ W	700–800	W + S	terra firme	1500	oxisol	0	1	1	500	20	L.A.	Museo Noel Kempff	4.91	N/A	N/A
Huanchaca Dos, plot 2	HCC-22	Bolivia	14°35′ S	60°44′ W	700–800	W + S	terra firme	1500	oxisol	0	1	1	500	20	L.A.	Museo Noel Kempff	4.89	N/A	N/A
Las Londras, plot 1	LSL-01	Bolivia	14°24′	61°09′ W	170	W + S	seasonally flooded	1500	ultisol	1	1	1	500	20	L.A.	Museo Noel Kempff	4.95	N/A	N/A
Las Londras, plot 2	LSL-02	Bolivia	14°24′	61°09′ W	170	W + S	seasonally flooded	1500	ultisol	1	1	1	500	20	L.A.	Museo Noel Kempff	4.95	N/A	N/A
Los Fierros Bosque I	LFB-01	Bolivia	14°37′ S	60°52′ W	225	W + S	terra firme	1500	oxisol	0	1	1	500	20	T.K.	Museo Noel Kempff	7.78	N/A	N/A
Los Fierros Bosque II	LFB-02	Bolivia	14°33′ S	60°56′ W	225	W + S	terra firme	1500	oxisol	0	1	1	500	20	T.K.	Museo Noel Kempff	7.76	N/A	N/A
BDFFP, 1101 Gaviao	BDF-03	Brazil	2°24′ S	59°54′ W	75	E + C	terra firme	2200	oxisol	0	1	1	100	100	W.L.	Smithsonian Institution	18.17	10.24	7.92
BDFFP, 1102 Gaviao	BDF-04	Brazil	2°24′ S	59°54′ W	75	E + C	terra firme	2200	oxisol	0	1	1	100	100	W.L.	Smithsonian Institution	18.17	10.25	7.92
BDFFP, 1103 Gaviao	BDF-05	Brazil	2°24′ S	59°54′ W	75	E + C	terra firme	2200	oxisol	0	1	1	100	100	W.L.	Smithsonian Institution	18.08	10.42	7.67
BDFFP, 1113 Florestal	BDF-09	Brazil	2°24′ S	59°54′ W	75	E + C	terra firme	2200	oxisol	0	1	1	100	100	W.L.	Smithsonian Institution	10.25	5.08	5.17
BDFFP, 1201 Gaviao	BDF-06	Brazil	2°24′ S	59°54′ W	75	E + C	terra firme	2200	oxisol	0	1	3	100	100	W.L.	Smithsonian Institution	18.00	10.08	7.92
BDFFP, 1301 Florestal 1	BDF-10	Brazil	2°24′ S	59°54′ W	75	E + C	terra firme	2200	oxisol	0	1	1	100	100	W.L.	Smithsonian Institution	13.67	3.75	9.92
BDFFP, 1301 Florestal 3	BDF-12	Brazil	2°24′ S	59°54′ W	75	E + C	terra firme	2200	oxisol	0	1	2	100	100	W.L.	Smithsonian Institution	13.67	3.75	9.92
BDFFP, 2303 Faz. Dimona 4–6	BDF-01	Brazil	2°24′ S	59°54′ W	75	E + C	terra firme	2200	oxisol	0	1	2	100	100	W.L.	Smithsonian Institution	12.42	5.33	7.09

(*Continued*.)

Table 1. (*Continued.*)

site name	site code	country	latitude	longitude	altitude (m)	region	forest type[a]	rainfall (mm)	soil order	soil (0 = poor, 1 = richer)	seasonality (0 = aseasonal, 1 = seasonal)	area (ha)	max. plot dimension (m)	min. plot dimension (m)	principal investigator	institution/ publication	monitoring period (years)	census interval 1 (years)	census interval 2 (years)
BDFFP, 3304 Porto Alegre	BDF-14	Brazil	2°30′ S	59°54′ W	75	E + C	terra firme	2200	oxisol	0	1	2	100	100	W.L.	Smithsonian Institution	14.17	8.08	6.08
BDFFP, 3402 Cabo Frio	BDF-13	Brazil	2°30′ S	59°54′ W	75	E + C	terra firme	2200	oxisol	0	1	9	100	100	W.L.	Smithsonian Institution	13.02	5.30	7.72
Bionte 1	BNT-01	Brazil	2°38′ S	60°10′ W	73	E + C	terra firme	2200	oxisol	0	1	1	100	100	N.H.	INPA	12.70	4.80	7.90
Bionte 2	BNT-02	Brazil	2°38′ S	60°10′ W	73	E + C	terra firme	2200	oxisol	0	1	1	100	100	N.H.	INPA	12.70	4.80	7.90
Bionte 4	BNT-04	Brazil	2°38′ S	60°10′ W	73	E + C	terra firme	2200	oxisol	0	1	1	100	100	N.H.	INPA	12.70	4.80	7.90
Bionte T4 B1 SB3	BNT-06	Brazil	2°38′ S	60°10′ W	73	E + C	terra firme	2200	oxisol	0	1	1	100	100	N.H.	INPA	7.00	4.00	3.00
Bionte T4 B2 SB1	BNT-05	Brazil	2°38′ S	60°10′ W	73	E + C	terra firme	2200	oxisol	0	1	1	100	100	N.H.	INPA	7.00	4.00	3.00
Bionte T4 B4 SB4	BNT-07	Brazil	2°38′ S	60°10′ W	73	E + C	terra firme	2200	oxisol	0	1	1	100	100	N.H.	INPA	7.00	4.00	3.00
Caxiuana 1	CAX-01	Brazil	1°42′ S	51°32′ W	15	E + C	terra firme	2400	oxisol	0	1	1	1000	10	S.A.	Museu Goeldi	8.38	5.00	3.38
Caxiuana 2	CAX-02	Brazil	1°42′ S	51°32′ W	15	E + C	terra firme	2400	oxisol	0	1	1	1000	10	S.A.	Museu Goeldi	4.00	N/A	N/A
Jacaranda, plots 1–5	JAC-01	Brazil	2°38′ S	60°10′ W	73	E + C	terra firme, valleys, swamp	2200	oxisol	0	1	5	2500	20	N.H.	INPA	6.00	4.00	2.00
Jacaranda, plots 6–10	JAC-02	Brazil	2°38′ S	60°10′ W	73	E + C	terra firme, valleys, swamp	2200	oxisol	0	1	5	2500	20	N.H.	INPA	6.00	4.00	2.00
Jari 1	JRI-01	Brazil	1°00′ S	52°03′ W	82	E + C	terra firme	2346	oxisol	0	1	1	100	100	N.S.	CIFOR, EMBRAPA	10.50	5.00	5.50
Mocambo	MBO-01	Brazil	1°27′ S	48°28′ W	24	E + C	terra firme	3189	ultisol?	1	1	2	200	100	published	Pires & Prance (1977)	15.00	N/A	N/A
Tapajos, RP014, 1–4[b]	TAP-01	Brazil	2°45′ S	55°00′ W	100	E + C	terra firme	1800	oxisol	0	1	1	50	50	N.S.	CIFOR, EMBRAPA	12.00	6.00	6.00
Tapajos, RP014, 5–8[b]	TAP-02	Brazil	2°45′ S	55°00′ W	100	E + C	terra firme	1800	oxisol	0	1	1	50	50	N.S.	CIFOR, EMBRAPA	12.00	6.00	6.00
Tapajos, RP014, 9–12[b]	TAP-03	Brazil	2°45′ S	55°00′ W	100	E + C	terra firme	1800	oxisol	0	1	1	50	50	N.S.	CIFOR, EMBRAPA	12.00	6.00	6.00
Anangu, A1	ANN-01	Ecuador	0°32′ S	76°26′ W	250	W + S	seasonally flooded	3252	ultisol?	1	0	1	2100	PCQ	published	Korning & Balslev (1994)	8.50	N/A	N/A
Anangu, A2	ANN-02	Ecuador	0°32′ S	76°26′ W	310	W + S	terra firme	3252	ultisol	1	0	1	4000	PCQ	published	Korning & Balslev (1994)	8.50	N/A	N/A
Anangu, A3	ANN-03	Ecuador	0°32′ S	76°26′ W	370	W + S	terra firme	3252	ultisol	1	0	1	100	100	published	Korning & Balslev (1994)	4.92	N/A	N/A

(*Continued.*)

Table 1. (*Continued.*)

site name	site code	country	latitude	longitude	altitude (m)	region	forest type[a]	rainfall (mm)	soil order	soil (0 = poor, 1 = richer)	seasonality (0 = aseasonal, 1 = seasonal)	area (ha)	max. plot dimension (m)	min. plot dimension (m)	principal investigator	institution/ publication	monitoring period (years)	census interval 1 (years)	census interval 2 (years)
Bogi 1	BOG-01	Ecuador	0°42′ S	76°26′ W	271	W + S	terra firme	3252	inceptisol	1	0	1	1000	10	N.P.	Duke University	5.83	N/A	N/A
Bogi 2	BOG-02	Ecuador	0°42′ S	76°25′ W	270	W + S	terra firme	3252	inceptisol	1	0	11	1000	10	N.P.	Duke University	5.83	N/A	N/A
Cuyabeno	CYB-01	Ecuador	0°00′ S	76°12′ W	265	W + S	terra firme	3252	inceptisol	1	0	1	100	100	published	Korning & Balslev (1994)	2.54	N/A	N/A
Jatun Sacha 2	JAS-02	Ecuador	1°04′ S	77°36′ W	450	W + S	terra firme	4013	ultisol/ inceptisol	1	0	1	100	100	D.N.	Herbario Nacional	14.42	6.92	7.50
Jatun Sacha 3	JAS-03	Ecuador	1°04′ S	77°40′ W	450	W + S	terra firme	4013	ultisol/ inceptisol	1	0	1	100	100	D.N.	Herbario Nacional	13.17	9.63	3.54
Jatun Sacha 4	JAS-04	Ecuador	1°04′ S	77°40′ W	450	W + S	terra firme	4013	ultisol/ inceptisol	1	0	0.92	100	100	D.N.	Herbario Nacional	11.55	3.95	7.60
Jatun Sacha 5	JAS-05	Ecuador	1°04′ S	77°40′ W	450	W + S	terra firme	4013	entisol	1	0	1	100	100	D.N.	Herbario Nacional	12.67	5.08	7.58
Tiputini 2	TIP-02	Ecuador	0°38′ S	76°08′ W	246	W + S	terra firme	3252	inceptisol	1	0	0.8	100	100	N.P.	Duke University	4.42	N/A	N/A
Tiputini 3	TIP-03	Ecuador	0°38′ S	76°08′ W	248	W + S	seasonally flooded	3252	entisol	1	0	1	100	100	N.P.	Duke University	4.00	N/A	N/A
Nouragues GP	NOR-02	French Guiana	4°05′ N	52°40′ W	110	E + C	terra firme	2997	oxisol	0	1	10	1000	100	J.Ch., J.O.	CNRS	7.52	N/A	N/A
Nouragues PP	NOR-01	French Guiana	4°05′ N	52°40′ W	110	E + C	terra firme	2997	oxisol	0	1	12	400	300	J.Ch., J.O.	CNRS	9.55	N/A	N/A
Paracou	PAR	French Guiana	5°15′ N	52°50′ W	19	E + C	terra firme	3200	oxisol?	0	1	18.75	250	250	published	Favrichon *et al.* (1997)	11.00	N/A	N/A
Saint Elie Transect 1	ELI-01	French Guiana	5°30′ N	53°00′ W	40	E + C	terra firme	3120	oxisol?	0	1	0.78	390	20	published	Pelissier & Riera (1993)	10.00	N/A	N/A
Saint Elie Transect 2	ELI-02	French Guiana	5°30′ N	53°00′ W	40	E + C	terra firme	3120	oxisol?	0	1	1	500	20	published	Pelissier & Riera (1993)	10.00	N/A	N/A
Allpahuayo A, poorly drained	ALP-11	Peru	3°57′ S	73°26′ W	114	W + S	terra firme	2763	ultisol	1	0	0.44	500	20	O.P., R.V.	Leeds, JBM	10.15	5.25	4.9
Allpahuayo A, well drained	ALP-12	Peru	3°57′ S	73°26′ W	125	W + S	terra firme	2763	entisol (psamment)	0	0	0.4	500	20	O.P., R.V.	Leeds, JBM	10.15	5.25	4.9
Allpahuayo B, clayey	ALP-22	Peru	3°57′ S	73°26′ W	114	W + S	terra firme	2763	ultisol	1	0	0.44	500	20	O.P., R.V.	Leeds, JBM	10.16	5.25	4.91
Allpahuayo B, sandy	ALP-21	Peru	3°57′ S	73°26′ W	125	W + S	terra firme	2763	entisol (psamment)	0	0	0.48	500	20	O.P., R.V.	Leeds, JBM	10.16	5.25	4.91
Altos de Maizal	ALM-01	Peru	11°48′ S	71°28′ W	400	W + S	terra firme	2300	ultisol	1	1	2	200	100	J.T., P.N.	Duke University	5.00	N/A	N/A
Cocha Salvador Manu	MNU-08	Peru	11°59′ S	71°11′ W	400	W + S	rarely flooded	2300	entisol	1	1	2	200	100	J.T., P.N.	Duke University	10.07	5.04	5.03
Cuzco Amazonico, CUZAM1E	CUZ-01	Peru	12°35′ S	69°09′ W	200	W + S	terra firme	2417	inceptisol	1	1	1	500	20	O.P., R.V.	Leeds, JBM	9.38	5.23	4.14
Cuzco Amazonico, CUZAM1U	CUZ-02	Peru	12°35′ S	69°09′ W	200	W + S	terra firme	2417	inceptisol	1	1	1	500	20	O.P., R.V.	Leeds, JBM	9.35	5.21	4.14

(*Continued.*)

Table 1. (*Continued.*)

site name	site code	country	latitude	longitude	altitude (m)	region	forest type[a]	rainfall (mm)	soil order	soil (0 = poor, 1 = richer)	seasonality (0 = aseasonal, 1 = seasonal)	area (ha)	max. plot dimension (m)	min. plot dimension (m)	principal investigator	institution/ publication	monitoring period (years)	census interval 1 (years)	census interval 2 (years)
Cuzco Amazonico, CUZAM2E	CUZ-03	Peru	12°34′ S	69°08′ W	200	W + S	terra firme	2417	inceptisol	1	1	1	500	20	O.P., R.V.	Leeds, JBM	9.37	5.22	4.15
Cuzco Amazonico, CUZAM2U	CUZ-04	Peru	12°34′ S	69°08′ W	200	W + S	terra firme	2417	inceptisol	1	1	1	500	20	O.P., R.V.	Leeds, JBM	9.34	5.18	4.16
Infierno	INF-01	Peru	12°44′ S	69°42′ W	226	W + S	terra firme	2300	inceptisol	1	1	1	1000	10	M.A.	New York Botanical Garden	7.08	N/A	N/A
Jenaro Herrera: Spichiger	JEN-10	Peru	4°55′ S	73°44′ W	120	W + S	terra firme	2521	oxisol	0	0	1	100	100	published	Spichiger *et al.* (1996)	5.00	N/A	N/A
Jenaro Herrera, Restinga plot 3	JEN-03	Peru	4°55′ S	73°44′ W	110	W + S	seasonally flooded	2452	entisol	1	0	1	100	100	published	Nebel *et al.* (2001)	4.04	N/A	N/A
Jenaro Herrera, Restinga, plot 6	JEN-06	Peru	4°55′ S	73°44′ W	108	W + S	seasonally flooded	2452	entisol	1	0	1	100	100	published	Nebel *et al.* (2001)	3.87	N/A	N/A
Jenaro Herrera, Tahuampa plot 9	JEN-09	Peru	4°55′ S	73°44′ W	106	W + S	seasonally flooded	2452	entisol	1	0	1	100	100	published	Nebel *et al.* (2001)	4.04	N/A	N/A
Manu, clay	MNU-02	Peru	11°52′ S	71°21′ W	312	W + S	terra firme	2300	ultisol	1	1	0.34	< 100	< 50	J.T., P.N.	Duke University	15.00	10.00	5.00
Manu, Cocha Cashu Trail 12	MNU-05	Peru	11°52′ S	71°21′ W	312	W + S	rarely flooded	2300	entisol	1	1	2	150	150	J.T., P.N.	Duke University	10.00	5.00	5.00
Manu, Cocha Cashu Trail 2 & 31	MNU-06	Peru	11°52′ S	71°21′ W	312	W + S	rarely flooded	2300	entisol	1	1	2.25	150	150	J.T., P.N.	Duke University	10.00	5.00	5.00
Manu, Cocha Cashu Trail 3	MNU-01	Peru	11°52′ S	71°21′ W	312	W + S	rarely flooded	2300	entisol	1	1	0.97	160	60	J.T., P.N.	Duke University	25.75	15.75	10.00
Manu, terra firme ravine	MNU-04	Peru	11°53′ S	71°21′ W	312	W + S	terra firme	2300	ultisol	1	1	2	200	100	J.T., P.N.	Duke University	10.00	5.00	5.00
Manu, terra firme terrace	MNU-03	Peru	11°53′ S	71°21′ W	312	W + S	terra firme	2300	ultisol	1	1	2	200	100	J.T., P.N.	Duke University	10.00	5.00	5.00
Manu, trans-Manu upland	MNU-07	Peru	11°53′ S	71°21′ W	312	W + S	terra firme	2300	ultisol	1	1	1	100	100	P.N., J.T.	UNSAAC, Duke University	3.00	N/A	N/A
Mishana	MSH-01	Peru	3°47′ S	73°30′ W	114	W + S	terra firme	2763	spodosol/ ultisol	1	0	1	100	100	O.P., R.V.	Leeds, JBM	7.67	N/A	N/A
Pakitza, Manu River, plot 1	PAK-01	Peru	11°55′ S	71°15′ W	313	W + S	terra firme	2300	ultisol?	1	1	1	100	100	J.Co.	Smithsonian Institution	4.00	N/A	N/A
Pakitza, Manu River, plot 2	PAK-02	Peru	11°55′ S	71°15′ W	313	W + S	rarely flooded	2300	entisol?	1	1	1	100	100	J.Co.	Smithsonian Institution	4.00	N/A	N/A
Pakitza, Manu river, swamp	PAK-03	Peru	11°55′ S	71°15′ W	313	W + S	swamp	2300	eutrophic histosol?	1	1	1	100	100	J.Co.	Smithsonian Institution	4.00	N/A	N/A
Sucusari A	SUC-01	Peru	3°26′ S	72°54′ W	107	W + S	terra firme	2671	ultisol	1	0	1	500	20	O.P., R.V.	Leeds, JBM	8.93	3.95	4.98
Sucusari B	SUC-02	Peru	3°26′ S	72°54′ W	107	W + S	terra firme	2671	ultisol	1	0	1	500	20	O.P., R.V.	Leeds, JBM	8.93	3.95	4.99
Tambopata plot four	TAM-06	Peru	12°50′ S	69°18′ W	220	W + S	terra firme	2300	inceptisol	1	1	0.96	100	100	O.P., R.V.	Leeds, JBM	16.84	7.83	9.01
Tambopata plot one	TAM-02	Peru	12°50′ S	69°17′ W	220	W + S	terra firme	2300	inceptisol	1	1	1	100	100	O.P., R.V.	Leeds, JBM	20.71	11.7	9.01

(*Continued.*)

Table 1. (*Continued.*)

site name	site code	country	latitude	longitude	altitude (m)	region	forest type[a]	rainfall (mm)	soil order	soil (0 = poor, 1 = richer)	seasonality (0 = aseasonal, 1 = seasonal)	area (ha)	max. plot dimension (m)	min. plot dimension (m)	principal investigator	institution/ publication	monitoring period (years)	census interval 1 (years)	census interval 2 (years)
Tambopata plot six	TAM-07	Peru	12°50′ S	69°16′ W	220	W + S	terra firme	2300	oxisol	1	1	1	100	100	O.P., R.V.	Leeds, JBM	14.97	7.78	7.18
Tambopata plot three	TAM-05	Peru	12°50′ S	69°17′ W	220	W + S	terra firme	2300	ultisol	1	1	1	100	100	O.P., R.V.	Leeds, JBM	16.86	7.84	9.02
Tambopata plot two swamp	TAM-03	Peru	12°50′ S	69°17′ W	220	W + S	swamp	2300	histosol (dystrophic)	0	1	0.58	100	100	O.P., R.V.	Leeds, JBM	15.00	6.98	7.98
Tambopata plot two swamp edge	TAM-04	Peru	12°50′ S	69°17′ W	220	W + S	terra firme	2300	inceptisol	1	1	0.42	100	100	O.P., R.V.	Leeds, JBM	14.96	6.98	7.98
Tambopata plot zero	TAM-01	Peru	12°50′ S	69°17′ W	220	W + S	terra firme	2300	inceptisol	1	1	1	100	100	O.P., R.V.	Leeds, JBM	16.81	7.75	9.06
Yanamono A	YAN-01	Peru	3°26′ S	72°51′ W	104	W + S	terra firme	2671	cambisol/ mollisol	1	0	1	120	100	O.P., R.V.	Leeds, JBM	17.59	7.83	9.76
CELOS 67/9A plot 8	CEL-08	Suriname	5°13′ N	55°40′ W	66	E + C	terra firme	2201	ultisol	1	1	0.64	80	80	published	de Graaf *et al.* (1999)	28.00	?	?
Cano Rosalba, Z1, CR1	CRS-01	Venezuela	9°15′ N	72° W	60	E + C	terra firme	3380	oxisol	0	1	1	100	100	published	Veillon (1985)	2.02	N/A	N/A
Cano Rosalba, Z2, CR2	CRS-02	Venezuela	9°15′ N	72° W	35	E + C	terra firme	3000	inceptisol	1	1	1	100	100	published	Veillon (1985)	1.99	N/A	N/A
El Dorado km 91	ELD-12	Venezuela	6°30′ N	61°30′ W	210	E + C	terra firme	3200	oxisol?	0	1	0.5	50	50	A. Torres, S. Brown	Univ. de los Andes, Winrock	22.89	9.63	13.26
El Dorado km 98	ELD-34	Venezuela	6°30′ N	61°30′ W	380	E + C	terra firme	3200	oxisol?	0	1	0.5	50	50	A. Torres, S. Brown	Univ. de los Andes, Winrock	9.63	4.66	4.98
Rio Grande	RIO-12	Venezuela	8° N	61°45’ W	270	E + C	terra firme	2500	oxisol?	0	1	0.5	50	50	A. Torres, S. Brown	Univ. de los Andes, Winrock	22.88	9.62	13.26
San Carlos de Rio Negro, SC1	SCR-01	Venezuela	1°56′ N	67°03′ W	122	E + C	terra firme	3520	oxisol	0	0	1	100	100	published	Uhl *et al.* (1985)	10.71	5.25	5.08
San Carlos de Rio Negro, SC2	SCR-02	Venezuela	1°45′ N	67° W	122	E + C	terra firme	3520	spodosol	0	0	0.25	25	25	published	Veillon (1985)	4.01	N/A	N/A
San Carlos de Rio Negro, SC3	SCR-03	Venezuela	1°45′ N	67° W	117	E + C	terra firme	3520	spodosol	0	0	2	200	50	published	Heuveldop & Neumann (1983)	4.00	N/A	N/A

[a] Terra firme, defined as presumed not to have experienced fluvial flooding in at least 250 years.

[b] Tapajos: these are 12 ha × 0.25 ha plots laid out in a randomized fashion over an area of 300 m × 1200 m; at the time of analysis treated as 3 × 1 ha units.

Table 2. Site-by-site summary structural and dynamic properties, all sites.
(Data are the best available to the lead author at the time of final analyses, but are subject to future revision as a result of additional censuses and continued error-checking. Date of final analyses for this paper, *ca*. 1 March 2003.)

site name	country	site code	first census (*n* censuses)	'majestic forest' bias possible?[a]	monitoring period (years)	basal area start (m^2 ha^{-1})	stems start (ha^{-1})	recruitment[b] (% yr^{-1})	mortality[b] (% yr^{-1})	turnover[b] (% yr^{-1})	recruitment, interval corrected[b] (% yr^{-1})	mortality, interval corrected[b] (% yr^{-1})	turnover, interval corrected[b] (% yr^{-1})
BDFFP, 1102 Gaviao	Brazil	BDF-04	1981.13 (4)	Y?, g?	18.17	28.39	590	2.49	2.81	2.65	3.14	3.54	3.34
Cerro Pelao 1	Bolivia	CRP-01	1994.21 (3)	Y?, d?	7.25	20.30	552	1.87	3.32	2.59	2.19	3.89	3.03
Cerro Pelao 2	Bolivia	CRP-02	1994.27 (3)	N, df	7.19	24.09	472	3.05	2.30	2.67	3.57	2.69	3.13
Chore 1	Bolivia	CHO-01	1996.53 (2)	N, cf	4.91	14.08	565	2.39	2.61	2.50	2.71	2.96	2.84
Huanchaca Dos, plot 1	Bolivia	HCC-21	1996.52 (2)	N, cef	4.91	24.69	529	2.38	2.85	2.61	2.70	3.24	2.96
Huanchaca Dos, plot 2	Bolivia	HCC-22	1996.54 (2)	N, cef	4.89	26.66	644	1.18	1.79	1.48	1.34	2.03	1.68
Las Londras, plot 1	Bolivia	LSL-01	1996.53 (2)	N, cf	4.95	17.52	560	1.56	2.86	2.21	1.77	3.25	2.51
Las Londras, plot 2	Bolivia	LSL-02	1996.53 (2)	N, cf	4.95	20.45	630	1.25	1.19	1.22	1.42	1.35	1.39
Los Fierros Bosque I	Bolivia	LFB-01	1993.62 (3)	N, cf	7.78	23.57	557	2.86	3.36	3.11	3.37	3.96	3.66
Los Fierros Bosque II	Bolivia	LFB-02	1993.65 (3)	N, cf	7.76	28.03	540	2.82	2.73	2.78	3.32	3.22	3.28
BDFFP, 1101 Gaviao	Brazil	BDF-03	1981.13 (4)	N, fg	18.17	28.39	593	1.10	1.21	1.15	1.39	1.53	1.45
BDFFP, 1103 Gaviao	Brazil	BDF-05	1981.21 (4)	N, fg	18.08	25.28	650	0.93	1.84	1.12	1.18	2.32	1.41
BDFFP, 1113 Florestal	Brazil	BDF-09	1987.04 (3)	N, fg	10.25	29.49	571	0.67	1.25	0.96	0.81	1.51	1.16
BDFFP, 1201 Gaviao	Brazil	BDF-06	1981.29 (4)	N, fg	18.00	25.48	632	1.17	1.48	1.33	1.47	1.87	1.68
BDFFP, 1301 Florestal 1	Brazil	BDF-10	1983.46 (3)	N, fg	13.67	27.47	632	1.49	1.40	1.44	1.84	1.73	1.78
BDFFP, 1301 Florestal 2	Brazil	BDF-11	1983.46 (3)	N, fg	13.67	28.85	629	0.61	0.68	0.65	0.75	0.84	0.80
BDFFP, 1301 Florestal 3	Brazil	BDF-12	1983.46 (3)	N, fg	13.67	28.45	617	0.60	0.61	0.60	0.74	0.75	0.74
BDFFP, 2303 Faz. Dimona 4–6	Brazil	BDF-01	1985.29 (4)	N, dfg	12.42	30.15	688	1.23	1.18	1.20	1.50	1.44	1.47
BDFFP, 3304 Porto Alegre	Brazil	BDF-14	1984.21 (5)	N, beg	14.17	32.03	651	1.25	1.29	1.27	1.55	1.59	1.57
BDFFP, 3402 Cabo Frio	Brazil	BDF-13	1985.86 (4)	N, defg	13.02	26.52	565	1.31	0.98	1.14	1.61	1.20	1.40
Bionte 1	Brazil	BNT-01	1986.50 (11)	N, af	12.70	28.04	561	1.07	0.91	0.99	1.31	1.12	1.21
Bionte 2	Brazil	BNT-02	1986.50 (11)	N, af	12.70	30.14	692	0.64	0.64	0.64	0.78	0.78	0.78
Bionte 4	Brazil	BNT-04	1986.50 (10)	N, af	12.70	27.76	608	1.07	1.22	1.14	1.31	1.50	1.40
Bionte T4 B1 SB3	Brazil	BNT-06	1986.50 (5)	N, a	7.00	32.33	576	1.21	1.43	1.32	1.41	1.67	1.54
Bionte T4 B2 SB1	Brazil	BNT-05	1986.50 (5)	N, af	7.00	26.05	565	1.72	1.52	1.62	2.01	1.78	1.89
Bionte T4 B4 SB4	Brazil	BNT-07	1986.50 (5)	N, af	7.00	30.59	643	1.23	1.01	1.12	1.44	1.18	1.31

(*Continued*.)

Table 2. (*Continued.*)

site name	country	site code	first census (*n* censuses)	'majestic forest' bias possible?[a]	monitoring period (years)	basal area start (m^2 ha^{-1})	stems start (ha^{-1})	recruitment[b] (% yr^{-1})	mortality[b] (% yr^{-1})	turnover[b] (% yr^{-1})	recruitment, interval corrected[b] (% yr^{-1})	mortality, interval corrected[b] (% yr^{-1})	turnover, interval corrected[b] (% yr^{-1})
Caxiuana 1	Brazil	CAX-01	1994.50 (3)	N, cfg	8.38	30.07	524	0.78	0.90	0.84	0.93	1.06	1.00
Caxiuana 2	Brazil	CAX-02	1995.50 (2)	N, cg	4.00	33.11	508	1.56	1.31	1.44	1.74	1.46	1.61
Jacaranda, plots 1–5	Brazil	JAC-01	1996.50 (2)	N, cg	6.00	27.51	593	1.61	1.03	1.32	1.86	1.19	1.53
Jacaranda, plots 6–10	Brazil	JAC-02	1996.50 (3)	N, cg	6.00	26.60	573	1.34	1.11	1.23	1.55	1.28	1.41
Jari 1	Brazil	JRI-01	1985.50 (6)	N, bfg	10.50	32.99	572	1.59	1.17	1.38	1.92	1.41	1.67
Mocambo	Brazil	MBO-01	1956.50 (2)	N, deg	15.00	27.70	453	0.93	1.37	1.15	1.15	1.70	1.43
Tapajos, RP014, 1–4[c]	Brazil	TAP-01	1983.50 (4)	N, af	12.00	23.61	527	1.56	0.69	1.13	1.90	0.84	1.38
Tapajos, RP014, 5–8[c]	Brazil	TAP-02	1983.50 (4)	N, af	12.00	27.82	479	1.63	0.61	1.12	1.99	0.74	1.37
Tapajos, RP014, 9–12[c]	Brazil	TAP-03	1983.50 (4)	N, af	12.00	31.25	491	1.50	0.82	1.16	1.83	1.00	1.42
Añangu, A1	Ecuador	ANN-01	1982.48 (2)	N, cg	8.50	36.80	417	N/A	3.08	3.08	N/A	3.66	3.66
Añangu, A2	Ecuador	ANN-02	1982.48 (2)	N, cg	8.50	33.82	728	N/A	1.88	1.88	N/A	2.23	2.23
Añangu, A3	Ecuador	ANN-03	1986.04 (2)	N, fg	4.92	22.20	734	1.80	1.89	1.84	2.04	2.15	2.09
Bogi 1	Ecuador	BOG-01	1996.29 (2)	N, cfg	5.83	28.40	544	2.88	2.08	2.48	3.32	2.40	2.86
Bogi 2	Ecuador	BOG-02	1996.29 (2)	N, cfg	5.83	25.30	611	4.05	2.96	3.51	4.66	3.41	4.04
Cuyabeno	Ecuador	CYB-01	1988.40 (2)	N, fg	2.54	27.20	697	3.05	1.03	2.04	3.29	1.11	2.20
Jatun Sacha 2	Ecuador	JAS-02	1987.63 (4)	Y? g?	14.42	30.18	724	1.94	1.98	1.96	2.40	2.45	2.43
Jatun Sacha 3	Ecuador	JAS-03	1988.88 (4)	N, fg	13.17	27.96	648	2.09	1.92	2.00	2.57	2.36	2.46
Jatun Sacha 4	Ecuador	JAS-04	1990.45 (3)	N, ef	11.55	32.47	720	3.01	1.22	2.12	3.54	1.43	2.49
Jatun Sacha 5	Ecuador	JAS-05	1989.38 (4)	N, ef	12.67	30.90	536	2.53	2.10	2.31	3.10	2.57	2.83
Tiputini 2	Ecuador	TIP-02	1997.71 (2)	N, acf	4.42	27.18	626	2.37	2.04	2.20	2.67	2.30	2.48
Tiputini 3	Ecuador	TIP-03	1998.13 (2)	N, f	4.00	23.77	444	2.77	2.55	2.66	3.09	2.85	2.97
Nouragues GP	French Guiana	NOR-02	1993 and 1994 (2)	N, cf	7.52	28.13	493	1.23	2.07	1.65	1.45	2.43	1.94
Nouragues PP	French Guiana	NOR-01	1992.50 (2)	N, cf	9.55	30.28	524	1.13	1.51	1.32	1.35	1.81	1.58
Paracou	French Guiana	PAR	1984.50 (?)	N, cf	11.00	30.60	625	0.83	1.05	0.94	1.01	1.27	1.14
Saint Elie Transect 1	French Guiana	ELI-01	1981.50 (2)	N, c	10.00	35.83	615	0.82	0.85	0.83	0.99	1.02	1.00
Saint Elie Transect 2	French Guiana	ELI-02	1981.50 (2)	N, cf	10.00	37.94	609	0.95	1.02	0.98	1.14	1.23	1.18
Allpahuayo A poorly drained	Peru	ALP-11	1990.87 (3)	N, acf	10.15	27.36	580	2.26	2.69	2.48	2.72	3.24	2.99
Allpahuayo A, well drained	Peru	ALP-12	1990.87 (3)	N, ac	10.15	25.19	570	1.68	2.44	2.06	2.02	2.94	2.48

(*Continued.*)

Table 2. (*Continued.*)

site name	country	site code	first census (*n* censuses)	'majestic forest' bias possible?[a]	monitoring period (years)	basal area start ($m^2\ ha^{-1}$)	stems start (ha^{-1})	recruitment[b] (% yr^{-1})	mortality[b] (% yr^{-1})	turnover[b] (% yr^{-1})	recruitment, interval corrected[b] (% yr^{-1})	mortality, interval corrected[b] (% yr^{-1})	turnover, interval corrected[b] (% yr^{-1})
Allpahuayo B, clayey	Peru	ALP-22	1990.87 (3)	N, acf	10.16	25.49	614	2.32	1.93	2.12	2.79	2.32	2.55
Allpahuayo B, sandy	Peru	ALP-21	1990.87(3)	N, acf	10.16	26.88	575	2.47	2.05	2.26	2.97	2.47	2.72
Altos de Maizal	Peru	ALM-01	1994.75 (2)	N, df	5.00	30.99	672	1.04	1.68	1.36	1.18	1.91	1.55
Cocha Salvador Manu	Peru	MNU-08	1991.75 (3)	N, cf	10.07	36.81	563	1.52	1.33	1.43	1.83	1.60	1.71
Cuzco Amazonico, CUZAM1E	Peru	CUZ-01	1989.39 (3)	N, acf	9.38	25.41	489	2.56	1.70	2.13	3.06	2.03	2.55
Cuzco Amazonico, CUZAM1U	Peru	CUZ-02	1989.42 (3)	N, acf	9.35	25.27	509	2.08	1.51	1.8	2.49	1.81	2.15
Cuzco Amazonico, CUZAM2E	Peru	CUZ-03	1989.40 (3)	N, acf	9.37	21.69	470	2.72	2.13	2.43	3.25	2.55	2.91
Cuzco Amazonico, CUZAM2U	Peru	CUZ-04	1989.44 (3)	N, acf	9.34	27.26	571	2.57	2.13	2.35	3.07	2.55	2.81
Infierno	Peru	INF-01	1988.88 (2)	N, cg	7.08	N/A	809	1.94	2.08	2.01	2.27	2.43	2.35
Jenaro Herrera: Spichiger	Peru	JEN-10	1976.50 (2)	N, a	5.00	23.60	504	N/A	1.14	1.14	N/A	1.30	1.30
Jenaro Herrera, Restinga, Plot 3	Peru	JEN-03	1993.71 (4)	N, f	4.04	25.19	452	4.57	3.16	3.87	5.11	3.53	4.33
Jenaro Herrera, Restinga, Plot 6	Peru	JEN-06	1993.71 (4)	N, f	3.87	24.32	569	3.56	2.20	2.88	3.97	2.45	3.21
Jenaro Herrera, Tahuampa, Plot 9	Peru	JEN-09	1993.71 (4)	N, f	4.04	26.91	532	2.99	2.49	2.74	3.34	2.78	3.06
Manu, Cocha Cashu Trail 12	Peru	MNU-05	1989.99 (3)	N, df	10.00	33.59	599	1.84	1.63	1.73	2.21	1.96	2.08
Manu, Cocha Cashu Trail 2 & 31	Peru	MNU-06	1989.80 (3)	N, df	10.00	32.21	511	1.96	1.83	1.89	2.35	2.20	2.27
Manu, Cocha Cashu Trail 3	Peru	MNU-01	1975.00 (6)	N, f	25.75	28.56	549	2.31	2.31	2.31	3.00	2.99	2.99
Manu, clay	Peru	MNU-02	1974.50 (3)	N, f	15.00	30.61	610	2.32	2.79	2.56	2.88	3.46	3.18
Manu, trans-Manu upland	Peru	MNU-07	1986.60 (2)	Y? g?	3.00	N/A	617	3.53	2.99	3.26	3.85	3.26	3.56
Manu, terra firme ravine	Peru	MNU-04	1991.75 (3)	N, df	10.00	27.12	587	2.30	2.13	2.20	2.77	2.56	2.64
Manu, terra firme terrace	Peru	MNU-03	1991.75 (3)	N, df	10.00	25.90	578	3.34	3.13	3.24	4.02	3.76	3.89
Mishana	Peru	MSH-01	1983.04 (2)	N, f	7.67	28.66	829	1.39	1.58	1.49	1.64	1.86	1.75
Pakitza, Manu River, plot 2	Peru	PAK-02	1987.50 (2)	Y? g?	4.00	37.20	610	1.14	2.27	1.71	1.27	2.54	1.91
Pakitza, Manu River, plot 1	Peru	PAK-01	1987.50 (2)	Y? g?	4.00	27.11	550	1.59	2.66	2.13	1.78	2.97	2.38
Pakitza, Manu river, swamp	Peru	PAK-03	1987.50 (2)	Y? e? g?	4.00	29.98	714	3.94	2.01	2.97	4.40	2.25	3.32
Sucusari A	Peru	SUC-01	1992.13 (3)	N, ac	8.93	28.25	612	1.76	2.02	1.89	2.10	2.41	2.25

(*Continued.*)

Table 2. (*Continued.*)

site name	country	site code	first census (*n* censuses)	'majestic forest' bias possible?[a]	monitoring period (years)	basal area start ($m^2\ ha^{-1}$)	stems start (ha^{-1})	recruitment[b] (% yr^{-1})	mortality[b] (% yr^{-1})	turnover[b] (% yr^{-1})	recruitment, interval corrected[b] (% yr^{-1})	mortality, interval corrected[b] (% yr^{-1})	turnover, interval corrected[b] (% yr^{-1})
Sucusari B	Peru	SUC-02	1992.13 (3)	N, ac	8.93	29.46	607	2.25	2.53	2.39	2.68	3.01	2.85
Tambopata plot four	Peru	TAM-06	1983.71 (5)	N, efg	16.84	30.54	520	2.94	1.54	2.24	3.69	1.93	2.81
Tambopata plot one	Peru	TAM-02	1979.87 (8)	N, fg	20.71	27.44	576	2.12	1.50	1.81	2.70	1.91	2.31
Tambopata plot six	Peru	TAM-07	1983.76 (5)	N, fg	14.97	27.36	548	2.55	2.55	2.55	3.17	3.17	3.17
Tambopata plot three	Peru	TAM-05	1983.70 (6)	N, fg	16.86	24.27	548	2.59	2.33	2.46	3.25	2.92	3.08
Tambopata plot two swamp	Peru	TAM-03	1983.79 (4)	N, eg	15.00	N/A	617	0.81	1.09	0.95	1.01	1.35	1.18
Tambopata plot two swamp edge	Peru	TAM-04	1983.79 (4)	N, af	14.96	28.56	705	2.26	2.42	2.34	2.81	3.00	2.91
Tambopata plot zero	Peru	TAM-01	1983.78 (6)	N, fg	16.81	26.91	555	2.49	2.18	2.33	3.12	2.73	2.92
Yanamono A	Peru	YAN-01	1983.46 (6)	N, efg	17.59	30.95	570	2.44	2.47	2.46	3.07	3.11	3.09
CELOS 67/9A plot8	Suriname	CEL-08	1967.50 (?)	N, a	18.00	N/A	N/A	N/A	1.70	1.70	N/A	1.70	1.70
Cano Rosalba, Z1, CR1	Venezuela	CRS-01	1970.68 (2)	N, f	2.02	17.29	532	2.21	0.66	1.43	2.34	0.70	1.51
Cano Rosalba, Z2, CR2	Venezuela	CRS-02	1970.71 (2)	N, f	1.99	28.61	266	1.54	1.73	1.64	1.63	1.83	1.73
El Dorado km 91	Venezuela	ELD-12	1971.55 (15)	N, f	22.89	27.02	468	1.11	0.82	0.96	1.43	1.05	1.23
El Dorado km 98	Venezuela	ELD-34	1971.56 (11)	N, f	9.63	23.74	492	2.89	1.54	2.22	3.46	1.85	2.66
Rio Grande	Venezuela	RIO-12	1971.58 (16)	N, f	22.88	28.17	540	1.20	0.86	1.03	1.54	1.10	1.32
San Carlos de Rio Negro, SC1	Venezuela	SCR-01	1975.71 (2)	N, af?	10.71	27.80	786	1.43	1.14	1.29	1.73	1.38	1.56
San Carlos de Rio Negro, SC2	Venezuela	SCR-02	1976.14 (2)	N, af	4.01	31.89	680	0.74	0.44	0.59	0.83	0.49	0.66
San Carlos de Rio Negro, SC3	Venezuela	SCR-03	1975.50 (2)	N, d	4.00	33.05	964	1.54	1.63	1.58	1.72	1.82	1.77

[a] a, pre-selected randomly or systematically on a larger grid; b, randomized with respect to the forest growth phase; c, 300 m or more long; d, 2 ha or more, much larger than the typical grain of gap-phase dynamics; e, sampling most of the total area of the target stratum; f, gained basal area in the monitoring period; g, consciously selected to be unbiased with respect to topography and other microsite factors. In remaining plots there is a possibility that stem dynamic patterns might have been affected by unconscious 'majestic forest' bias when the plot location was selected. Note that these descriptions may be incomplete; they represent the best of our knowledge at the time of writing and some are subject to uncertainty or revision if more information becomes available.

[b] Rates are calculated over the total observation period for the plot, treating it as a single interval.

[c] Tapajos: these are 12 ha × 0.25 ha plots laid out in a randomized fashion over an area of 300 m × 1200 m; at the time of analysis treated as 3 × 1 ha units.

Table 3. Tests of increase in dynamic parameters.
(Results are given for *t*-tests without assuming equal variance, or for non-parametric equivalents when assumptions of normality are clearly violated. For raw data, census-interval corrected data and majestic-forest corrected data, we compare the first year in which ⩾10 sites monitored with the last, using two sample *t*-tests or Mann–Whitney *U*-tests. For all data corrected for site-switching, we compare the end interval with the start interval for all multi-interval sites except those with the end interval starting in 1976 or earlier, using paired *t*-tests or Wilcoxon signed-rank tests. See text for further details.)

	first interval rates		final interval rates		final–initial difference
	mean ± s.e. of mean (% yr^{-1})	*n*, mean mid-year of monitoring	mean ± s.e. of mean (% yr^{-1})	*n*, mean mid-year of monitoring	mean ± 95% CI (% yr^{-1}) (median for non-parametric comparisons)
(*a*) turnover					
pan-Amazon					
raw data: 1976–2001	1.22 ± 0.13	10, 1977	2.34 ± 0.11	31, 1999	1.12 ± 0.34, $t = 6.75$, $p = 0.000$, d.f. = 23
corrected for census-interval only: 1976–2001	1.30 ± 0.21	10, 1977	2.67 ± 0.13	32, 1999	1.24 ± 0.39, $t = 5.58$, $p = 0.000$, d.f. = 14
corrected for majestic forest effects only: 1976–2001	1.24 ± 0.13	10, 1977	2.35 ± 0.12	29, 1999	1.23 ± 0.33, $t = 6.46$, $p = 0.000$, d.f. = 25
corrected for site-switching only	1.42 ± 0.08	56, 1987	1.91 ± 0.11	56, 1997	0.49 ± 0.18, $t = 5.38$, $p = 0.000$, $n = 56$
corrected for census-interval, site-switching and majestic forest effects	1.65 ± 0.09	55, 1987	2.11 ± 0.12	55, 1997	0.46 ± 0.28, $t = 5.03$, $p = 0.000$, $n = 55$
west and south Amazonia					
raw data: 1983–2001	1.94 ± 0.18	13, 1984	2.48 ± 0.11	27, 1999	0.54 ± 0.43, $t = 2.61$, $p = 0.017$, d.f. = 20**
corrected for census-interval, site-switching and majestic forest effects	2.18 ± 0.10	27, 1987	2.80 ± 0.13	27, 1997	0.62 ± 0.32, $t = 4.12$, $p = 0.000$, $n = 27$
east and central Amazonia					
raw data: 1981–1999	1.01 ± 0.10	11, 1984	1.38 ± 0.19	14, 1996	+0.38 ± 0.43, $W = 112$, $p = 0.08$, $n = 25$
corrected for census-interval, site-switching and majestic forest effects	1.20 ± 0.07	28, 1986	1.43 ± 0.10	28, 1996	+0.24 ± 0.20, $t = 2.50$, $p = 0.02$, $n = 28$
richer soils					
raw data: 1983–2001	2.01 ± 0.16	11, 1986	2.44 ± 0.13	20, 1999	+0.42 ± 0.42, $t = 2.05$, $p = 0.05$, d.f. = 21
corrected for census-interval, site-switching and majestic forest effects	2.20 ± 0.11	24, 1989	2.83 ± 0.13	24, 1998	+0.66 ± 0.28, $t = 4.15$, $p = 0.000$, $n = 44$
poorer soils					
raw data: 1981–2001	0.97 ± 0.08	11, 1983	2.17 ± 0.20	12, 1999	+1.20 ± 0.46, $t = 5.73$, $p = 0.000$, d.f. = 13
Corrected for census-interval, site-switching and majestic forest effects	1.22 ± 0.08	31, 1986	1.54 ± 0.12	31, 1996	+0.32 ± 0.17, $t = 2.99$, $p = 0.003$, $n = 31$
aseasonal climate					
raw data: 1990–2001	1.94 ± 0.16	13, 1990	2.58 ± 0.11	15, 1999	+0.64 ± 0.40, $t = 3.30$, $p = 0.003$, d.f. = 24*
corrected for census-interval, site-switching and majestic forest effects	2.08 ± 0.13	10, 1991	2.78 ± 0.19	10, 1998	+0.69 ± 0.49, $t = 3.21$, $p = 0.011$, $n = 10$
seasonal climate					
raw data: 1981–2001	1.17 ± 0.14	13, 1982	2.19 ± 0.18	16, 1999	+0.91 ± 0.51, $t = 4.42$, $p = 0.002$, d.f. = 25
corrected for census-interval, site-switching and majestic forest effects	1.55 ± 0.10	45, 1985	1.96 ± 0.13	45, 1996	+0.41 ± 0.20, $t = 4.15$, $p = 0.000$, $n = 45$

(*Continued*.)

Table 3. (*Continued.*)

	first interval rates		final interval rates		final–initial difference
	mean ± s.e. of mean (% yr^{-1})	*n*, mean mid-year of monitoring	mean ± s.e. of mean (% yr^{-1})	*n*, mean mid-year of monitoring	mean ± 95% CI (% yr^{-1}) (median for non-parametric comparisons)
(*b*) recruitment					
pan-Amazon					
raw data: 1979–2001	1.35 ± 0.15	10, 1981	2.33 ± 0.13	32, 1999	+0.98 ± 0.43, $t = 4.86$, $p = 0.000$, d.f. = 21
corrected for census-interval, site-switching and majestic forest effects	1.70 ± 0.11	57, 1987	2.34 ± 0.15	57, 1997	+0.64 ± 0.28, $t = 4.45$, $p = 0.000$, $n = 57$
west and south Amazonia					
raw data: 1983–2001	1.82 ± 0.22	10, 1985	2.45 ± 0.14	27, 1999	+0.64 ± 0.57, $t = 2.39$, $p = 0.03$, d.f. = 15**
corrected for census-interval, site-switching and majestic forest effects	2.24 ± 0.14	27, 1988	2.86 ± 0.18	27, 1997	+0.62 ± 0.39, $t = 3.30$, $p = 0.003$, $n = 27$
east and central Amazonia					
raw data: 1981, 1999	0.87 ± 0.10	10, 1984	1.43 ± 0.28	14, 1996	+0.55 ± 0.60, $t = 1.91$, $p = 0.07$, d.f. = 6**
corrected for census-interval, site-switching and majestic forest effects	1.23 ± 0.10	27, 1986	1.60 ± 0.11	27, 1996	+0.38 ± 0.30, $t = 2.64$, $p = 0.014$, $n = 27$
richer soils					
raw data: 1983–2001	1.92 ± 0.23	10, 1986	2.50 ± 0.16	20, 1999	+0.55 ± 0.59, $t = 1.95$, $p = 0.06$, d.f. = 17
corrected for census-interval, site-switching and majestic forest effects	2.30 ± 0.14	25, 1989	3.01 ± 0.18	25, 1999	+0.69 ± 0.44, $t = 3.09$, $p = 0.003$, $n = 25$
poorer soils					
raw data: 1981–2001	0.87 ± 0.10	10, 1983	2.10 ± 0.22	12, 1999	+1.22 ± 0.51, $t = 5.12$, $p = 0.000$, d.f. = 15
corrected for census-interval, site-switching and majestic forest effects	1.26 ± 0.10	29, 1986	1.67 ± 0.12	29, 1996	+0.41 ± 0.27, $t = 3.03$, $p = 0.005$, $n = 29$
aseasonal climate					
raw data: 1990–2001	1.96 ± 0.20	11, 1991	2.66 ± 0.15	15, 1999	+0.70 ± 0.31, $W = 101.0$, $p = 0.006$, $n = 20$**
corrected for census-interval, site-switching and majestic forest effects	2.12 ± 0.10	10, 1990	2.69 ± 0.21	10, 1997	+0.57 ± 0.48, $t = 2.67$, $p = 0.022$, $n = 10$
seasonal climate					
raw data: 1981–2001	1.03 ± 0.20	11, 1983	2.04 ± 0.19	17, 1999	+1.01 ± 0.55, $t = 3.61$, $p = 0.001$, d.f. = 23
corrected for census-interval, site-switching and majestic forest effects	1.60 ± 0.13	46, 1986	2.25 ± 0.17	41, 1996	+0.65 ± 0.34, $t = 3.75$, $p = 0.001$, $n = 46$
(*c*) mortality					
pan-Amazon					
raw data: 1976–2001	1.16 ± 0.14	10, 1981	2.30 ± 0.14	31, 1999	+1.14 ± 0.39, $t = 5.97$, $p = 0.000$, d.f. = 25
corrected for census-interval, site-switching and majestic forest effects	1.58 ± 0.10	52, 1987	1.91 ± 0.13	52, 1997	+0.32 ± 0.19, $Z = 360$, $p = 0.001$, $n = 55$
west and south Amazonia					
raw data: 1983–2001	1.85 ± 0.18	12, 1985	2.50 ± 0.13	27, 1999	+0.65 ± 0.46, $t = 2.94$, $p = 0.007$, d.f. = 23
corrected for census-interval, site-switching and majestic forest effects	2.03 ± 0.13	27, 1988	2.59 ± 0.14	24, 1997	+0.56 ± 0.35, $t = 3.31$, $p = 0.003$, $n = 27$

(*Continued.*)

Table 3. (*Continued*).

	first interval rates		final interval rates		final–initial difference
	mean ± s.e. of mean (% yr^{-1})	*n*, mean mid-year of monitoring	mean ± s.e. of mean (% yr^{-1})	*n*, mean mid-year of monitoring	mean ± 95% CI (% yr^{-1}) (median for non-parametric comparisons)
east and central Amazonia					
raw data: 1981–1999	1.12 ± 0.11	12, 1984	1.33 ± 0.13	14, 1996	+0.21 ± 0.33, $t = 1.24$, $p = 0.23$, d.f. = 23
corrected for census-interval, site-switching and majestic forest effects	1.16 ± 0.08	28, 1986	1.27 ± 0.09	28, 1996	+0.11 ± 0.20, $t = 1.01$, $p = 0.33$, $n = 28$
richer soils					
raw data: 1983–2001	1.98 ± 0.15	11, 1986	2.40 ± 0.15	20, 1999	+0.42 ± 0.43, $t = 2.01$, $p = 0.056$, d.f. = 25
corrected for census-interval, site-switching and majestic forest effects	2.12 ± 0.12	24, 1990	2.55 ± 0.12	21, 1999	+0.42 ± 0.30, $t = 2.89$, $p = 0.009$, $n = 24$
poorer soils					
raw data: 1981–2001	1.06 ± 0.10	12, 1983	2.24 ± 0.26	12, 1999	+1.18 ± 0.60, $t = 4.22$, $p = 0.001$, d.f. = 14
corrected for census-interval, site-switching and majestic forest effects	1.16 ± 0.07	31, 1986	1.41 ± 0.14	31, 1996	+0.32 ± 0.19, $Z = 365$, $p = 0.023$, $n = 31$
aseasonal climate					
raw data: 1990–2001	1.84 ± 0.18	15, 1991	2.49 ± 0.17	13, 1999	+0.66 ± 0.51, $t = 2.66$, $p = 0.013$, d.f. = 25*
corrected for census-interval, site-switching and majestic forest effects	2.04 ± 0.18	10, 1990	2.86 ± 0.29	10, 1997	+0.82 ± 0.81, $t = 2.29$, $p = 0.048$, $n = 10$
seasonal climate					
raw data 1981–2001	1.26 ± 0.11	13, 1983	2.21 ± 0.21	17, 1999	+0.94 ± 0.46, $t = 4.26$, $p = 0.000$, d.f. = 23
corrected for census-interval, site-switching and majestic forest effects	1.48 ± 0.10	45, 1985	1.70 ± 0.11	45, 1996	+0.22 ± 0.18, $Z = 763$, $p = 0.006$, $n = 45$

*p-values should be interpreted with caution because seven of the sites monitored in 1990 were also monitored in 2001.
**p-values should be interpreted with caution because four of the sites monitored in the start year were also monitored in the end year.

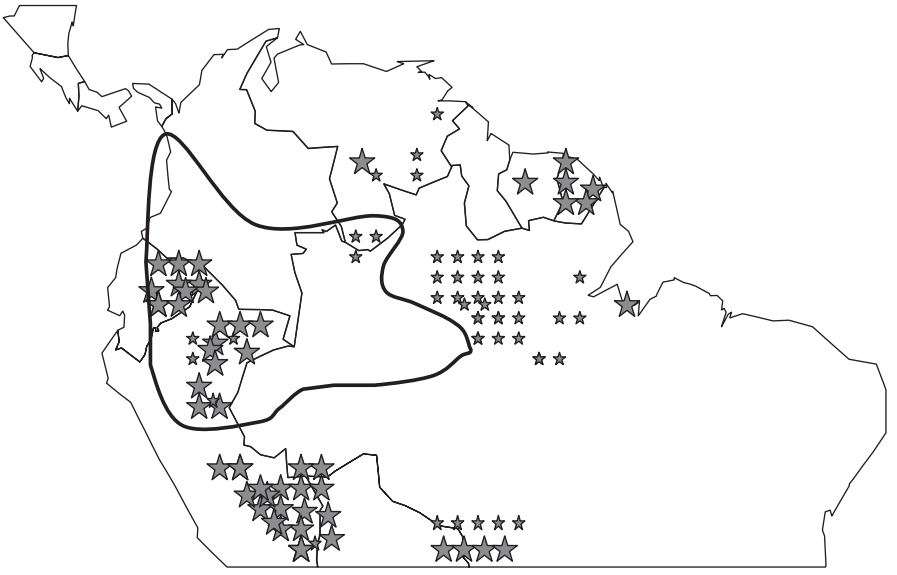

Figure 1. Map of location of sites in Amazonia and contiguous forested zones. The map shows the approximate boundary between the region where precipitation averages less than one month a year with less than 100 mm ('aseasonal', inside the line) from the rest of Amazonia ('seasonal', outside the line). Sites with poor soils (oxisols, spodosols and oligotrophic histosols) are represented by small stars, sites with richer soils are represented by large stars.

For data that were not corrected for site-switching we used simple two-sample Student's *t*-tests or the non-parametric equivalent (Mann–Whitney *U*-test), comparing values recorded at all sites monitored at the start of the period (e.g. 1976) with values at all sites monitored at the end of the period (2001). For data corrected for site-switching we used paired Student's *t*-tests or the non-parametric equivalent (Wilcoxon tests), evaluating change across all sites monitored for at least two intervals by comparing the final interval rate with the first interval rate for the same site. These statistical tests supplement graphical display of time-dependent patterns for each major pan-Amazon and regional analysis. Exploratory comparisons of annual mean mortality and recruitment rates are also used to indicate potential regional-scale lags between the ecological processes. The focus here is on detecting broad spatial and temporal patterns, rather than determining causes: the data are not yet of sufficient quality to disaggregate the potential environmental and spatial drivers of turnover processes or to pinpoint annual fluctuations, but they are sufficient to test whether change is confined to specific Amazonian environments or if it is a general phenomenon, and whether process rates are changing at different rates.

3. RESULTS

Ninety-seven sites met our criteria for inclusion, of which 61 with at least two intervals are the main focus of analyses (table 1; electronic Appendix A). Sites are distributed across the region, but with clusters in seasonal eastern Amazonia with oxisols, in seasonal southwest Amazonia with mostly richer soils, and in aseasonal northwest Amazonia with mostly richer soils (figure 1). In total the data represent 1640 hectare years of monitoring by more than 20 research groups.

Across all 97 sites the distribution of recruitment and mortality rates is skewed slightly positively, especially for recruitment (figure 2). Both average *ca*. 2% per year (table 2), but recruitment rates are marginally greater than mortality rates, using only sites with both mortality and recruitment values (Wilcoxon signed-rank test, $Z = 2359$, $p < 0.05$, $n = 93$, for both uncorrected and census-interval corrected values).

When results are plotted from individual sites, turnover rates vary substantially from site-to-site and interval-to-interval (figure 3), suggesting that large samples of sites may be needed to statistically distinguish large-scale patterns in time and space. However, despite the inherent noise in recruitment and mortality processes, taken together these data show that turnover rates have increased substantially across all Amazonian sites regardless of the method of data treatment (figure 4; table 3). Each correction produces different patterns in terms of magnitude of overall change and inter-annual fluctuations. Nevertheless, irrespective of whether the procedures are applied singly or in combination, the overall result of turnover increase remains highly significant ($p < 0.001$). Thus, correcting for census interval effects causes all rates to be shifted upwards (figure 4*b*), but otherwise this has no impact on the overall pattern shown in the raw data (figure 4*a*) because there is no trend in the distribution of census interval lengths through time (figure 5). Removing the possible majestic forest sites slightly shortens the period available for comparison and appears to dampen the fluctuations (figure 4*c*), but otherwise has no impact compared with the raw data. As expected, eliminating site-switching greatly reduces the supra-annual fluctuations (figure 4*d*). It also simultaneously reduces the apparent rate of change and the variance within any given year, so that the net effect is that significance levels are not substantially altered. We assumed zero change when we stretched the turnover data from each site to eliminate site-switching, so the aggregate graph is likely to underestimate the actual rate of any secular change across Amazonian forests during the period. This is especially so towards the start and end of the period when most plots were not being monitored (figure 6), thus flattening the trendline. Finally, when we correct for all three potential

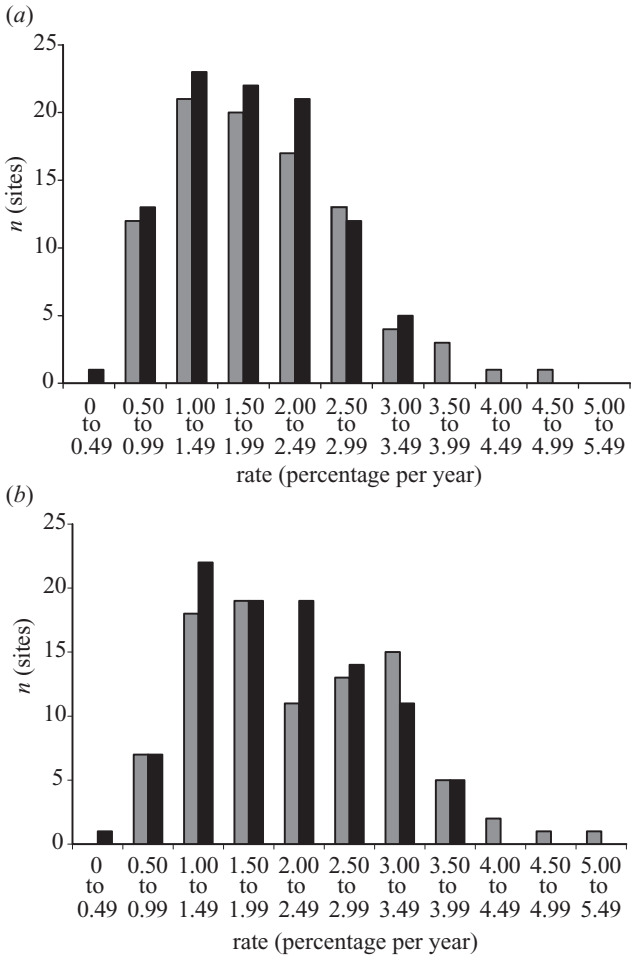

Figure 2. Frequency distribution of turnover rates across all Amazonian sites for their full monitoring period. The histograms include one value for each plot, calculated as the whole-period rate parameter for that plot. See text for details. Shaded bars, recruitment; black bars, mortality. (*a*) Uncorrected for census interval, (*b*) corrected for census interval.

effects (figure 4*e*), the result is remarkably similar to correcting for site-switching only, except that the line is shifted upwards. Therefore most of the variability in the raw data is caused by site-switching rather than any other effect.

The remaining results—broken down by process, spatial region and environmental attributes—are given after correcting for all three potential artefacts.

Both recruitment and mortality have increased across all sites (figure 7), with mean recruitment rates exceeding mean mortality rates throughout the period. This difference is not significant initially but becomes so by the end of the period (paired *t*-test for all 55 multi-census sites: for first interval rates, $t = 1.51$, $p < 0.15$; for final interval rates, $t = 2.90$, $p < 0.01$). Elsewhere (Lewis *et al.* 2004*a*) we use within-plot analyses to show that a logical corollary of this—increased stem density—is also apparent.

Turnover is nearly twice as high in the west and south as it is in east and central Amazonia (median values 2.60, 1.35% yr^{-1}, respectively; 95% CIs for difference 0.93 to 1.56% yr^{-1}, two sample *t*-test, $t = 7.94$, $p < 0.001$, d.f. = 43; test includes all census-corrected sites monitored in 1995 except those with potential majestic forest effects). Turnover rates have increased significantly in both regions (figure 8; table 3). The absolute rate of change is greater in the west and south (figure 8; Mann–Whitney *U*-test, $W = 657$, $p < 0.03$, $n = 55$; test compares regions using census-corrected end versus start turnover rate increases standardized by inventory length). In the west and south, mortality and recruitment have both increased significantly (figure 9*a*); in east and central Amazonia mortality and recruitment trends are positive but only significantly so for recruitment (figure 9*b*).

The east–west differences and the within-region trends in turnover, recruitment and mortality are largely mirrored by the patterns among and within the soil-based categories (figures 10 and 11). This is because poor soils tend to dominate in the east and central forests and richer soils are more common in the west and south (Irion 1978). Thus richer soil forests are nearly twice as dynamic as poor soil forests (median turnover rates 2.72, 1.37% yr^{-1}, respectively; 95% CIs for difference 1.06 to 1.65% yr^{-1}, two sample *t*-test, $t = 9.23$, $p < 0.001$, d.f. = 39; test includes all census-corrected sites monitored in 1995 except those with potential majestic forest effects). Recruitment and mortality have tended to increase on both substrates but with the largest absolute increases on richer soils and in recruitment rates (table 3).

Only the northwestern quadrant of Amazonia is generally aseasonal, and accordingly our aseasonal dataset is both smaller and less extensive through time than the seasonal one. Aseasonal Amazon forests are more dynamic than seasonal Amazon forests but not significantly so (mean turnover rates 2.64, 2.12% yr^{-1}, respectively; 95% CIs for difference −0.06 to 1.09% yr^{-1}, two sample *t*-test, $t = 1.88$, $p < 0.08$, d.f. = 18; test includes all census-corrected sites monitored in 1995 except those with potential majestic forest effects). Regardless, forests in both climate regimes have become significantly more dynamic (figure 12; table 3). In both the seasonal and aseasonal Amazon, both recruitment and mortality have increased significantly (figure 13*a*,*b*).

We have redrawn the mortality and recruitment figures by calculating the mean differences between the processes when each curve is shifted to the left or right by *x* years while holding the other constant (figure 14). The point at which the difference curve intersects the year axis (mean difference zero) indicates the mean lag in the system. This provides a graphical display of the temporal relation between the two curves, with the proviso that the multi-annual census intervals will tend to smooth these relations. At the pan-Amazon scale, mean mortality rates lag mean recruitment rates by a period of *ca.* 15 years (figure 14*a*). Both recruitment and mortality have increased in the south and west but with a pronounced asynchronicity: mortality lags recruitment by nearly 10 years (figure 14*b*). Mortality rates also lag recruitment rates in the east and central Amazon (figure 14*c*), but the lag appears to be longer and the effect is weaker and less coherent than in the south and west.

Out of the four potential majestic forest sites, only one (BDF-04) had a detectable effect on temporal patterns of dynamics when compared with the main analyses that correct for all possible effects. This 1 ha terra firme plot experienced semi-catastrophic mortality caused by unusual flooding (20% of stems died over a 4 year period), followed by a big recruitment pulse. Including this site

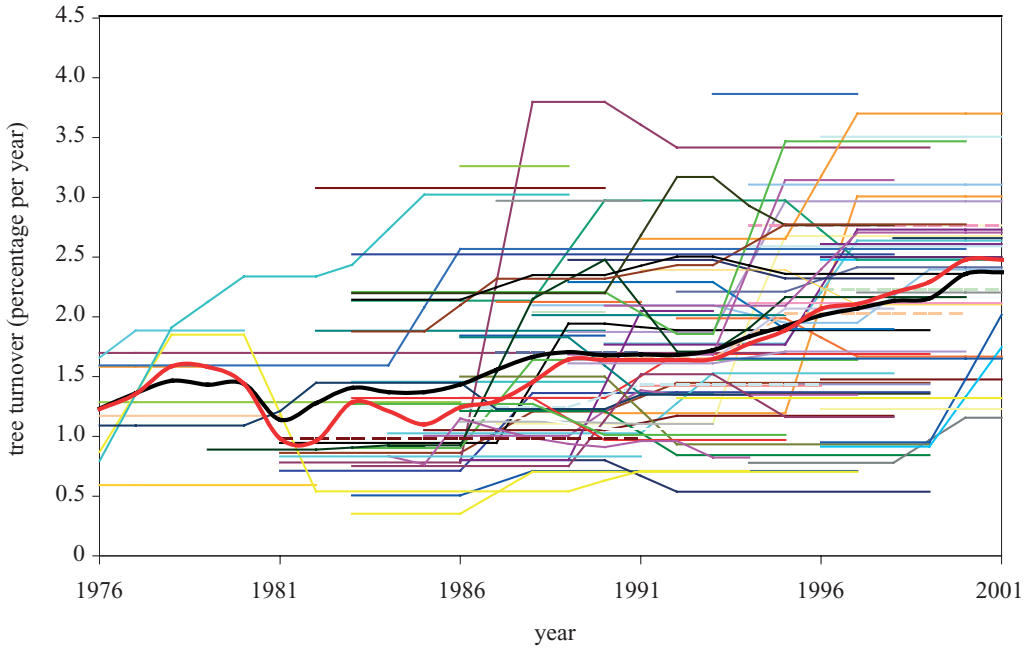

Figure 3. Interval-by-interval turnover rates for all sites in table 1, not corrected for census interval. In each year in which a plot was censused, we estimated its turnover rate as the mean of the rates recorded in the interval that ended and the interval that started in that year. Thick black line, mean; thick red line, median.

(and BDF-08) in the east and central Amazon analyses did not alter the conclusion that recruitment rates have increased here and that mortality rates have not, nor that the dominant regional pattern is for mortality to lag recruitment at supra-decadal scales (figure 14*d*, cf. figure 14*c*). Finally, the spatial distribution of plots is clearly non-random, and this could impact our results (if, for example, plots happened to be located by chance in areas with accelerating and synchronized dynamics as a result of landscape-scale processes). Although a full analysis of spatial autocorrelation is beyond the scope of this paper, in the companion paper (Lewis *et al.* 2004*a*) we have assessed its likely impact by selecting larger and larger clusters of plots as the basic unit and asking whether the mean values of the change parameters vary. Parameter estimates are insensitive to the degree of aggregation of sample units, indicating, for example, that the large concentration of plots north of Manaus in central Amazonia is not disproportionately influencing change parameters, and that our assumption that plot dynamics are largely independent from one another is a reasonable one.

4. DISCUSSION

The results show that the mature forests of Amazonia have experienced accelerated tree turnover during the past one to three decades. This finding is consistent with earlier findings at different time-scales and over larger spatial extents: tropical forest plots were on average twice as dynamic in the 1990s as in the 1950s, and increases have occurred in both the Old and New World tropics (Phillips & Gentry 1994; Phillips 1996). The current analysis also expands upon these earlier findings in several important ways.

First, the consistent patterns observed here suggest that the previously reported increase in tropical tree turnover rates (Phillips & Gentry 1994; Phillips 1996) cannot be substantially driven by any of the most debated artefactual concerns. These are the tendency for turnover rates to appear greater when measured over shorter interval censuses (Phillips 1995; Sheil 1995*a*; Sheil & May 1996; Lewis *et al.* 2004*c*), the possible preference of some ecologists to select high-biomass 'majestic' forest that subsequently develops gaps and accelerated mortality and recruitment through endogenous sylvigenetic processes (Condit 1997; Phillips & Sheil 1997; Phillips *et al.* 1997, 2002*a*), and progressive 'switching' of monitoring effort through time to intrinsically more dynamic forests (Condit 1997).

Second, the increasing turnover result sheds light on the increasing biomass result (Phillips *et al.* 1998*b*; Baker *et al.* 2004*b*), and vice versa. Thus, the net increase in biomass in Amazon plots is unlikely to reflect widespread natural recovery from earlier catastrophic disturbance, because succession should involve *reduced* recruitment rates of small trees as maturing forests thin. Conversely, progressive fragmentation and advancing edge effects—changes that accelerate turnover by killing large trees (Laurance *et al.* 2000; Laurance 2004)—cannot be responsible for the turnover increases in our data because most plots with increasing turnover are also gaining biomass (Lewis *et al.* 2004*a*). In summary, the coincidence of increasing turnover with increasing biomass makes it difficult to explain either as an artefact of sampling bias or landscape processes.

Third, we have demonstrated that the increase in turnover is not simply an outcome of an increase in mortality or an increase in recruitment. For the Amazon, at least, it is both. Forest dynamic processes have therefore accelerated in a concerted manner.

Fourth, we have found that, regardless of time-related trends, turnover rates of tropical forest trees also vary systematically with environmental and/or regional factors. Turnover rates are highest on richer soils, in aseasonal

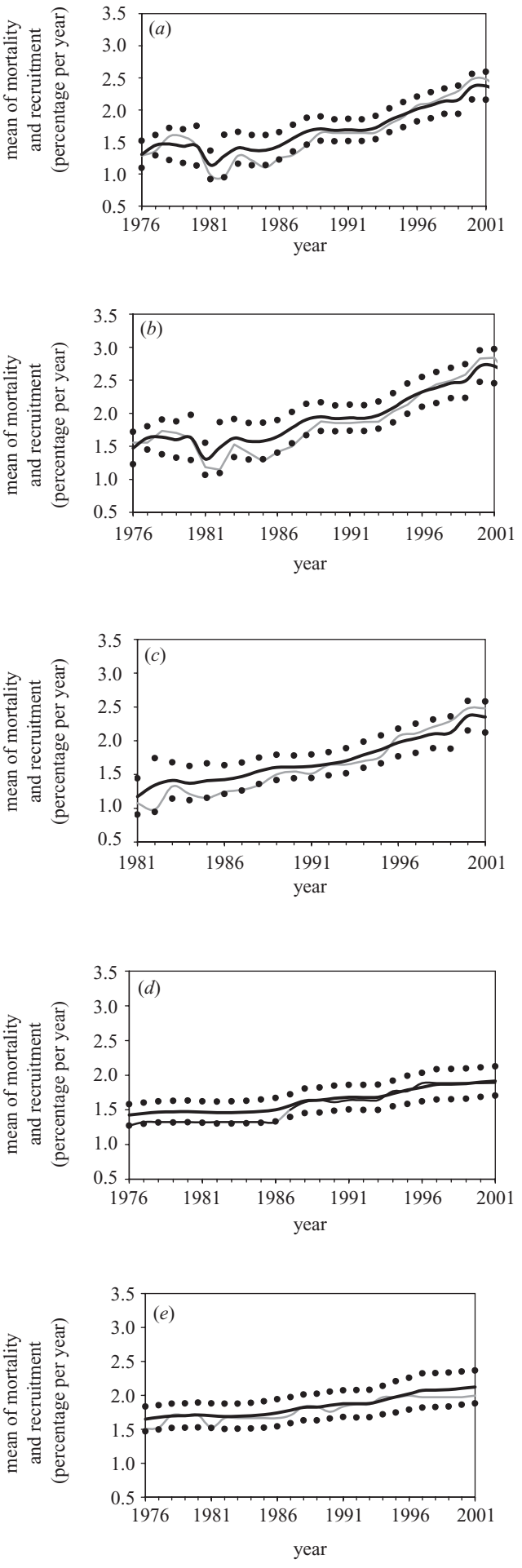

Figure 4. Pan-Amazon turnover rates. (*a*) All sites, with no census-interval correction or smoothing of site-switching; (*b*) all sites, only census-interval corrected; (*c*) only potential majestic forest sites removed; (*d*) only sites with a single interval removed, and all multi-census sites corrected for site-switching; and (*e*) corrected for census-interval, site-switching, and majestic forest effects. Grey line, median; black line, mean; black dots, 95% CI.

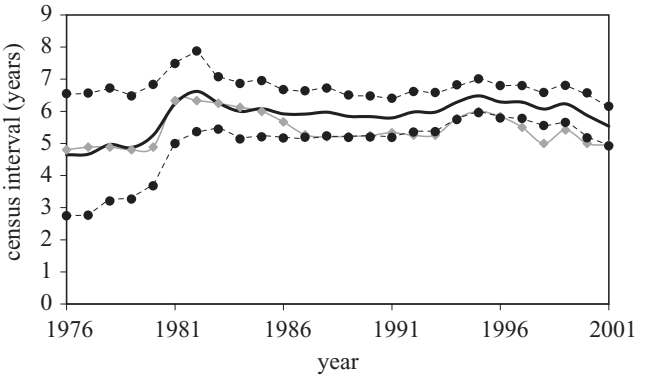

Figure 5. Mean and median census-interval periods for all sites monitored in each year, 1976–2001. All sites. Light grey dots and solid line, median interval; black line, mean; black dots, 95% CI.

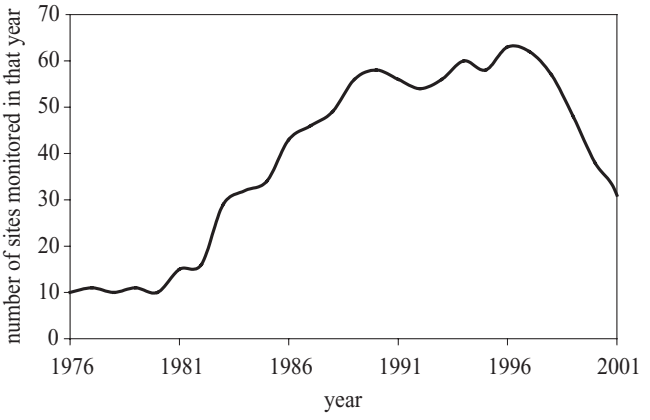

Figure 6. Number of Amazon sites monitored in each year, 1976–2001. All sites.

forests, and in southern and western Amazonia, with long-term process rates varying across the basin by a factor of two (table 3). Moreover, despite these systematic differences in Amazonian tree population dynamics, it appears that across Amazonia change has occurred simultaneously in a consistent direction.

Fifth, these findings show how essential geographically distributed long-term research programmes are in tropical ecology. Even when defined very broadly, no single region, soil class or climate regime can represent 'typical' conditions for the lowland Amazon. However lengthy, well-replicated and carefully conducted they may be, studies at landscape scales cannot be used to test hypotheses of regional- and continental-scale change.

Discriminating between the potential causes of these differences will be difficult because the design of the Amazon 'experiment' is not balanced: most richer soils,

for example, are located in areas relatively immune to ENSO inter-annual climate fluctuations. Still, the results here move us closer to tackling the exciting and critical questions of what factors drive tree dynamics in tropical forests in general, and what factors are driving the ecological changes in particular. The spatial patterns in forest dynamics might imply a macroecological response to prevailing climate and soil conditions, such that ample moisture supply and good soil nutrition support greater above-ground forest productivity in the west and the south, which in turn supports faster turnover rates (Phillips *et al.* 1994). Wood density is lower in the west and south (Baker *et al.* 2004*a*), but even after correcting for wood density the 'slow' forests of central Amazonia have lower above-ground wood production than the 'fast' forests of the west and south (Malhi *et al.* 2004). This is consistent with the finding from a broad sample of tropical trees that wood density does not influence rates of biomass production across trees (Enquist *et al.* 1999). Non-resource factors, such as windstorms (Nelson *et al.* 1994), saturated soil conditions and topography (Gale & Barford 1999) may also contribute to higher turnover rates in the west. Biogeographic factors may also play a role. Several families dominant on the richer soils in the southwest (e.g. Cecropiaceae, Mimosaceae, Malvaceae) have typically low wood densities and high mortality rates. By contrast, families with Guyanan shield centres of diversity (e.g. Caesalpinaceae, Lecythidaceae, Chrysobalanaceae) exhibit more 'stress-tolerant' growth strategies with high wood density, large seeds and seedling banks in shaded and nutrient-poor environments (ter Steege & Hammond 2001; Baker *et al.* 2004*a*). At the community level, there is a clear northeast–southwest Amazon floristic gradient in familial dominance (Terborgh & Andresen 1998; ter Steege *et al.* 2000). So one important question is whether it is resource availability driving these biogeographic patterns or whether the historical pattern of evolution has driven the ecological differences? Whereas relative densities of species vary along the spatial gradient, no significant tree family and very few genera appear to be actually restricted to either Guyana or to the southwest, indicating that there have been no significant long-term barriers to migration. This suggests that the edaphic resource gradient is likely to be the cause of the floristic gradient, perhaps mediated through the effects of soil quality on tree turnover rates favouring some phylogenetically conserved growth and regeneration strategies over others.

(a) *Mechanisms of forest dynamics*

The data we have assembled can also provide some insight into the mechanisms of forest dynamics in the Amazon. Tree turnover is an emergent property of underlying forest structural, floristic and dynamic processes. Considered at its most simple we can envision two extreme situations: (i) a system driven entirely by catastrophic mortality, in which exogenous disturbance events such as fire, drought, flood and storm determine forest structure and dynamics (cf. Connell 1978); or (ii) a system driven entirely by endogenous growth and recruitment processes, in which resource supply provides the ultimate driver for forest ecology so that trees mostly die competing for these resources (cf. Enquist & Niklas 2001). Which of these models best approximates reality in the Amazon? We know of course that both processes operate—weather extremes kill trees but competition for resources can be intense—but it should be possible to test which mode is dominant at the regional scale. One approach would be to examine tree-by-tree mortality records to determine spatial patterns in proximate causes of death (e.g. Korning & Balslev 1994), but we do not yet have the data to attempt this across the Amazon. Another approach is to assess temporal lags between mortality and recruitment within plots and within regions. More specifically then, a further question that can be asked is whether catastrophic disturbances occur frequently enough and synchronously enough to generate large-scale lags of recruitment following mortality? Or, are they so rare and random that instead pulses of recruitment lead pulses of mortality? The results from the pan-Amazon and regional subsets show that mean mortality rates lag mean recruitment rates (figure 14*a*,*b*,*c*), implying that recruitment is leading turnover and therefore possibly driving the increase in turnover too. Including potential majestic forest sites in the analysis shows that in some patches recruitment pulses certainly follow extreme mortality events (figure 14*d*), but does not alter the current dominant regional pattern of mortality lagging recruitment.

We need to consider an alternative explanation for this pattern. Imagine that a catastrophic mortality event sets synchronized recruitment of a cohort of light-demanding trees, then there will be high mortality rates of small trees in the developing stand, followed by deaths of the few big dominant trees, leading to another pulse in recruits, and then high mortality rates by self-thinning, and so on (Sheil 2003). Assuming that this wave-like pattern of forest ontogeny dominates in Amazonia, *and* that our plots tend to start around the point that a few big trees are dying and finish around the point that self-thinning mortality is accelerating, *then* the pattern of recruitment leading mortality during the particular time-window glimpsed by the plots could actually reflect a longer-term mortality-led process initiated originally by a much earlier large-scale climate event across the Amazon. This ontogenetic argument generates several testable predictions. The key process is death of a few big trees near the start of the time-window. Therefore, we should also find: (i) declines in the relative importance of long-lived pioneer taxa; (ii) net losses in the number of big trees; (iii) *stem* mortality rates increasing, but *biomass* mortality rates dropping from an early peak; and (iv) stand biomass dropping steeply early in the monitoring period, then slowly recovering. We have not yet collated all the life-history data needed to carry out the floristic test proposed (i), but results of the other tests are not consistent with this model: the number of big trees has not decreased on average (ii) (cf. Phillips *et al.* 1997, fig. 1; Phillips *et al.* 2002*a*, p. 582); biomass mortality rates tend to increase during the monitoring period (iii) (cf. Lewis *et al.* 2004*a*, fig. 4); and rates of net change in biomass are independent of time elapsed since the plot was established (iv) (cf. Phillips *et al.* 2002*a*, fig. 2).

So, we argue that the ghosts of deaths past cannot easily explain the *general* syndrome of concerted dynamic and structural change in old-growth Amazon forests. Notwithstanding this, mortality-led dynamics certainly do occur in the Amazon, and all *individual* stands must still be adjusting in subtle ways to past disturbances. How frequent are

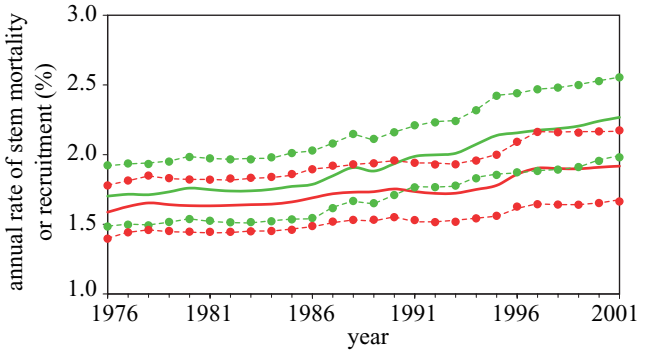

Figure 7. Recruitment and mortality, Amazonia 1976–2001. Both recruitment and mortality rates have increased. Corrected for census-interval, site-switching and majestic forest effects. Solid green line, recruitment mean; green dots, recruitment 95% CI; solid red line, mortality mean; red dots, mortality 95% CI.

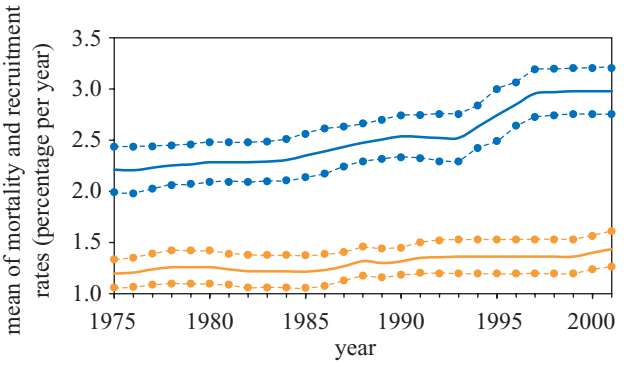

Figure 8. Trends in turnover in west and south Amazonia and east and central Amazonia. Turnover has increased significantly in both regions, but is much higher in the south and west than in the east and central Amazon throughout the period. Corrected for census-interval, site-switching and majestic forest effects. Orange line, east and central mean; orange dots, east and central 95% CI; blue line, west mean; blue dots, west 95% CI.

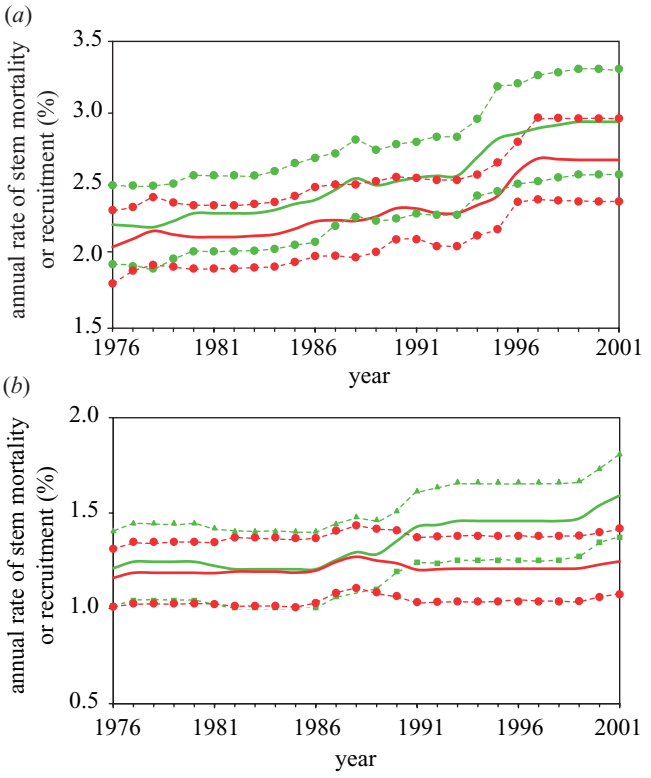

Figure 9. (*a*) Recruitment and mortality, west and south Amazonia. Both recruitment and mortality rates have increased. (*b*) Recruitment and mortality, east and central Amazonia. Only recruitment rates have increased significantly. Corrected for census-interval, site-switching and majestic forest effects. Note the different scales. Solid green line, recruitment mean; green dots, recruitment 95% CI; solid red line, mortality mean; red dots, mortality 95% CI.

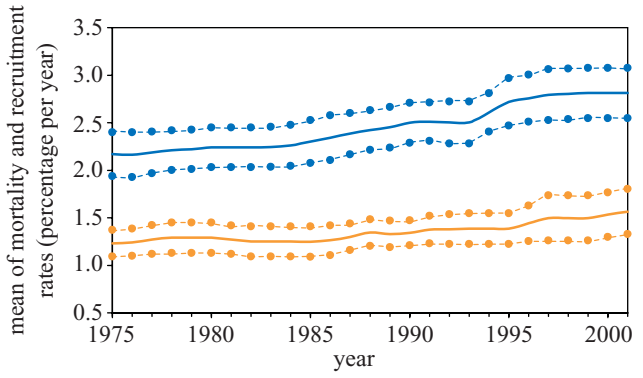

Figure 10. Turnover through time in poor soil (spodosol, oxisol, histosol) compared with richer soil (ultisol, inceptisol, entisol, eutrophic histosol) Amazonia. Corrected for census-interval, site-switching and majestic forest effects. Blue line, rich soil mean; blue dots, rich soil 95% CI; orange line, poor soil mean; orange dots, poor soil 95% CI.

catastrophic disturbances? In principle, long-term monitoring of plots should provide better estimates of their frequency and impact than anecdotal reports of individual events. In some of our central Amazon plots increased rainfall and wind storms associated with La Niña brought increased risk of death by flooding (BDF-04) and windthrow (JAC-01, JAC-02: N. Higuchi, personal observation). Likewise, in the Manu region of southwestern Amazonia, occasional extreme storm events can topple emergent trees over large areas (Foster & Terborgh 1998). But in 1640 hectare years of monitoring, we have yet to observe really catastrophic disturbance in any of our plots. Although space and time are not perfectly substitutable, this implies that such events have been very rare, asynchronous, and localized for at least the past 20 years. Further analysis at finer scales and over longer time periods is clearly needed to develop rigorous tests of the 'catastrophic' versus 'resource supply' models of forest dynamics.

However, late twentieth-century Amazonia is perhaps not an ideal setting for testing equilibrium or stochastic models of forest behaviour, because the whole system is undergoing a shift as turnover rates accelerate and forest basal area increases. The shift is apparently both ubiquitous but also asymmetric: turnover rates have risen most in absolute terms in the already-dynamic forests of the south and west, and is being led by recruitment changes, with recruitment exceeding mortality in most forest zones for most of the time. Seedlings and saplings are not being monitored in most of our plots so we cannot tell if the recruitment gains result from increased growth of

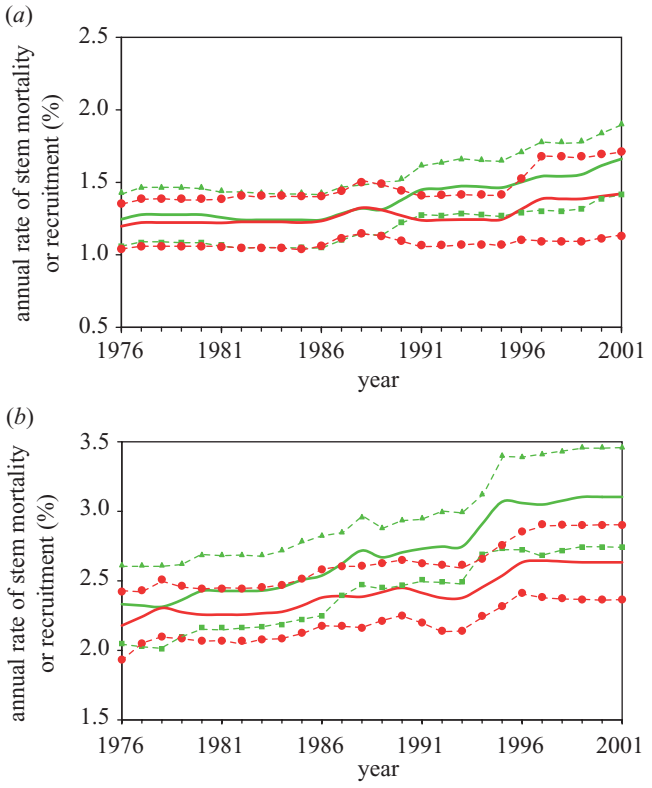

Figure 11. (*a*) Recruitment and mortality through time, poor soil Amazonia (spodosols and oxisols). (*b*) Recruitment and mortality through time, richer soil Amazonia (ultisol, inceptisol, entisol, histosol Amazonia). Corrected for census-interval, site-switching and majestic forest effects. Note the different scales. Solid green line, recruitment mean; green dots, recruitment 95% CI; solid red line, mortality mean; red dots, mortality 95% CI.

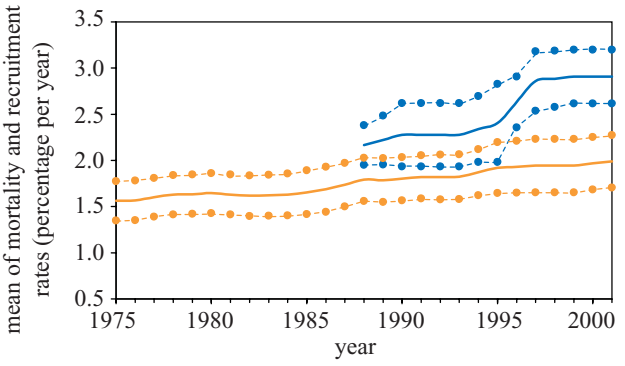

Figure 12. Turnover through time, aseasonal versus seasonal Amazonia. Corrected for census-interval, site-switching and majestic forest effects. Blue line, aseasonal Amazonia mean; blue dots, aseasonal 95% CI; orange line, seasonal Amazonia mean; orange dots, seasonal 95% CI.

seedlings and saplings or lower mortality rates, but the latter is unlikely as mortality rates have generally increased for trees 10 cm or more in diameter. The fact that growth and mortality rates are higher on more productive soils (this paper; Phillips *et al.* 1994; Malhi *et al.* 2004) indicates that spatial variation in growth rates is primarily caused by factors that influence growth of plants, and therefore that temporal variation may be too. The patterns of Amazon change in dynamics and stand structure also

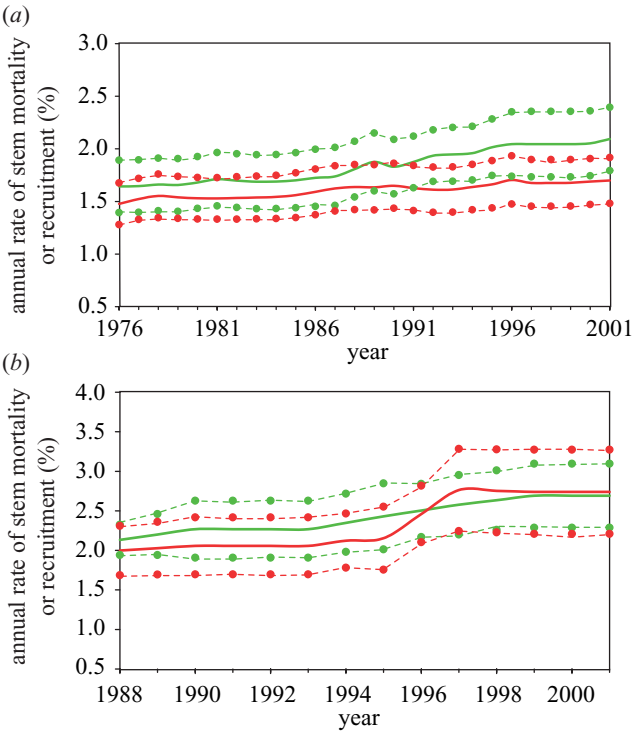

Figure 13. (*a*) Recruitment and mortality through time, seasonal Amazonia. (*b*) Recruitment and mortality through time, aseasonal Amazonia. Corrected for census-interval, site-switching and majestic forest effects. Note the different scales. Solid green line, recruitment mean; green dots, recruitment 95% CI; solid red line, mortality mean; red dots, mortality 95% CI.

conform to common-sense predictions for a growth driver (Lewis *et al.* 2004*a*,*b*). Here, growth rates across all size-classes and therefore recruitment rates into the 10 cm size-class respond instantaneously to an increase in resource provision, with adult mortality lagging as the system approaches, perhaps, a new equilibrium at higher biomass and turnover (Lloyd & Farquhar 1996; Chambers *et al.* 2001). Given an equal proportional effect in all forests, the absolute effect should be greater in faster forests and therefore the signal easier to detect (given a similar magnitude of 'noise' across forests), which is what we observe (cf. for example western versus eastern Amazon significance levels for the final-interval versus first-interval change in recruitment and mortality rates; table 3). Similarly, faster systems should respond to a stimulating effect in a more synchronized manner than slower systems. Mortality and recruitment curves do appear to be more closely synchronized with one another in the faster forests. Southern and western Amazonia have a fast response of mortality to recruitment, and mean rates match each other for only a narrow envelope of lag periods (figure 14*b*). In eastern and central Amazonia there is a slow response of mortality to recruitment, and mean rates are quite well matched for a wide range of lag periods (figure 14*c*,*d*). Although the lag analyses involve too many assumptions to attach statistical confidence, the patterns are in line with common sense predictions. To the extent that the processes are causatively linked we can use these patterns to predict stem mortality patterns into the future. The results imply that stem mortality rates must eventually

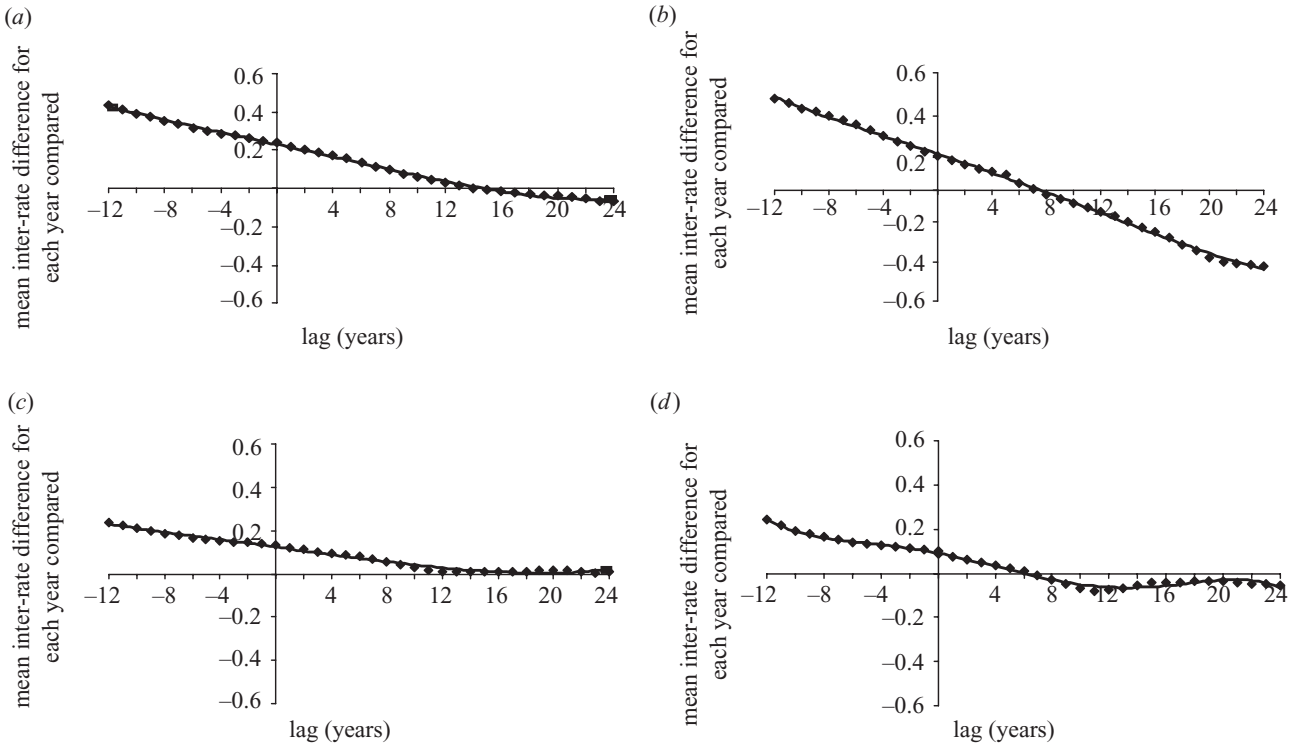

Figure 14. The temporal relationship between mean mortality and recruitment rates across all sites, after correcting for site-switching and census-interval effects and (except (*d*)) for majestic forest effects. Positive values for the *y*-intercept indicate recruitment leading mortality. See text for details. (*a*) Pan-Amazon, mortality lags recruitment by 15 years; (*b*) south and west Amazonia, mortality strongly lags recruitment by 7–9 years; (*c*) east and central Amazonia, mortality weakly lags recruitment by at least 10 years; and (*d*) east and central Amazonia, mortality still lags recruitment weakly (including the potentially majestic forest sites BDF-04 and BDF-08).

increase in the east as the swollen cohort resulting from the recent (and future?) pulse of elevated recruitment works its way through the system.

(b) *Causes of changes in forest dynamics*

What might the environmental parameter(s) driving these changes be? We have two sets of circumstantial evidence to guide us. First, *a priori* knowledge of changes in drivers and their likely ecophysiological effects (Lewis *et al.* 2004*b*; Malhi & Wright 2004) allows us to estimate the potential impact of any given process. Second, the geographical and temporal pattern of response provides further clues. Change has occurred over large areas (different regions of Amazonia and beyond) for at least two decades, even though detecting trends in individual sites is notoriously difficult because of a high ratio of noise to signal (Phillips 1996; Hall *et al.* 1998). Therefore the driver must be either a set of coincident yet independent local changes at dozens of sites, or more parsimoniously a single 'global' environmental change. Combining both strands of evidence suggests we should probably reject most aspects of climate change as the dominant driver. Amazon moisture regimes have not changed significantly, and although Amazonia is shown to have warmed by *ca.* 0.26 ± 0.07 °C per decade since 1976 (Malhi & Wright 2004), the impacts of a modest warming on tropical growth (increase or decrease) are not certain (Lewis *et al.* 2004*b*), bearing in mind that tropical warming needs to boost growth to be a candidate. ENSO cycles certainly affect mortality and recruitment rates in some forests, but it is difficult to see how they can be driving increased turnover on continental and multi-decadal time-scales. The immediate impact of meteorological extremes on forest dynamics is typically by short-term reductions in growth and increases in mortality (e.g. the La Niña flooding in BDF-04), whereas in fact mortality gains are lagging recruitment gains. Also, ENSO events only marginally affect south and west Amazon, but turnover gains have occurred there. Climate cycles with longer periodicity also affect the Amazon, such as a 24–28 year cycle (Botta *et al.* 2002) and supra-millennial cycles with orbital forcing (Mayle *et al.* 2000). Some role for these cannot be ruled out, but the magnitude and sign of the changes in moisture and temperature regimes that they engender vary across the region. We lack a plausible mechanistic explanation of how these changes can cause forests across the region to respond simultaneously with increased stem recruitment (this paper), increased stem density (Lewis *et al.* 2004*a*), increased rates of basal area growth and mortality (Lewis *et al.* 2004*a*), net gains in biomass (Baker *et al.* 2004*b*) and increased relative dominance of lianas (Phillips *et al.* 2002*b*). Some other candidate growth drivers (deposition of nitrogen and other nutrients through biomass burning, increased Saharan dust deposition) are too poorly characterized, ecophysiologically uncertain and probably too spatially localized to be able to make a coherent case, although again contributory effects cannot be ruled out. By elimination, two growth drivers remain as serious candidates. We discuss them in turn.

First, the only large-scale growth driver known to have increased across the tropics is atmospheric CO_2, and elevated concentrations of CO_2 may plausibly be stimulating

forest growth through increased canopy photosynthetic rates. However, the annual increase in turnover in Amazon plots is *ca*. $2.8 \pm 1.7\%$ (from table 3: calculated for the period 1987–1997 with pan-Amazon turnover rates corrected for potential artefacts). This is an order of magnitude greater than would be predicted on the basis of 1 : 1 scaling of growth effects recorded in pot, growth chamber or small-scale free air carbon dioxide enrichment (FACE) experiments (Curtis & Wang 1998). But what scaling *should* we expect? This is a controversial area (see Chambers & Silver (2004) and Körner (2004) for different interpretations), but we suggest that there are several reasons for suspecting that a 1 : 1 scaling to real-life growth rates (Lewis *et al*. 2004*a*) and recruitment rates (this paper) in tropical forests may be unduly conservative. First, growth stimulation for tropical trees *in situ* in response to increasing CO_2 concentrations may be particularly large owing to a strong sensitivity of photosynthesis to intercellular CO_2 concentrations at the high and increasing leaf temperatures experienced in this biome (Long 1991; Lloyd *et al*. 1995; Grace *et al*. 1996). Second, CO_2 fertilization experiments involve shocking simple communities with a sudden increase in CO_2, whereas in reality complex forests have experienced a slow increase during which compositional and allocational shifts may occur to optimize the use of the increasing resource. Third, such experiments expose plants to ambient CO_2 concentrations about twice those ever experienced in the past 20–60 Myr of evolutionary history, whereas in reality forests have experienced an increase from low concentrations at which CO_2 is more limiting. A fourth factor is the likelihood that tropical trees expend a disproportionately large proportion of their assimilated carbon on autotrophic respiration rather than growth (Lloyd & Farquhar 1996; Chambers *et al*. 2004). The argument here is that, especially as the tropical forest canopy may be already closed with any increases in leaf area of little consequence, much of this extra carbon being acquired as atmospheric CO_2 concentrations increase may be being channelled into new stem growth. As new stem growth typically constitutes a relatively small proportion of the overall annual net primary production (Malhi *et al*. 2004), the *proportional* increase in stem growth rates in response to increasing CO_2 concentrations may be much greater than the *proportional* increase in photosynthesis itself (Lloyd & Farquhar 1996). Fifth, although some workers have assumed that nutrient limitations (especially phosphorus) should constrain tropical forest growth responses to increasing CO_2 concentrations (e.g. Friedlingstein *et al*. 1995) there is little evidence to show that this should be the case (Lloyd *et al*. 2001). Sixth, photosynthetic and growth responses to CO_2 of young tropical plants may be particularly large close to the light compensation point (Würth *et al*. 1998; Granados & Körner 2002), so proportional impacts in the understorey may be substantial.

The above theoretical considerations suggest that a portion of the increase in tropical forest recruitment rates occurring over the past 25 years that we document may have a physiological explanation in increasing availability of CO_2. However, even if we accept these arguments, they are clearly not sufficient to explain the magnitude of change witnessed. Similarly, the increasing dominance of large lianas recently documented for western Amazonia (Phillips *et al*. 2002*b*) appears too rapid to be generated solely by first-order responses to gradual CO_2 enrichment (but see also Granados & Körner 2002). Recent satellite-based measurements suggest that a second key growth driver, sunlight, may have been increasing in much of Amazonia (Wielicki *et al*. 2002), and a modelling study suggests that Amazon net primary productivity could be responding to an increase in photosynthetically active radiation (Nemani *et al*. 2003).

The CO_2 and sunlight explanations are not mutually exclusive (growth responses to CO_2 could improve synergistically with increased radiation), but because the first is universal and the second has a strong spatial pattern, we can posit clearly distinct predictions that should allow us to eventually discriminate their ecological footprints. Thus: if a CO_2 effect is dominant we expect to see growth and dynamics responses everywhere we look in the tropics (except where constrained by large climate change); if a radiation effect is dominant we expect to see growth and dynamics responses approximately in proportion to simultaneous local radiation trends. To perform such tests will require estimating growth rates and growth trends for permanent plots across the biome, building on the kind of cumulative, collaborative and careful work by field biologists that has been synthesized here. An initial attempt can be made using existing data, but we will need investment comparable to that being made in monitoring the climate to be able to fully discriminate the contributions of multi-decadal climate cycles from those of long-term trends. Truly long-term commitments to on-the-ground ecosystem monitoring are essential for understanding the profound changes that forests will experience through the twenty-first century.

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GLOSSARY

CI: confidence interval
ENSO: El Niño–Southern Oscillation

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