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Lewis, S.L., Phillips, O.L., Baker, T.R. et al. (2004) Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical Transactions Of The Royal Society Of London Series B - Biological Sciences*, 359 (1443). pp. 421-436. ISSN: 1471-2970

<https://doi.org/10.1098/rstb.2003.1431>

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Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots

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Several widespread changes in the ecology of old-growth tropical forests have recently been documented for the late twentieth century, in particular an increase in stem turnover (pan-tropical), and an increase in above-ground biomass (neotropical). Whether these changes are synchronous and whether changes in growth are also occurring is not known. We analysed stand-level changes within 50 long-term monitoring plots from across South America spanning 1971–2002. We show that: (i) basal area (BA: sum of the cross-sectional areas of all trees in a plot) increased significantly over time (by $0.10 \pm 0.04 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$, mean \pm 95% CI); as did both (ii) stand-level BA growth rates (sum of the increments of BA of surviving trees and BA of new trees that recruited into a plot); and (iii) stand-level BA mortality rates (sum of the cross-sectional areas of all trees that died in a plot). Similar patterns were observed on a per-stem basis: (i) stem density (number of stems per hectare; 1 hectare is 10^4 m^2) increased significantly over time ($0.94 \pm 0.63 \text{ stems ha}^{-1} \text{ yr}^{-1}$); as did both (ii) stem recruitment rates; and (iii) stem mortality rates. In relative terms, the pools of BA and stem density increased by $0.38 \pm 0.15\%$ and $0.18 \pm 0.12\% \text{ yr}^{-1}$, respectively. The fluxes into and out of these pools—stand-level BA growth, stand-level BA mortality, stem recruitment and stem mortality rates—increased, in relative terms, by an order of magnitude more. The gain terms (BA growth, stem recruitment) consistently exceeded the loss terms (BA loss, stem mortality) throughout the period, suggesting that whatever process is driving these changes was already acting before the plot network was established. Large long-term increases in stand-level BA growth and simultaneous increases in stand BA and stem density imply a continent-wide increase in resource availability which is increasing net primary productivity and altering forest dynamics. Continent-wide changes in incoming solar radiation, and increases in atmospheric concentrations of CO_2 and air temperatures may have increased resource supply over recent decades, thus causing accelerated growth and increased dynamism across the world's largest tract of tropical forest.

Keywords: carbon; permanent sample plot; turnover; mortality; recruitment; biomass

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One contribution of 17 to a Theme Issue 'Tropical forests and global atmospheric change'.

1. INTRODUCTION

Significant areas of tropical forest have been conventionally considered to represent a 'natural', 'pristine' or 'undisturbed' state. However, these areas may be impacted by human-induced changes to major biogeochemical cycles such as the global carbon, water and nitrogen cycles, or other 'unseen' impacts such as the impacts of habitat fragmentation or increased hunting pressure (Phillips 1997; Vitousek *et al.* 1997; Prentice *et al.* 2001; Galloway *et al.* 2002; Laurance 2004; Barlow & Peres 2004; Lewis *et al.* 2004). If consistent biome-wide changes are occurring, these could have profound impacts on the global carbon cycle, the rate of climate change and biodiversity, as tropical forests store and process large quantities of carbon and harbour more than 50% of the world's species (Heywood 1995; Malhi *et al.* 1999; Malhi & Grace 2000).

The physical, chemical and biological environment that tropical trees grow in has altered appreciably over recent decades (Lewis *et al.* 2004). Several studies have compiled data from long-term monitoring plots in tropical forests suggesting large-scale ecological change over the past two to five decades. (i) A pan-tropical increase in stem turnover rates (Phillips & Gentry 1994; Phillips 1996). (ii) A neotropical increase in above-ground woody biomass (Phillips *et al.* 1998, 2002a; Baker *et al.* 2004a). (iii) An Amazon-wide increase in stem recruitment (Phillips *et al.* 2004). (iv) An Amazon-wide increase in stem mortality (Phillips *et al.* 2004). (v) A western Amazon increase in large liana biomass and density (Phillips *et al.* 2002b). These results have generated an evolving debate about whether tropical forests are showing widespread directional changes caused by one or more widespread changes to the environment, or whether the observed patterns can be explained by methodological problems, mathematical artefacts or statistical errors (Sheil 1995a; Phillips 1995; Condit 1997; Phillips & Sheil 1997; Clark 2002, 2004; Phillips *et al.* 2002a,b, 2004; Baker *et al.* 2004a,b; Chambers & Silver 2004; Lewis *et al.* 2004). Several basic questions remain. Have there been widespread increases in forest growth? Are these structural and dynamic changes synchronous within the same plots? Are the changes all widespread? If so, do they share a common cause?

We document changes in stand-level processes of growth, recruitment and mortality within individual plots from across a network of plots in South America. This provides new information in three respects. First, previous studies on stem turnover and above-ground biomass (Phillips & Gentry 1994; Phillips *et al.* 1998) did not share the same plot dataset, thus we do not know if those changes were occurring simultaneously within the same plots. Second, by choosing only plots with at least two census intervals, it is possible to specifically look at rates of change without potentially confounding the results by including different plots in the dataset over time (Condit 1997). Third, we have standardized our dataset to use only three inventories with two approximately equal census interval lengths, so that any changes detected cannot be attributable to census interval effects on rate parameter estimation (Sheil 1995a; Sheil & May 1996). Thus in this study, we have factored out three potentially important limitations compared with previous studies using compilations of plot data.

When considering potential changes in forest dynamics it can be useful to view the forest, at the stand level, as a simple system consisting of a BA pool (BA: sum of the cross-sectional areas of all trees in a plot) with the size of the pool changing as BA is added to the pool by stem-increment growth and new recruitment fluxes, and subtracted from by mortality losses. Thus, we define growth (all the factors that increase the BA pool) as the sum of the increments of BA of surviving stems *and* newly recruited stems over a census interval. We call this *stand-level BA growth* (expressed as an annual rate). Likewise, we define the losses of BA from the BA pool as the sum of BA of all trees that die over a census interval, and call this *stand-level BA mortality*. Using these definitions, it can be seen that the documented increase in the BA pool (above-ground biomass) in South American forests (Phillips *et al.* 1998, 2002a; Baker *et al.* 2004a) must be caused by stand-level BA growth rates exceeding stand-level BA mortality rates. However, changes in the growth and mortality fluxes have not been investigated (cf. Phillips *et al.* 1998, 2002a; Baker *et al.* 2004a). In the simplest case, the increase in the BA pool may be caused by either an increase in stand-level BA growth with no change in stand-level BA mortality, or no change in stand-level BA growth and a decrease in stand-level BA mortality rates. However, many different combinations of rates of change in growth and mortality fluxes can also potentially lead to the same BA increment response (figure 1). Thus, a key objective for this paper is to document, for the first time, how growth and mortality fluxes have changed in South American tropical forests over recent decades.

We also apply the same simple modelling system to stems: a pool of stems (stem density), which can be added to by stem recruitment (flux in) and subtracted from by stem mortality (flux out). For South American tropical forests, we already know something about the size of the stem pool and the direction of the fluxes, but the direction and rate of change of the pool has not been investigated (cf. Phillips & Gentry 1994; Phillips 1996; Phillips *et al.* 2004).

A further advantage of looking at both changes in the pools and fluxes of BA and stems simultaneously within the same group of monitoring plots is that it is likely to allow us to exclude some of the competing interpretations of recent widespread changes in the dynamics and carbon balance of tropical forests. For example, if the documented increase in above-ground biomass (Baker *et al.* 2004a) is caused by forests recovering from disturbance events that occurred before the plots were monitored (Körner 2003), then logically the growth flux must exceed the mortality flux. However, no large changes in stand-level BA growth or BA mortality rates would be expected over time. Indeed, as the forest recovers from disturbance, the rate of increase in the biomass pool would be expected to decline over time, possibly caused by either a small reduction in the growth flux or a small increase in the mortality flux. By contrast, if sustained increases in resource levels such as atmospheric CO₂ are driving these changes, as has been suggested (Phillips *et al.* 1998, 2002a), then in addition to the growth flux exceeding the mortality flux we would predict an increase in the growth

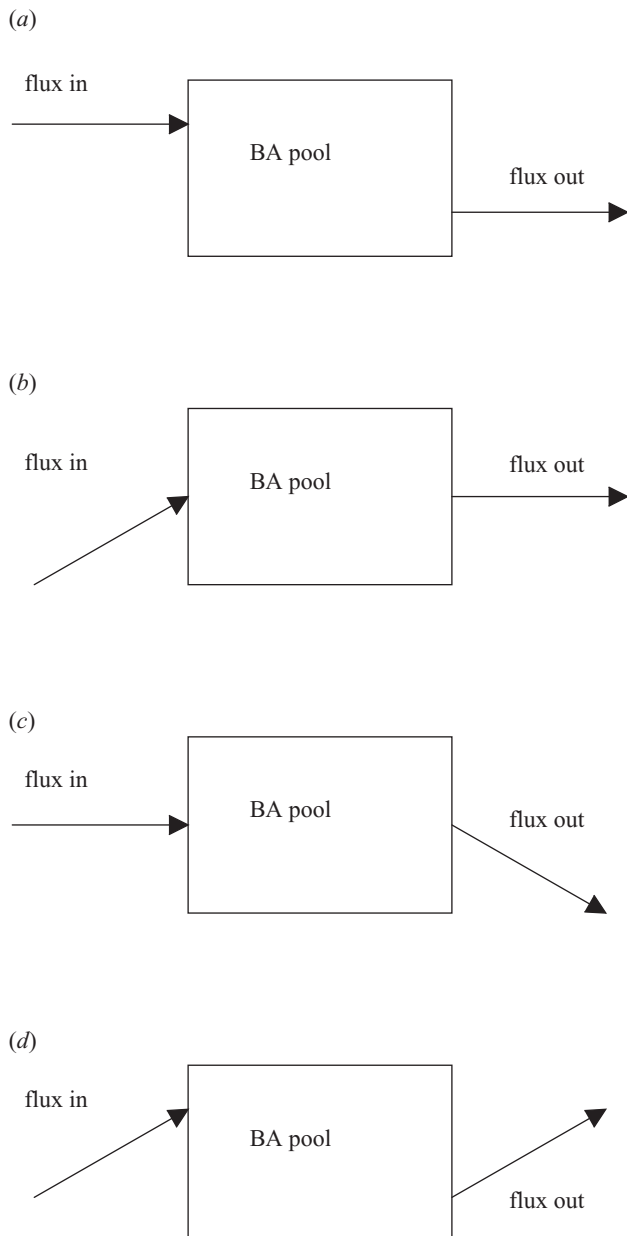


Figure 1. Schematic representations of four different scenarios where the BA of a forest (BA pool) increases. The box represents the BA pool, the line represents a flux in (additions from tree growth and recruitment) or a flux out (from mortality). The heights of the lines represent the size of the flux, and the slopes of the lines represent the rate of change of the flux over time. Knowledge of the residence time of BA in the pool is also needed to estimate the change in pool size.

flux over time (as the trees respond to increased resource levels). It is also possible to make further *a priori* predictions that could be used to separate the two hypotheses. For example, if increasing atmospheric CO₂ concentrations are driving changes in forest dynamics, then an increase in the stem flux into the stem pool (i.e. recruitment) may be expected as plants increase their light-use efficiency, especially under low light levels (Würth *et al.* 1998). Although recovery from past disturbances and rising CO₂ concentrations are only two of many hypotheses that may explain recent changes in tropical forest structure and dynamics, each is likely to leave a

consistent, coherent ‘fingerprint’ on tropical forests (Parmesan & Yohe 2003; Lewis *et al.* 2004). Analyses of suites of parameters from networks of monitoring plots should therefore allow us to eliminate some hypotheses of the causes of widespread changes in tropical forest structure and dynamics, and help us choose new analyses to further test remaining competing hypotheses.

2. METHODS

(a) Forest monitoring sites

We compiled data (table 1) from the RAINFOR network of plots across South America (Malhi *et al.* 2002). We included all forest inventories that we know of that conform to all the following criteria:

- (i) located in the Amazon Basin or contiguous forested areas;
- (ii) located in apparently mature humid tropical forest;
- (iii) no known major human impacts such as selective logging, mining or habitat fragmentation;
- (iv) elevation 1000 m or less above mean sea-level;
- (v) six months or less dry season (defined as less than 100 mm of rainfall per month; data from Malhi & Wright 2004);
- (vi) plots 0.25 ha or more in size; and
- (vii) two consecutive census intervals at least 2 years long.

All nearby plots that were individually 0.25 ha or less were combined (eleven sites, site codes: ALP, TAP, JRI, ELD and RIO). We included eight mature forests on Holocene floodplains that are no longer flooded (site codes: CUZ-01, 02, 03, 04, TAM-01, 02, 04, 06), and five that are occasionally flooded (site codes: JAS-05, MNU-01, 05, 06, 08). Our sample does not include any plots in seasonally flooded or swamp forest. The 50 plots used in the analyses are listed in table 1. Locations are shown in figure 2.

Details on measurement methodologies are given elsewhere (Phillips *et al.* 2002a, 2004; Baker *et al.* 2004a,b; Malhi *et al.* 2004). For six plots (site codes MNU), a non-standard method was used: measurements were generally made including buttresses in all censuses. To correct for this we developed a size-dependent logarithmic correction algorithm, based on a set of approximately 100 large trees correctly measured above buttresses by one of us in the same plots (Chave 2004). The correction algorithm was applied in the same way to all potentially buttressed trees, excluding non-buttressed taxa, and for all censuses. This correction entails some random error but should provide unbiased estimates of stand-level BA variables. In addition, there has been some discussion over whether or not the three plots from Venezuela that we use (ELD-12, 34 and RIO-12) were consistently measured above buttresses (see Veillon 1985; Clark 2002; Phillips *et al.* 2002a). We can confirm that measurements were made above buttresses after 1978 (Phillips *et al.* 2002a), and investigations into the protocols used in earlier censuses done by one of us (A.T.L.) who has worked extensively with the plots also confirms that before 1978 the protocols required diameter measurement or estimation above buttresses. This is reflected in the data, which show none of the features that would be expected from a change in protocols (high density of very large trees, high stand BA values, large decreases in diameters of individual trees after 1978). However, to be conservative we repeated our analyses both with and without the six MNU and three Venezuelan plots.

Table 1. Plots used in the analyses, initial values and flux rates.

(Data are the best available as of 1 March 2003, but are subject to future revision as a result of additional censuses and continued error checking. dec, decimal.)

plot name	code	country	latitude (dec)	longitude (dec)	size (ha)	first census	mid census	final census	BA start (m ² ha ⁻¹)	stems start (ha ⁻¹)	stand	stand	stand	stand	stem	stem	stem	stem
											growth interval 1	growth interval 2	mortality interval 1	mortality interval 2	recruits interval 1	recruits interval 2	morta- lity interval 1	morta- lity interval 2
BDFFP, 2303 Dimona 4-5 ^a	BDF-01	Brazil	-2.40	-60.00	2.00	1985.29	1990.62	1997.71	30.15	688	1.17	1.58	1.73	1.05	0.84	1.60	1.37	1.11
BDFFP, 1101 Gaviao	BDF-03	Brazil	-2.40	-59.90	1.00	1981.13	1991.37	1999.29	28.39	593	1.21	1.56	1.08	1.24	0.83	1.40	0.90	1.55
BDFFP, 1102 Gaviao	BDF-04	Brazil	-2.40	-59.90	1.00	1981.13	1991.37	1999.29	28.08	590	1.13	2.44	3.77	1.81	0.69	4.64	3.25	2.19
BDFFP, 1103 Gaviao	BDF-05	Brazil	-2.40	-59.90	1.00	1981.21	1991.62	1999.29	25.28	650	1.30	1.64	1.27	1.11	0.54	1.41	1.47	1.32
BDFFP, 1201 Gaviao ^a	BDF-06	Brazil	-2.40	-59.90	3.00	1981.29	1991.37	1999.29	25.48	632	1.50	1.68	1.10	1.95	0.84	1.52	1.18	1.78
BDFFP, 1109 Gaviao	BDF-08	Brazil	-2.40	-59.90	1.00	1981.63	1991.55	1999.46	28.47	590	1.13	1.10	1.46	1.06	0.87	2.25	1.67	1.53
BDFFP, 1301.1 Florestal	BDF-10	Brazil	-2.40	-59.90	1.00	1983.46	1987.21	1997.13	27.47	621	1.00	1.57	0.60	1.45	1.00	1.67	0.83	1.61
BDFFP, 1301.4, 5, 6 ^a Florestal	BDF-11	Brazil	-2.40	-59.90	3.00	1983.46	1987.21	1997.13	28.85	629	0.90	1.16	0.33	0.84	0.53	0.65	0.49	0.78
BDFFP, 1301.7, 8 Florestal ^a	BDF-12	Brazil	-2.40	-59.90	2.00	1983.46	1987.21	1997.13	28.45	617	0.76	1.15	0.93	0.75	0.35	0.70	0.37	0.70
BDFFP, 3402 Cabo Frio	BDF-13	Brazil	-2.40	-60.00	9.00	1985.86	1991.16	1998.88	26.42	568	1.34	1.40	0.84	0.84	1.24	1.34	0.87	1.04
BDFFP, 3304 Porto Alegre ^a	BDF-14	Brazil	-2.40	-60.00	2.00	1984.21	1992.29	1998.38	32.05	651	1.00	1.67	1.62	1.55	0.81	1.77	1.22	1.29
Bionte 1	BNT-01	Brazil	-2.63	-60.17	1.00	1986.50	1991.50	1999.50	28.04	561	1.61	1.43	0.62	0.69	1.54	0.82	0.99	0.89
Bionte 2	BNT-02	Brazil	-2.63	-60.17	1.00	1986.50	1991.50	1999.50	30.14	692	1.43	1.38	0.56	0.75	1.06	0.41	0.61	0.68
Bionte 4	BNT-04	Brazil	-2.63	-60.17	1.00	1986.50	1991.50	1999.50	27.76	608	1.69	1.69	1.84	1.05	1.60	0.81	1.53	1.08
Caxiuana 1	CAX-01	Brazil	-1.70	-51.53	1.00	1994.50	1999.50	2002.84	30.07	524	0.98	1.15	0.61	1.04	0.51	1.16	0.86	0.93
Jacaranda 1-5	JAC-01	Brazil	-2.63	-60.17	5.00	1996.50	2000.50	2002.50	27.51	593	1.13	1.90	1.24	2.14	1.01	2.80	0.92	1.24
Jacaranda 6-10	JAC-02	Brazil	-2.63	-60.17	5.00	1996.50	2000.50	2002.50	26.60	573	1.01	1.98	1.14	2.18	0.97	2.09	0.87	1.57
Jari 1 ^b	JRI-01	Brazil	-1.00	-52.05	1.00	1985.50	1990.50	1996.00	32.99	572	1.18	1.38	0.79	1.66	1.52	1.59	0.97	1.28
Tapajos, RP014, 1-4 ^c	TAP-01	Brazil	-3.31	-54.94	1.00	1983.50	1989.50	1995.50	23.61	527	1.99	1.80	0.49	1.13	1.63	1.46	0.68	0.67
Tapajos, RP014, 5-8 ^c	TAP-02	Brazil	-3.31	-54.94	1.00	1983.50	1989.50	1995.50	27.82	479	2.00	1.27	0.66	0.63	1.86	1.45	0.78	0.50
Tapajos, RP014, 9-12 ^c	TAP-03	Brazil	-3.31	-54.94	1.00	1983.50	1989.50	1995.50	31.25	491	1.63	1.37	0.64	0.77	1.64	1.33	0.91	0.70
Jatun Sacha 1	JAS-02	Ecuador	-1.07	-77.60	1.00	1987.63	1994.54	2002.04	30.18	724	1.83	3.28	1.54	3.73	1.14	2.61	1.08	2.74
Jatun Sacha 3	JAS-03	Ecuador	-1.07	-77.67	1.00	1988.88	1994.29	2002.04	27.96	648	3.30	2.89	2.45	2.33	1.79	2.39	2.40	1.69
Jatun Sacha 5	JAS-05	Ecuador	-1.07	-77.67	1.00	1989.38	1994.46	2002.04	30.90	534	2.65	3.54	1.61	2.50	1.87	2.97	1.76	2.32
Allpahuayo A clayey ^d	ALP-11	Peru	-3.95	-73.43	0.44	1990.87	1996.13	2001.03	27.36	580	1.80	2.49	1.54	2.58	2.05	2.30	2.13	3.12
Allpahuayo A, sandy ^d	ALP-12	Peru	-3.95	-73.43	0.40	1990.87	1996.13	2001.03	25.19	570	2.14	2.57	0.93	4.53	1.36	2.05	1.03	3.97
Allpahuayo B, sandy ^d	ALP-21	Peru	-3.95	-73.43	0.48	1990.87	1996.13	2001.04	26.88	575	2.14	3.07	2.72	2.12	1.80	3.13	1.73	2.34
Allpahuayo B, clayey ^d	ALP-22	Peru	-3.95	-73.43	0.44	1990.87	1996.13	2001.04	25.49	614	2.59	2.06	1.64	2.06	2.09	2.71	1.46	2.57
Cuzco Amazonico, CUZAM1E	CUZ-01	Peru	-12.50	-68.95	1.00	1989.39	1994.63	1998.77	25.41	489	2.31	2.95	1.40	1.55	2.79	2.24	1.80	1.55
Cuzco Amazonico, CUZAM1U	CUZ-02	Peru	-12.50	-68.95	1.00	1989.42	1994.63	1998.77	25.27	509	2.53	3.55	1.01	2.86	1.92	2.36	1.37	1.77
Cuzco Amazonico, CUZAM2E	CUZ-03	Peru	-12.49	-69.11	1.00	1989.40	1994.62	1998.77	21.69	470	3.17	3.93	1.76	1.40	2.76	2.70	2.20	1.97
Cuzco Amazonico, CUZAM2U	CUZ-04	Peru	-12.49	-69.11	1.00	1989.44	1994.62	1998.78	27.26	571	2.44	3.51	2.34	1.91	1.47	3.90	1.92	2.35
Manu, Trail 3	MNU-01	Peru	-11.88	-71.35	0.97	1975.00	1990.75	2000.75	28.56	549	2.09	2.04	1.72	2.28	2.15	2.50	2.19	2.45

(Continued.)

Table 1. (Continued.)

plot name	code	country	latitude (dec)	longitude (dec)	size (ha)	first census	mid census	final census	BA start (m ² ha ⁻¹)	stems start (ha ⁻¹)	stand BA growth interval 1	stand BA growth interval 2	stand BA mortality interval 1	stand BA mortality interval 2	stem recruits interval 1	stem recruits interval 2	stem morta- lity interval 1	stem morta- lity interval 2
Manu, terra firme terrace	MNU-03	Peru	-11.88	-71.35	2.00	1991.75	1996.75	2001.75	25.90	578	2.71	3.27	2.60	2.99	3.24	3.55	3.00	3.34
Manu, terra firme ravine	MNU-04	Peru	-11.88	-71.35	2.00	1991.75	1996.75	2001.63	27.12	587	2.43	2.36	1.73	2.08	2.84	1.78	2.02	2.34
Manu, Trail 12	MNU-05	Peru	-11.88	-71.35	2.00	1989.99	1994.99	1999.99	33.59	599	1.77	1.27	1.11	1.32	2.03	1.53	1.24	1.92
Manu, Trail 2 & 31	MNU-06	Peru	-11.88	-71.35	2.25	1989.80	1994.80	1999.80	32.21	511	1.77	1.90	0.98	1.71	1.79	2.06	1.67	1.92
Manu, Cocha Salvador	MNU-08	Peru	-11.88	-71.35	2.00	1991.80	1996.83	2001.87	36.81	563	1.47	1.61	1.40	1.06	1.52	1.55	1.20	1.48
Sucusari A	SUC-01	Peru	-3.23	-72.90	1.00	1992.13	1996.08	2001.06	28.25	612	2.44	2.00	2.75	2.01	1.86	1.53	2.11	1.80
Sucusari B	SUC-02	Peru	-3.23	-72.90	1.00	1992.13	1996.08	2001.07	29.46	606	2.45	2.09	1.92	3.70	2.33	2.07	2.09	2.77
Tambopata plot zero	TAM-01	Peru	-12.85	-69.28	1.00	1983.78	1991.53	2000.59	26.91	555	2.40	2.89	3.01	1.60	2.15	2.87	2.31	2.15
Tambopata plot one	TAM-02	Peru	-12.83	-69.28	1.00	1979.87	1991.58	2000.58	27.44	576	1.82	2.05	1.42	1.59	1.68	2.55	1.35	1.57
Tambopata plot two	TAM-04	Peru	-12.83	-69.28	0.42	1983.79	1990.76	1998.75	28.56	705	2.48	2.91	3.10	1.76	2.28	2.59	2.77	2.46
Tambopata plot three	TAM-05	Peru	-12.83	-69.28	1.00	1983.70	1991.54	2000.56	24.27	548	2.21	2.76	1.87	2.06	2.13	3.19	2.32	2.27
Tambopata plot four	TAM-06	Peru	-12.83	-69.30	0.96	1983.71	1991.54	2000.55	30.54	520	1.98	2.39	1.58	0.90	2.73	3.37	1.69	1.47
Tambopata plot six	TAM-07	Peru	-12.83	-69.27	1.00	1983.76	1991.54	1998.73	27.36	548	2.50	2.71	2.25	2.19	2.18	2.96	2.22	2.91
Yanamono A	YAN-01	Peru	-3.43	-72.85	1.00	1983.46	1991.29	2001.05	30.95	570	2.82	2.48	2.45	2.31	2.00	3.06	2.54	2.69
El Dorado, km 91 plot EDL-01, 02 ^c	ELD-12	Venezuela	6.50	-61.50	0.50	1971.55	1981.18	1994.44	27.69	492	1.76	1.62	1.01	0.51	1.09	0.76	0.93	0.47
El Dorado, km 98 plot EDL-03, 04 ^c	ELD-34	Venezuela	6.50	-61.50	0.50	1971.56	1976.21	1981.19	25.29	622	2.58	2.95	1.01	4.29	1.47	1.74	1.06	2.00
Rio Grande RIO-01, 02 ^c	RIO-12	Venezuela	8.00	-61.75	0.50	1971.58	1981.20	1994.46	29.45	570	1.81	1.73	0.82	1.94	1.27	1.15	0.91	1.46

^a These sites comprise non-contiguous 1 ha plots separated by less than 200 m; they are treated as one plot.

^b Twenty-five 10 m × 10 m subplots, within each of four nearby 1 ha plots.

^c Twelve 0.25 ha plots laid out in a randomized design over an area of 300 m × 1200 m; treated as 3 × 1 ha units.

^d Allpahuayo A and B both contain two distinct soil types that are treated separately in these analyses.

^e These sites comprise two nearby non-contiguous 0.25 ha plots.

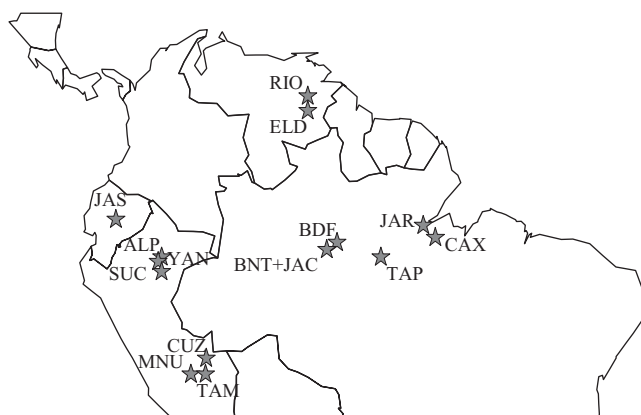


Figure 2. The location of the study plots. Codes RIO, JAR, CAX and YAN have one plot each, EDL, JAC and SUC have two plots, TAP, BNT and JAS, have three plots, ALP and CUZ have four plots, MNU and TAM have six plots and BDF has 11 plots.

(b) Approach and definitions

We consider the forest as a simple system of a pool of BA with a flux into and flux out of the BA pool (figure 1). We define the pool of BA as the sum of the cross-sectional areas of all trees with a dbh of 10 cm or more (dbh, 1.3 m or above deformities) in a plot (in square metres per hectare). The amount of growth occurring is the flux into the BA pool. We define growth as the sum of the increments of BA of all surviving trees and the sum of BA of all newly recruited trees into a plot over the census interval (in square metres per hectare per year). We call this stand-level BA growth. This represents all the additions of BA to the system per unit time per unit area. Note that stand-level BA growth, as defined here, will also be influenced by changes in recruitment into the 10 cm dbh size-class but this component is relatively small: the 50 plot mean stand-level BA growth is $0.51 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$, whereas recruitment averages $9.4 \text{ stems ha}^{-1} \text{ yr}^{-1}$, thus contributing *ca.* $0.08 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ to stand-level BA growth (*ca.* 15%). The flux out of the system is caused by tree mortality. We define stand-level BA mortality as the sum of BA of all trees of dbh of 10 cm or more that died in a plot over the census interval (in $\text{m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$).

Figure 1 shows how the changes in the size of the BA pool can be similar even though the fluxes in and out may be very different. Thus, for the forests studied we seek to discover:

- (i) the size of the BA pool;
- (ii) the direction and rate of change in the size of the pool;
- (iii) the mean flux into the BA pool, i.e. stand-level BA growth rate;
- (iv) the mean flux out of the BA pool, i.e. stand-level BA mortality rate;
- (v) the direction and rate of change of stand-level BA growth rates;
- (vi) the direction and rate of change of stand-level BA mortality rates.

Overall, we are interested in determining the rate at which the fluxes determining the size of the BA pool are themselves changing. Most importantly, we are interested in knowing if the observed changes in BA pool are due to an acceleration or deceleration of the rates of growth and/or mortality, and whether changes in growth rates precede changes in mortality rates or vice versa.

We treat stems in the same way, i.e. as a pool of stems with fluxes into and out of the pool. The pool is the number of stems of greater than 10 cm dbh per hectare. The flux into the stem pool is the stem recruitment rate, the number of stems attaining 10 cm or more dbh over the census interval. The flux out of the stem pool is the stem mortality rate, the number of stems dying, over the census interval.

Thus, for each forest plot with three censuses (i.e. two intervals) we have calculated the pools at each census date and the fluxes for both census intervals, that is:

- (i) BA at each census;
- (ii) stand-level BA growth rates for both census intervals;
- (iii) stand-level BA mortality rates for both census intervals;
- (iv) stem density at each census;
- (v) stem recruitment rates for both census intervals; and
- (vi) stem mortality rates for both census intervals.

If more than three censuses were available we selected the mid-census inventory that provided two approximately equal census intervals, with a bias towards choosing slightly longer second census intervals where possible. This ensures that any results showing increases in the fluxes cannot be attributed to census interval-length effects (Sheil & May 1996).

For each pool, we need to directly compare the size of the fluxes in and out, as is commonly done in studies of mortality and recruitment. Hence, we calculate

$$\lambda = \frac{\ln n_0 - \ln(n_0 - D_t)}{t} \times 100, \quad (3.1)$$

where λ is the exponential mortality coefficient (expressed as per cent per year), n_0 is the number of stems at the start of the census interval, D_t is the number of stems dying over the census interval, and t is the census interval length (in years) (Sheil *et al.* 1995).

For stem recruitment, we use the inverse of mortality:

$$\mu = \frac{\ln n_t - \ln(n_0 - D_t)}{t}, \quad (3.2)$$

where n_t is the number of stems at the end of the census interval. We use equivalent formulae for the fluxes of BA, substituting BA at the start of the census for n_0 , substituting BA lost through stems dying over the census interval (stand-level BA mortality) for D_t , and substituting the total BA at the end of the census interval for n_t . This allows direct comparisons of stand-level BA growth, stand-level BA mortality, stem recruitment and stem mortality (i.e. the direct comparison of fluxes whether on a stem or BA basis).

To compare *changes* in the fluxes we use two methods. We report (i) absolute changes, the rate over the first census interval subtracted from the rate over the second census interval; and (ii) relative changes, by applying the method used to calculate relative growth rates (Evans 1972). Thus for stand-level BA growth rates (SBAG), the annual relative change is

$$\Delta\text{SBAG} = \frac{\ln(\text{SBAG}_{i2}) - \ln(\text{SBAG}_{i1})}{m_{i2} - m_{i1}} \times 100, \quad (3.3)$$

expressed in per cent per year. The subscripts $i1$ and $i2$ denote census intervals one and two, respectively, and m is the mid-year of the census interval in years.

To compare *changes* in the pools (BA or stems) we calculate absolute changes in the same way as for the fluxes. To calculate

relative changes, we use the difference in the pool scaled by the initial size of the pool and the census interval, as has commonly been used elsewhere, again expressed in per cent per year (Malhi & Grace 2000; Hamilton *et al.* 2002). Using equation (3.3) to calculate changes in the pools makes very little difference to the mean values. The mean relative change in BA is $0.36 \pm 0.14\% \text{ yr}^{-1}$ or $0.38 \pm 0.15\% \text{ yr}^{-1}$ assuming either a \log_e or linear relationship, respectively.

(c) Statistical analysis

For each of our analyses we checked that our data were normally distributed. Overall, the static variables (pools), changes in static variables over time (e.g. relative change in BA), dynamic variables (fluxes) and changes in dynamic variables over time (e.g. differences between rates in the first and second census intervals) that we use in the analyses, were all approximately normal but tended to have a right skew. No category of parameter was grossly non-normal. Explorations of a variety of transformations did not consistently move the data to become more normal. Thus, we used untransformed data and mostly employed parametric *t*-tests on paired observations in our statistical analyses. When analysing the full set of 50 plots we used two-tailed tests of significance, as either increases or decreases in parameters were expected. When we analysed subsets of the data for consistency with the trends from the full dataset, for example, to assess potential sampling biases, we used one-tailed tests of significance as we had an *a priori* expectation of change in a given direction.

In the first set of analyses we compared the flux rates over the first and second census intervals, firstly as BA, and secondly on a stem basis. Throughout § 4, we report BA, stand BA growth and mortality rates in square metres per hectare per year in the main body of the text. Likewise, we report stem density, and stem recruitment and stem mortality rates in stems per hectare per year in the main body of the text. This notation allows comparisons with other studies, which commonly report BA and growth using these units. In the figures and tables we give rates using equations (3.1) and (3.2), in per cent per year, as this allows the direct comparison of fluxes on both a per stem and a per BA basis. This notation allows comparisons with other studies as stem recruitment and mortality rates are commonly reported using these equations.

In the first set of analyses, we also plot each flux (stand BA growth, stand BA mortality, stem recruitment and stem mortality) against calendar year. We used linear regression to relate each parameter to the mid-year of each census interval for each plot. This linear relation was used to obtain an estimated parameter rate for each year from 1985 to 1999 (when more than half the plots were monitored). When extrapolating beyond the limits of the data for a given plot we constrained values by not exceeding the highest ($4.64\% \text{ yr}^{-1}$) and lowest ($0.33\% \text{ yr}^{-1}$) rates in our dataset. This procedure avoids the problem of 'site switching' (as not all plots were monitored in all years) and ensures that each plot has a rate estimate for each year rather than constant values followed by large instantaneous changes each time a new census is completed.

In § 4c, we analyse changes in the fluxes and pools of faster growing and more dynamic forests compared with slower growing and less dynamic forests. South American tropical forests vary widely in their growth rates (Malhi *et al.* 2004) and dynamics (Phillips 1996). Furthermore, faster growing forests are, on average, more dynamic than slower growing forests (cf. forests reported in both Phillips 1996 and Malhi *et al.* 2004). If South

American tropical forests are indeed changing because of a long-term environmental change affecting growth or mortality rates, then other factors being equal, such changes should manifest themselves earlier and more readily in faster-growing and more dynamic forests than slower growing and less dynamic forests. This is because similar proportional changes would be absolutely larger in more dynamic forests, and because any changes occurring would more rapidly percolate through the system. To test our predictions for faster growing and more dynamic plots, compared with slower growing and less dynamic plots, we grouped our 50 plots into a 'slow dynamics' group and 'fast dynamics' group.

The plot network shows large-scale bias in plot location across South America, as some areas are well sampled, others less so (figure 2). In § 4d we investigate whether this bias is causing the changes in the pools and fluxes we observe (figure 2). If a few well-sampled areas are changing, while other poorly sampled areas are not, we may obtain significant results for plots from across South America when in fact only landscape-scale changes are occurring. We test whether our data are robust to this sampling bias by progressively clustering plots together based on distance criteria. If the mean values of estimated parameters were not affected by clustering this would suggest that any patterns documented are robust for spatial coverage. We group plots in four ways to give a decreasing number of clusters:

- (i) each non-contiguous plot defined as a 'cluster';
- (ii) group all plots within *ca.* 20 km radii (13 clusters with codes: ALP, BDF, BNT & JAC, CAX, CUZ, ELD, JAR, JAS, MNU, RIO, TAM, TAP, and YAN & SUC);
- (iii) group all plots within *ca.* 200 km radii, and define such areas as a cluster (six clusters: Ecuador, north Peru, south Peru, central Amazonia, eastern Amazonia, Venezuela); and
- (iv) group all plots from western (more than 69° W), eastern (less than 55° W) and central (more than 55° W and less than 69° W) South America (three clusters).

3. RESULTS

(a) Basal area

The average date of the first, mid and final censuses was late 1985, early 1992 and early 1999, respectively. The earliest start date was 1971; five plots started in the 1970s, 33 in the 1980s and 12 in the 1990s. The final census was between 1994 and 2002 for all plots except ELD-34, which was concluded in 1981. The first census interval was, on average, 6.4 ± 0.7 years ($\pm 95\% \text{ CI}$; range of 3.8–15.8), and the second 6.8 ± 0.7 years (range of 2.0–13.3). Thus, the results are conservative, in an overall sense, for census interval effects. The average plot size was 1.50 ± 0.41 ha (range of 0.4–9). Eight plots were 0.4–0.5 ha, 29 plots were 0.96–1 ha and 13 were 2 ha or more.

The mean BA of the 50 plots was $28.2 \pm 0.75 \text{ m}^2 \text{ ha}^{-1}$ (range of 21.7–36.8) at the first census interval and was significantly higher at $29.5 \pm 0.88 \text{ m}^2 \text{ ha}^{-1}$ by the final census interval ($t = 4.93$, $p < 0.0001$, d.f. 49; 41 out of 50 plots increased). The mean size of the flux into the BA pool, stand-level BA growth, was $0.51 \pm 0.04 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$. The mean flux out, stand-level BA mortality, was $0.41 \pm 0.04 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$. Hence, for the study period, BA increased by $0.10 \pm 0.04 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$, or a relative increase of

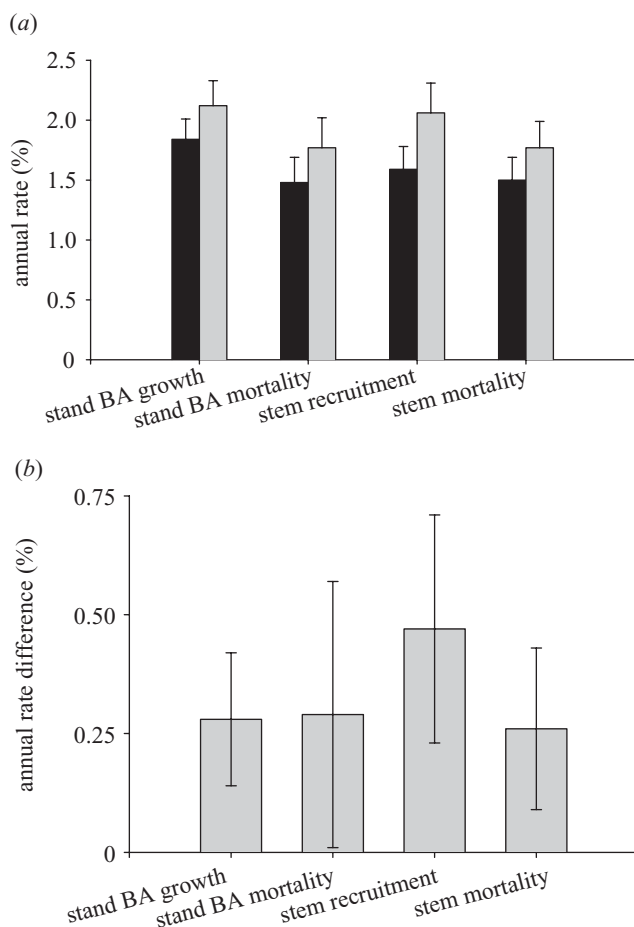


Figure 3. (a) Annualized rates of stand-level BA growth, stand-level BA mortality, stem recruitment and stem mortality from two consecutive census intervals (black bars, interval 1; grey bars, interval 2); (b) stand-level BA growth, stand-level BA mortality, stem recruitment and stem mortality over census interval one subtracted from that over interval two (rate difference), each from 50 plots with 95% CIs. The average mid-year of the first and second censuses was 1989 and 1996, respectively.

$0.38 \pm 0.15\% \text{ yr}^{-1}$ (change in the BA pool scaled by the initial BA pool and the census interval).

Across the 50 plots the stand-level BA growth rate increased significantly between the first and second census intervals, shown by subtracting the rate over interval one from that over interval two for each plot and noting that the 95% CI for this change parameter does not cross zero (figure 3; table 2; $t = 3.89$, $p = 0.0003$; 34 out of 50 plots increased). The wide confidence intervals associated with comparing the mean stand-level BA growth rates over intervals one and two are caused by the wide range of tropical forests sampled, for example, CAX-01 increased stand-level BA growth from 0.29 to $0.35 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$, while CUZ-03 increased from 0.68 to $0.94 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ (figure 3). Mean stand-level BA growth rate increased from $0.50 \pm 0.04 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ in the first census interval to $0.58 \pm 0.05 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ in the second. Plotting stand-level BA growth rate across calendar years shows the same increase (figure 4; table 2). In relative terms, the annual rate of increase in stand-level BA growth rate ($2.55 \pm 1.45\% \text{ yr}^{-1}$, using equation (3.3)) is almost an

order of magnitude larger than the change in the BA pool size itself ($0.38 \pm 0.15\% \text{ yr}^{-1}$; table 2).

Stand-level BA mortality rates increased significantly between the first and second census intervals (figure 3; table 2; $t = 2.01$, $p = 0.05$; 29 out of 50 plots increased). Note that although the differences in stand-level BA growth rates and stand-level BA mortality rates are similar, the absolute amounts are higher for additions compared with the losses (figure 3). Mean stand-level BA mortality rates increased from $0.40 \pm 0.05 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ in the first interval to $0.48 \pm 0.06 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ in the second. The rates of increase in stand-level BA growth rates and stand level BA mortality rates were very similar. However, stand-level BA growth rates were significantly higher than stand-level BA mortality rates in both intervals (by 0.11 ± 0.05 and $0.10 \pm 0.06 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ for census intervals one and two, respectively). Plotting stand-level BA mortality rates across calendar years, we again see an increase (figure 4; table 2). Using this dataset stand-level BA growth exceeded BA mortality, but by a detectable amount only after 1987 (figure 4). As was the case for stand-level BA growth rates, in relative terms, the change in stand BA mortality rates was an order of magnitude larger than the change in the size of the BA pool itself (table 2).

In summary, over the past 30 years the study plots have experienced a net increase in BA of $0.10 \pm 0.04 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$. This is not attributable to the documented increase in stand-level BA growth rates (which increased, on average, by $0.08 \pm 0.04 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ between the two censuses), as stand-level BA mortality rates, while much more variable, also increased by a similar amount (by $0.08 \pm 0.07 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ between the two censuses). The BA pool increased in this group of forests as growth rates exceeded mortality rates by $0.10 \pm 0.05 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ in the first census period, and this difference between growth and mortality rates continued over the second census period. These results correspond to the situation represented schematically as figure 1d.

(b) Stems

The mean number of stems per hectare across the 50 plots was 581 ± 16 (range of 470–724) at the first census, and was significantly higher at $592 \pm 14 \text{ ha}^{-1}$ at the final census ($t = 2.46$, $p = 0.017$, d.f. 49; 32 out of 50 plots increased). The mean size of the flux into the stem pool, stem recruitment, was $9.4 \pm 0.88 \text{ stems ha}^{-1} \text{ yr}^{-1}$ across the 50 plots over the entire monitoring period. The mean size of the flux out of the stem pool, stem mortality, was $8.4 \pm 0.89 \text{ stems ha}^{-1} \text{ yr}^{-1}$. Hence, for the study period, stem number increased by $0.94 \pm 0.63 \text{ stems ha}^{-1} \text{ yr}^{-1}$, or relatively speaking by $0.18 \pm 0.12\% \text{ yr}^{-1}$ (change in the BA pool scaled by the initial BA pool and the census interval). Thus, compared with the relative increase in the BA pool, the relative increase in stem density was less marked (mean difference between the relative change in the BA pool and the relative change in the stems pools was $0.19 \pm 0.11\%$).

Across the 50 plots stem recruitment rates increased significantly between the first and second census intervals (figure 3; table 2; $t = 3.86$, $p = 0.0003$, d.f. = 49; 37 out of

Table 2. Mean and 95% CIs for flux rates of BA and stems from 50 South America forest plots (in per cent per year).

flux	within plots			from linear regression procedures ^a		
	interval 1	interval 2	relative change ^b	1989	1998	relative change ^b
stand BA growth	1.87 ± 0.18	2.14 ± 0.21	2.55 ± 1.45	1.80 ± 0.20	2.18 ± 0.26	1.92 ± 1.21
stand BA mortality	1.50 ± 0.21	1.79 ± 0.25	4.03 ± 2.71	1.44 ± 0.27	1.76 ± 0.28	2.72 ± 2.33
stem recruitment	1.59 ± 0.19	2.06 ± 0.25	4.23 ± 2.53	1.59 ± 0.22	2.11 ± 0.30	2.73 ± 1.94
stem mortality	1.50 ± 0.19	1.77 ± 0.22	3.08 ± 1.81	1.41 ± 0.22	1.80 ± 0.26	2.63 ± 1.64

^a Between 1989 and 1998 more than three-quarters of the plots were being simultaneously monitored.

^b Using equation (3.3).

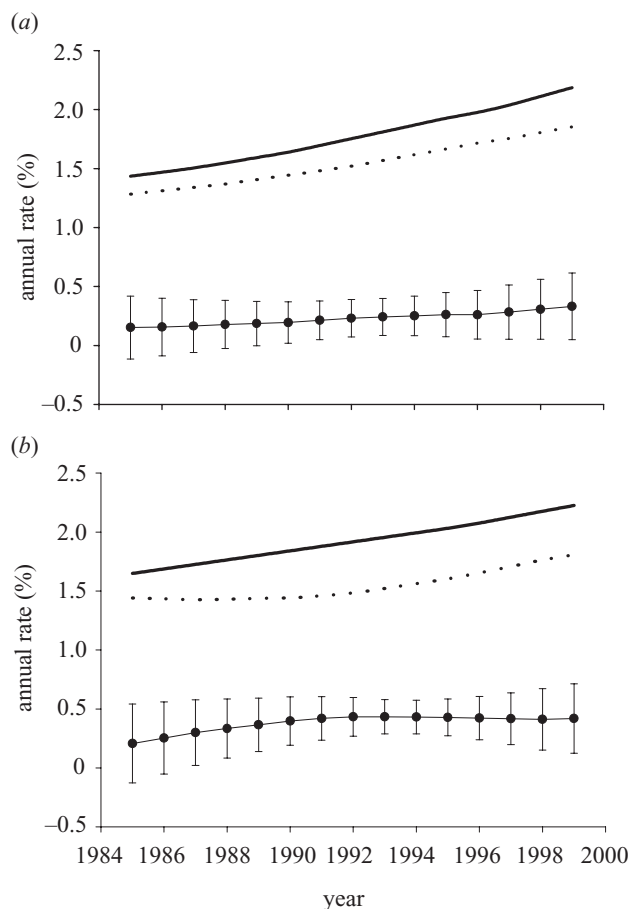


Figure 4. (a) Mean rates of stem recruitment and stem mortality and their difference, with 95% CI, and (b) stand-level BA growth and stand-level BA mortality and their difference, with 95% CI from 50 plots, against calendar year using a simple extrapolation method (see text). Solid lines, additions; dotted lines, losses; lines with error bars, difference.

50 plots increased). Mean stem recruitment rates increased from 8.7 ± 0.98 stems $\text{ha}^{-1} \text{yr}^{-1}$ in the first census interval to 11.3 ± 1.3 stems $\text{ha}^{-1} \text{yr}^{-1}$ in the second. Plotting stem recruitment across calendar years, we again see an increase (figure 4; table 2). The relative increase in stem recruitment rates ($4.23 \pm 2.53\% \text{yr}^{-1}$) is an order of magnitude greater than the change in the stem pool itself ($0.18 \pm 0.12\% \text{yr}^{-1}$; table 2).

Stem mortality rates increased significantly between the first and second census intervals (figure 3; table 2; $t = 2.97, p = 0.005$; d.f. = 49; 32 out of 50 plots increased).

Mean stem mortality increased from 8.2 ± 1.0 stems $\text{ha}^{-1} \text{yr}^{-1}$ in the first census interval to 9.6 ± 1.2 stems $\text{ha}^{-1} \text{yr}^{-1}$ in the second interval. The rate of increase in stem recruitment, although greater than the rate of increase in stem mortality, was not significantly so (an increase of 2.6 ± 1.3 stems $\text{ha}^{-1} \text{yr}^{-1}$ between census intervals one and two for stem recruitment compared with an increase of 1.4 ± 0.98 stems $\text{ha}^{-1} \text{yr}^{-1}$ between census intervals one and two for stem mortality, with a mean difference of 1.2 ± 1.6 stems $\text{ha}^{-1} \text{yr}^{-1}$). The mean difference between stem recruitment and mortality rates was slightly higher when calculated using two shorter census intervals compared with one long interval. This may be because: (i) stem recruitment and/or stem mortality rates are increasing nonlinearly; or (ii) because shorter census intervals increase recruitment and mortality rates by the similar relative amounts, so amplifying the absolute difference between the two. Plotting stem mortality rates across calendar years, we again see an increase (figure 4; table 2). Using this dataset, stem recruitment exceeded stem mortality, but by a detectable amount only after 1990 (figure 5). Again, the relative increase in stem mortality rates is approximately an order of magnitude greater than the change in the stem pool itself (table 2).

In summary, over the past 30 years the study plots have, on average, been characterized by an increase in stem density of 0.94 ± 0.63 stems $\text{ha}^{-1} \text{yr}^{-1}$. This is partly attributable to the increase in recruitment rates, which increased, on average, by 2.6 ± 1.3 stems $\text{ha}^{-1} \text{yr}^{-1}$ between the two censuses, but stem mortality also increased over the monitoring period, on average, by 1.4 ± 0.98 stems $\text{ha}^{-1} \text{yr}^{-1}$ between the two censuses. Stem density also increased because stem recruitment exceeded mortality by a statistically insignificant amount over the first census interval (0.5 ± 0.9 stems $\text{ha}^{-1} \text{yr}^{-1}$), then by a much greater and significant amount over the second census interval (1.7 ± 1.1 stems $\text{ha}^{-1} \text{yr}^{-1}$).

(c) *Fast versus slow forests*

To further understand the changes in dynamics documented for the group of forest plots as a whole we split the 50 plots into a faster growing and more dynamic group of plots and a slower growing and less dynamic group of plots (see § 2c). The ‘fast dynamics’ group of plots is approximately twice as dynamic and twice as fast growing as the ‘slow dynamics’ group (figure 5; table 3). Whereas, on average, the fluxes are twice as large in the fast group compared with the slow, the BA and stems pools are similar for both groups of forests (fast group, mean

Table 3. Mean and 95% CIs for flux rates of BA and stems from a relatively slow-growing un-dynamic group of forest plots and a relatively fast-growing dynamic group (in per cent per year).

flux	slow dynamics group, $n = 24$			fast dynamics group, $n = 26$		
	interval 1	interval 2	relative change	interval 1	interval 2	relative change
stand BA growth	1.37 ± 0.14	1.50 ± 0.10	2.56 ± 2.60	2.34 ± 0.18	2.73 ± 0.21	2.53 ± 1.47
stand BA mortality	1.00 ± 0.16	1.20 ± 0.19	4.07 ± 3.43	1.97 ± 0.28	2.34 ± 0.34	3.98 ± 4.22
stem recruitment	1.13 ± 0.18	1.38 ± 0.21	4.29 ± 4.54	2.02 ± 0.22	2.69 ± 0.27	4.18 ± 2.57
stem mortality	0.99 ± 0.13	1.15 ± 0.17	2.71 ± 2.51	1.98 ± 0.22	2.34 ± 0.23	3.42 ± 2.65

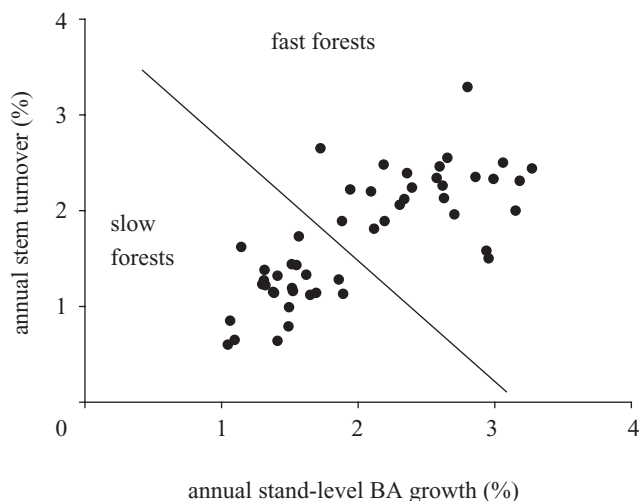


Figure 5. We group the 50 plots into two categories, relatively slow-growing and non-dynamic ('slow forests'), and relatively fast-growing and dynamic ('fast forests'), based on annualized stem turnover and stand-level BA growth calculated over the total census interval for each plot.

BA = $27.5 \text{ m}^{-2} \text{ ha}^{-1}$, mean stem density = 575; slow group, mean BA = 28.9, mean stem density = 585).

The fast and slow dynamics groups both significantly increased their BA pools by $0.40 \pm 0.25\% \text{ yr}^{-1}$ and $0.35 \pm 0.16\% \text{ yr}^{-1}$, respectively. Likewise, significant increases in stem density occurred at rates of $0.21 \pm 0.18\% \text{ yr}^{-1}$ and $0.16 \pm 0.15\% \text{ yr}^{-1}$ for the fast and slow groups, respectively.

The fast and slow groups also both exhibited significantly increased stand-level BA growth rates (figure 6, table 3; fast: $t = 3.65$, $p = 0.0006$, d.f. = 25; slow: $t = 1.73$, $p = 0.049$; d.f. = 23; one-tailed tests), with the fast dynamics group having significantly greater absolute increases in stand BA growth rates than the slow group (cf. figure 6; $t = 1.95$, $p = 0.029$, two-sample test, variances assumed unequal, one-tailed test). However, there is no significant difference in the relative increases in growth between the slow and fast groups (table 3). Both the fast and slow groups of forests also showed increases in stand-level BA mortality rates, although this increase was only significant for the slow group of forests (figure 6; table 3; fast: $t = 1.52$, $p = 0.07$, d.f. = 25; slow: $t = 1.79$, $p = 0.04$, d.f. = 23). The fast dynamics forests had greater absolute increases in stand BA mortality rates than the slow dynamics forests, but not significantly so (table 3; cf. figure 6; $t = 0.69$, $p = 0.25$). Again, when expressed in relative terms, increased stand BA mortality rates were similar for the two forest groups (table 3).

Both forest groups also showed significantly increased stem recruitment rates (figure 6; table 3; fast: $t = 3.84$, $p = 0.0008$, d.f. = 25; slow: $t = 1.86$, $p = 0.038$, d.f. = 23), with the fast group having significantly greater absolute increases in stem recruitment than the slow group of forests (table 3; cf. figure 6; $t = 1.93$, $p = 0.030$, two-sample test, variances assumed unequal, one-tailed test). However, the relative increases were not significantly different (table 3). Stem mortality rates increased significantly in both the fast and slow forest groups (figure 6; fast: $t = 2.44$, $p = 0.01$, d.f. = 25; slow: $t = 2.17$, $p = 0.02$, d.f. = 23). Although the more dynamic group of forests had greater absolute increases in stem mortality rates than the slower dynamic group, this difference was not significant (cf. figure 6; $t = 1.09$, $p = 0.14$). The relative increases in stem mortality rates were not different between the two groups of forests (table 3).

Overall, the group of faster growing, more dynamic forests showed highly significant increases in stand-level BA growth rates ($p = 0.0006$) and stem recruitment rates ($p = 0.0008$) whereas the p -values from all the other terms from both forest groups tended to be more marginal. Furthermore, the absolute increases in rates were significantly higher in the fast compared with the slow group of forests for stand-level BA growth rates and stem recruitment rates, but not for stand-level BA mortality rates or stem mortality rates. That is to say, the largest and most consistent changes in these forests have been, on average, the additions to the system, in terms of both BA and stems, and more specifically, the additions to the faster-growing and more dynamic forests. In absolute terms, the average flux increase was approximately twice as high in the fast group of forests than in the slow group (figure 6). However, in relative terms both groups of forest have changed similarly, having, on average, simultaneously increased stand-level BA growth, BA mortality, stem recruitment and stem mortality rates by similar amounts (figure 6; table 3).

(d) Further tests

Increasing stem turnover rates (mean of stem recruitment and stem mortality rates) and increasing above-ground biomass (BA pool) have both been demonstrated by using overlapping but different networks of plots (Phillips & Gentry 1994; Phillips *et al.* 1998). We show that both the BA pool and stem turnover rates increased simultaneously in 30 out of the 50 plots in the study (figure 7). In only one plot did BA and turnover rates decrease simultaneously, whereas 11 had increased BA and decreased turnover rates, and eight had decreased BA and increased turnover rates (figure 7).

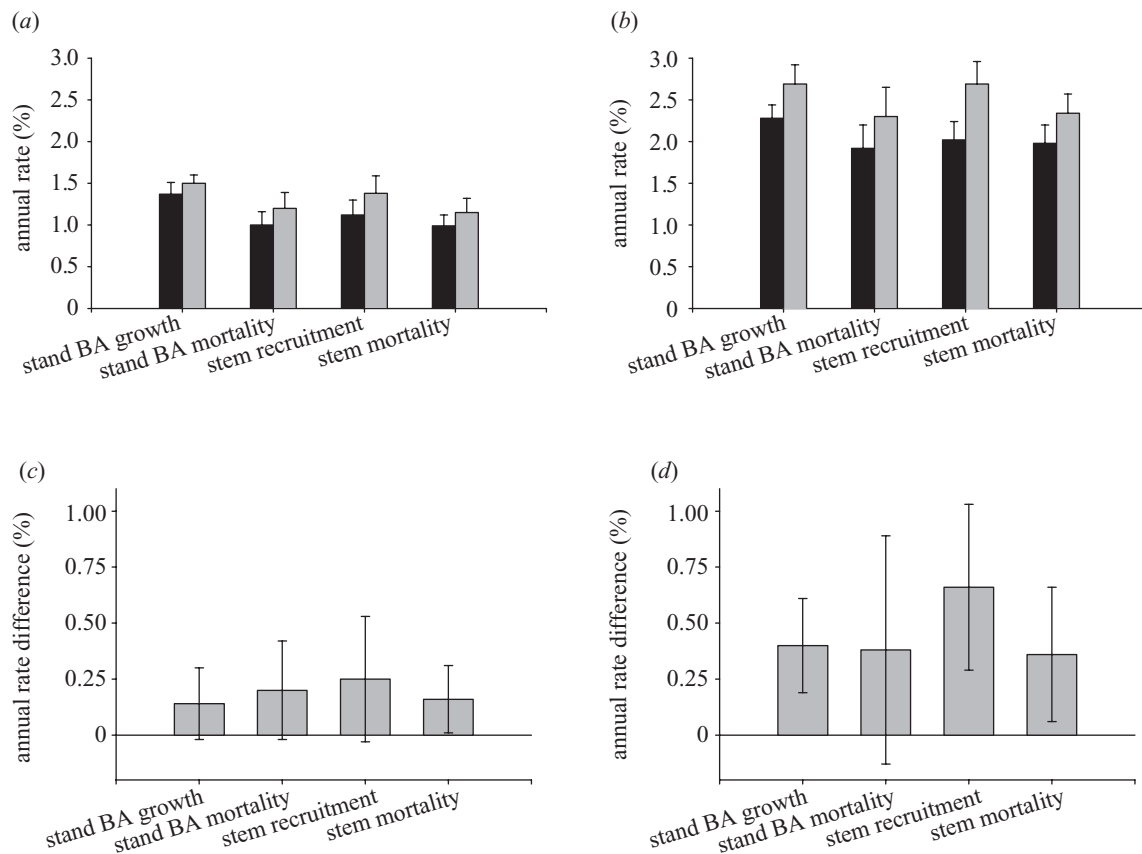


Figure 6. (a,b) Annualized rates of stand-level BA growth, stand-level BA mortality, stem recruitment and stem mortality (black bars, interval 1; grey bars, interval 2); (c,d) their difference over consecutive census intervals for plots grouped into 'slow dynamic' (a,c) and 'fast dynamic' (b,d) forests.

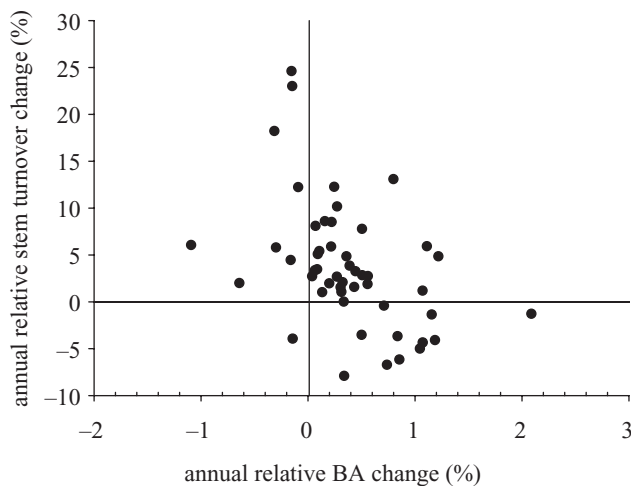


Figure 7. Most plots increased in stem turnover and BA (using equation (3.3)) simultaneously.

The network of plots show large-scale geographical biases in their location (figure 2). If our data are robust to this sampling bias then the mean values of parameters will remain similar as we progressively cluster plots together (see § 2c). Figure 8 shows that as plots are clustered there is no systematic pattern of change in the mean values of the changes in any of the flux rates or pools (i.e. no consistent increase or decrease as plots are progressively clustered). Therefore, the changes documented in stand-level BA growth rates, stand-level BA mortality

rates, stem recruitment rates, stem mortality rates and the net changes in the BA and stem pools are caused by changes in plots from across South America, and not simply by those in one or two well-sampled landscapes. Finally, note that the flux with the smallest confidence intervals at a given geographical scale is stand-level BA growth (figure 8). This suggests that stand-level BA growth is the flux that is increasing most consistently across South America.

4. DISCUSSION

We found a concerted, widespread and consistent directional change in the structure and dynamics of the 50 forest plots spanning South America (figures 3, 4, 6 and 8). We have shown for the first time that: (i) growth is increasing; (ii) simultaneous increases in growth, recruitment and mortality rates have occurred within the same plots; and (iii) these changes are widespread, occurring across several areas of South America (figure 8). Overall, the structure and dynamics of these forests have altered substantially over the three decades that they have been monitored.

The flux into the BA pool, stand-level BA growth, exceeded the flux out of the pool, stand-level BA mortality, and therefore the BA pool increased. This result is consistent both in direction and magnitude with other recent estimates of increases in above-ground biomass in South American tropical forests (Phillips *et al.* 1998, 2002a; Baker *et al.* 2004a). In addition, both the growth

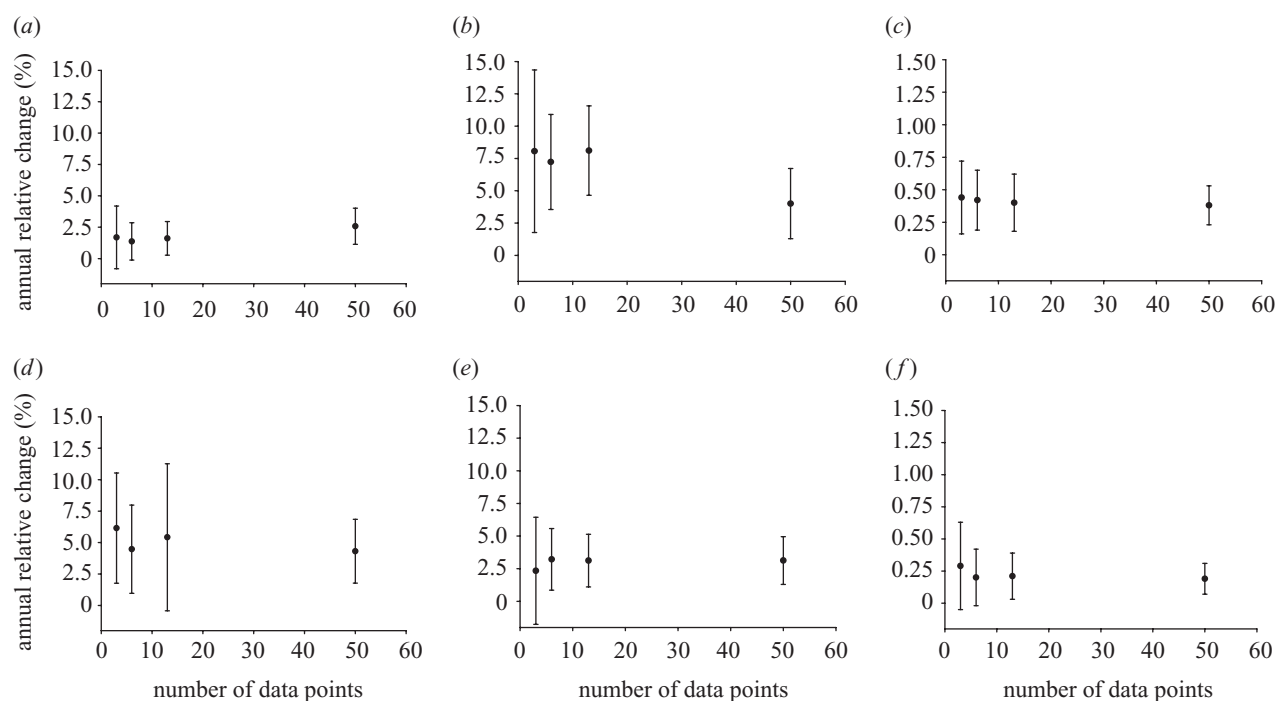


Figure 8. Mean relative changes and 95% CIs, for (a) stand-level BA growth; (b) stand-level BA mortality; (c) net BA change; (d) stem recruitment; (e) stem mortality; and (f) net stem change, whether replicates are defined as each non-contiguous plot ($n = 50$), plots clustered into 20 km radii ($n = 13$), plots clustered into 200 km radii ($n = 6$), or as longitudinal bands of east, west and central Amazonia ($n = 3$). Note the y -axis scale of the fluxes is an order of magnitude larger than the y -axis scale of the pools.

and mortality fluxes increased significantly and similarly to each other. Therefore, the size of the BA pool increased because stand-level BA growth rates were higher than stand-level BA mortality rates at the outset of the study and this difference was maintained through the study period (cf. the schema in figure 1*d*).

A similar, albeit slightly more complicated pattern, was shown for the stems pool and fluxes. Stem recruitment rates exceeded stem mortality rates, thus stem density increased. Again, both of these fluxes increased significantly over time, and the rates of change of these fluxes were not significantly different from one another. This increase in stem recruitment rates and stem mortality rates is consistent both in direction and magnitude, with previous estimates across the tropics showing that these fluxes approximately doubled from the 1950s to the 1990s (Phillips & Gentry 1994; Phillips 1996; Phillips *et al.* 2004). However, the increase in stem density was partly attributable to stem recruitment rates increasing faster than the increase in stem mortality rates (but not statistically significantly so), and partly attributable to stem recruitment rates being higher than stem mortality rates at the beginning of the study (again not statistically significantly so). The changes in both the stem and BA fluxes indicate that the current imbalance of additions and losses was occurring before the onset of monitoring the plots.

It has previously been suggested that *individual* patterns of change documented from long-term plot data may have been caused by: (i) statistical problems; (ii) biases and artefacts in the data; (iii) widespread recovery from past disturbances; or (iv) a widespread environmental change or changes. Any prospective cause or causes invoked must account for the multiple patterns we have documented

within the same plots. We compiled the dataset used to remove two pervasive statistical problems associated with analysing forest plot data with irregular census intervals. First, we deliberately chose census intervals so that the second census interval was, on average, slightly longer than the first. Therefore, census interval effects cannot explain the flux results (Sheil 1995*a*; Sheil & May 1996). Second, we monitored change within the same group of 50 plots over time, so potential biases associated with a lack of continuity of monitoring ('site-switching') cannot be driving the results (Condit 1997). A third major statistical issue is the large-scale geographical bias in the location of the plots. However, our tests using progressively larger clustering of plots showed that the mean changes are not driven by changes in only some well-sampled geographical areas (figure 8).

A variety of other methodological, analytical and artefactual biases may also potentially affect long-term monitoring data (Sheil 1995*b*). Although it is possible that an individual pattern of change may be caused by one of these artefacts, it is difficult to conceive artefacts that are causing the suite of changes we document. Furthermore, the most commonly discussed artefact that we have not accounted for in this study, which may be causing an increase in stem turnover rates (Phillips & Gentry 1994)—the potential location of plots in small areas of tall, easy-to-work-in forest ('majestic forest bias'; Phillips 1996)—has been carefully accounted for in newer analyses, and the trend of increasing forest dynamism holds (Phillips *et al.* 2004). Likewise, the most commonly discussed artefact that may be causing the increase in the BA pool and above-ground biomass (Phillips *et al.* 1998), poor diameter measurements of some trees (measuring around

buttresses; Clark 2002), has been shown to be theoretically implausible (Phillips *et al.* 2002a), and has been carefully assessed in newer analyses, and the trend of increasing above-ground biomass holds (Baker *et al.* 2004a). Finally, if we re-analyse our 50 plots, to either include only plots that could not have shown biases towards small areas of 'majestic forest' (i.e. those that are long transects, were located using a grid system, or are large enough to contain a mosaic of gap, building and mature phase forest, 2 ha or more), or to exclude plots that Clark (2002) had concerns over (see § 2a), the same qualitative results hold—both the size of the BA and stem pools and all four fluxes show increases. Although biases must affect the confidence we have in parameter estimates, we do not know of a bias or artefact, or set of biases and artefacts, that could plausibly cause the suite of changes within the same plots shown in this study.

We suggest a parsimonious explanation of our results. The data appear to show a coherent fingerprint of increasing growth, i.e. increasing NPP, across tropical South America, probably caused by a long-term increase in resource availability. The argument runs: increasing resource availability increases NPP, which increases stem growth rates. This accounts for the increase in stand BA growth rates and stem recruitment rates, and the fact that these show the 'clearest' signal in our dataset. Over time some of these faster-growing, larger trees die, as do some of the 'extra' recruits. This accounts for the increase in the fluxes out of the system, stand BA mortality rates and stem mortality rates. Thus, the system has increasing additions of BA and stems, while the losses lag behind, causing an increase in the BA and stems pools. The increase in the pools is determined by: (i) the rate of increase in stand BA growth and stem recruitment rates; (ii) the rate of increase in stand BA mortality and stem mortality rates; and (iii) the length of delay between the increase in inputs and those extra inputs leaving the system. Thus the much larger proportional increases in the fluxes compared with the more modest proportional changes in the pool sizes may be explained. Overall, the suite of results may be qualitatively explained by a long-term increase in a limiting resource.

Is a long-term increase in resource availability increasing NPP and growth, and accelerating forest dynamics a plausible scenario? First, stand BA growth is 10–30% of total NPP for mature tropical forests (Clark *et al.* 2001). Hence, it is reasonable to assume that the large increase in stand BA growth we document may reflect an increase in NPP. However, the increase in NPP may be smaller than the increase in stand BA growth if allocation patterns also change. For example, if a canopy is already closed, any extra (new) growth may be channelled into extra stem growth rather than more foliage production (Lloyd & Farquhar 1996). Second, this scenario implicitly assumes that tropical forests are resource-limited systems. This may or may not be the case (see Phillips *et al.* 2004, for a discussion of this). However, there is a body of evidence that this is generally the case for forests globally (Enquist & Niklas 2001). Third, there are 'smoking guns'; studies have shown that incoming solar radiation may have increased across tropical South America over the past two decades (by $0.37 \text{ W m}^{-2} \text{ yr}^{-1}$; Wielicki *et al.* 2002; Nemani *et al.* 2003), that air temperatures have increased (by

0.026 °C yr^{-1} ; Malhi & Wright 2004), and that atmospheric CO_2 concentrations have increased (by $1.5 \text{ p.p.m. yr}^{-1}$; Prentice *et al.* 2001), each of which may increase NPP (Lewis *et al.* 2004). Fourth, a long-term increase in resource availability increasing NPP may account for many of the specific results we see, notably that increases in stand BA growth and stem recruitment in the faster-growing and more dynamic forests were statistically the most significant changes (figure 6). Also, that the increase in stand BA growth is the most invariant flux when varying sampling across different geographical scales (figure 8). Fifth, researchers have independently predicted major parts of this basic scenario, mostly when considering the impacts of increasing CO_2 concentrations on forests, notably: (i) if the BA flux (growth) into the system increases, these larger trees eventually die, leading to a lag in the increase in BA fluxes out of the system, thus the BA pool increases while the resource remains non-limiting (Lloyd & Farquhar 1996; Chambers *et al.* 2001); (ii) that the changes in the fluxes are likely to be much larger than the changes in the pools (Körner 1998, 2004; Norby *et al.* 1999; Nemani *et al.* 2003); and (iii) that forests with more resources and faster growth will respond absolutely more, but not necessarily proportionately more, than forests with fewer resources and slower growth (Lloyd & Farquhar 1996, 2000).

Several authors have suggested that the impacts of disturbance, and recovery from disturbance, may account for either the increase in stem turnover rates (Sheil 1995a), or the increase in above-ground biomass (Körner 2003; Chambers & Silver 2004). Similarly, it has also been suggested that past disturbance may create waves of recruitment and mortality (Sheil 2003). Thus the results that we find could potentially be explained by a combination of a particular synchronous disturbance regime across South America, and with measurements at a substantial number of plots commencing just as a wave of recruitment was beginning, and final data points in this analysis occurring just as a wave of self-thinning mortality was beginning.

Phillips *et al.* (2004) discussed *a priori* predictions of other changes in such stands if this recovery from disturbance hypothesis is correct, and found no support for these predictions. In addition, it is difficult to explain the increases in stand BA growth and stem recruitment rates, while mortality rates are simultaneously increasing, through internal disturbance-and-succession processes. Furthermore, synchronous disturbance events are unlikely to lead to synchronous dynamics across all plots as the actual fluxes differ approximately fourfold (table 1). Thus, after disturbance events, the responses of the faster-growing and more dynamic forests are likely to be much faster than the slower growing and less dynamic forests. Finally, and perhaps most importantly, there is no 'smoking gun'; we know of no continent-wide disturbance event on which to base these scenarios. The most obvious candidate, ENSO events, show a strong spatial pattern across South America, running approximately northeast (strongly affected) to southwest (little affected) across the continent (Malhi & Wright 2004). Out of the plots in this study, those from eastern and central Amazonia are moderately to strongly affected by ENSO events, whereas those in western Amazonia are little affected, yet the largest absolute changes in dynamics have occurred in the

plots from western Amazonia (figure 6; all but two plots in the fast dynamics group were from western Amazonia).

Overall, we suggest that the simplest explanation, and our current working hypothesis to explain the concerted directional shifts in the structure and dynamics of this network of 50 plots, is that a long-term increase in resource availability has increased NPP, which is profoundly affecting these forests' dynamics. We note several important points about this. First, we chose, for statistical reasons, to use only three censuses even when more were available. We are confident that this does not affect the general trends we document, as other studies using all available censuses for plots in South America show that stem recruitment, stem mortality and the BA pool all increase significantly (Phillips 1996; Phillips *et al.* 1998, 2002a, 2004).

Second, we make clear that not every plot is increasing in both pools and all fluxes (table 1). The responses we document are averages. In only 17 out of 50 plots did stand BA growth, stand BA mortality, stem recruitment and stem mortality all increase simultaneously (while all fluxes decreased simultaneously in three plots). Furthermore, many combinations of flux and pool changes occurred. For example, in TAP-02 all fluxes decreased, while both the stems and BA pools increased, as the additions exceeded the losses over the monitoring period. These differences between plots are likely to be the outcome of many interacting causal agents, from the constantly changing environmental conditions forests experience, to biogeography and site history. Indeed, it should be quite possible to reconcile the paradigm of the dynamics of individual forest plots as being contingent on local processes and regional histories (e.g. Sheil & Burslem 2003) with the observation that they may all also be affected by global changes (cf. Parmesan & Yohe 2003).

Third, we note that for none of the three candidates for widespread increasing resource availability—solar radiation, temperature, CO₂—do we have good evidence to say *both* that the driver has actually changed *and* evidence that such a change will cause an increase in flux rates and pools (Lewis *et al.* 2004). The increase in incoming solar radiation comes from a single satellite dataset (Wielicki *et al.* 2002), which may contradict land-based sensors that show a decrease in incoming solar radiation (Stanhill & Cohen 2001; see Lewis *et al.* 2004, for a discussion). However, such a decrease in solar radiation may, counter-intuitively, increase NPP (Roderick *et al.* 2001; Gu *et al.* 2003). If the satellite data are correct, a modelling study suggests that the increase in NPP would increase similarly to that which we find in this study (Nemani *et al.* 2003). However, the changes in solar radiation documented from the satellites are thought to be a decadal-scale oscillation. Thus it is open to debate whether this apparent change in incoming solar radiation has occurred over a long enough period to have caused the patterns we and others document, notably the steady and pan-tropical increase in stem turnover rates since the 1950s (Phillips & Gentry 1994; Phillips 1996).

Temperature increases are undisputed, but evidence as to whether the *ca.* 0.5 °C increase in temperature over the monitoring period would be expected to increase or decrease NPP is unclear: photorespiration and respiration costs may increase as temperatures rise, which may reduce

NPP, or higher temperatures may increase soil nutrient availability which may increase NPP (Lewis *et al.* 2004).

Finally, the *ca.* 10% increase in CO₂ concentrations between 1980 and 2000 is undisputed. Carbon dioxide is a key substrate for photosynthesis, and higher CO₂ concentrations increase CO₂ : O₂ ratios thereby reducing photorespiration, and also increase the optimum temperature for photosynthesis, while higher CO₂ concentrations also increase water-use and nutrient-use efficiency (Drake *et al.* 1997; Saxe *et al.* 1998; Norby *et al.* 1999; Lewis *et al.* 2004). Although experiments show that elevated CO₂ concentrations increase plant growth under many conditions (Curtis & Wang 1998), including *in situ* tropical seedlings (Würth *et al.* 1998) and whole stands of temperate trees (Hamilton *et al.* 2002; Norby *et al.* 2002), experiments on whole stands of tropical forest trees have not been conducted. Thus, whether these positive experimental results are good evidence to suggest that the increases in stand BA growth and other fluxes we document are caused by increasing CO₂ concentrations is open to debate (Clark 2004; Chambers & Silver 2004; Lewis *et al.* 2004). The available literature allows for interpretations of the probable impact on NPP to be negligible to very large, as the effects of increasing CO₂ concentrations on tropical forests are likely to be nonlinear, and initiate multiple feedback loops at the leaf, whole plant and stand scales (Lewis *et al.* 2004).

In conclusion, we believe we have shown a consistent 'fingerprint' of increasing growth across a large sample of geographically widespread South American tropical forests over the 1980s and 1990s. These forests, on average, simultaneously increased growth, recruitment and mortality rates, and accumulated both stems and BA and hence are very likely to have been a carbon sink (see Baker *et al.* 2004a). The simplest explanation of this concerted increase in forest dynamics across South America is that increasing resource availability has increased NPP, which, in turn, has accelerated BA and stem dynamics and increased above-ground woody biomass. Whether these changes will persist, stabilize or reverse, and over what time-scales, is unknown. What the consequences of these changes have been for biodiversity is also not known. Whatever the mechanism, over recent decades, profound changes seem to have occurred across the world's largest tract of tropical forest.

The authors acknowledge the essential contributions of numerous field assistants over the past 25 years, and Professor Alwyn H. Gentry and Professor J. P. Veillon, both deceased, who established several of the plots analysed here. These analyses were supported by the UK Natural Environment Research Council (NER/A/S/2000/00532) and the EU Fifth Framework programme (CARBONSINK-LBA). The following provided financial, logistical and other support for data collection: Andrew W. Mellon Foundation, NASA-LBA Program, Conservation, Food, Health Foundation, MacArthur Foundation (BDF, Brazil); Brazils National Institute for Amazonian Research, MCT, the EU, DFID (UK), CNPq, Brazil (BNT, JAC, Brazil); Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Tropical Ecology, Assessment and Monitoring (TEAM) initiative, Centre for Applied Biodiversity Science, Conservation International, Museu Goeldi, Estacao Científica Ferreira Penna, (CAX, Brazil); Jari Celulose SA, Rubens Tocci, and Embrapa Jari (JAR, Brazil); Embrapa Amazônia Oriental (TAP, Brazil); Pew Charitable Trusts, Andrew Mellon Foundation (MNU, Peru); National

Geographic Society, Garden Club of America, Conservation International, NSF, the Mellon Foundation, American Philosophical Society, and the U.K. Natural Environment Research Council (CUZ, SUC, TAM, YAN, Peru); Liz Claiborne & Art Ortenberg Foundation, National Geographic Society (JAT, Ecuador). The authors thank Doug Sheil and two anonymous reviewers for their insightful and constructive reviews.

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GLOSSARY

- BA: basal area
 dbh: diameter at breast height
 ENSO: El Niño–Southern Oscillation
 NPP: net primary productivity