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Changes in tree species abundance in a Neotropical forest: impact of climate change

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ABSTRACT. The abundance of all tree and shrub species has been monitored for eight years in a 50 ha census plot in tropical moist forest in central Panama. Here we examine population trends of the 219 most numerous species in the plot, assessing the impact of a long-term drying trend. Population change was calculated as the mean rate of increase (or decrease) over eight years, considering either all stems ≥10 mm diameter at breast height (dbh) or just stems ≥100 mm dbh. For stems ≥10 mm, 40% of the species had mean growth rates <1% per year (either increasing or decreasing) and 12% had changes ≥5% per year. For stems ≥100 mm, the figures were 38% and 8%.

Species that specialize on the slopes of the plot, a moist microhabitat relative to the plateau, suffered significantly more declines in abundance than species that did not prefer slopes (stems ≥10 mm dbh). This pattern was due entirely to species of small stature: 91% of treelets and shrubs that were slope-specialists declined in abundance, but just 19% of non-slope treelets and shrubs declined. Among larger trees, slope and non-slope species fared equally. For stems ≥100 mm dbh, the slope effect vanished because there were few shrubs and treelets with stems ≥100 mm dbh. Another edaphic guild of species, those occurring preferentially in a small swamp in the centre of the plot, were no more likely to decline in abundance than non-swamp species, regardless of growth form. Species that preferentially colonize canopy gaps in the plot were slightly more likely to decrease in abundance than non-colonizing species (only for stems ≥10 mm dbh, not ≥100 mm). Despite this overall trend, however, several colonizing species had the most rapidly increasing populations in the plot.

The impact of a 25-year drying trend and an associated increase in the severity of the 4-month dry season is having an obvious impact on the BCI forest. At least 16 species of shrubs and treelets with affinities for moist microhabitats are headed for extinction in the plot. Presumably, these species invaded the forest during a wetter period prior to 1966. A severe drought of 1983 that caused unusually high tree mortality contributed to this trend, and may also have been responsible for sharp increases in abundance of a few gap-colonizers because it temporarily opened the forest canopy. The BCI forest is remarkably sensitive to a subtle climatic shift, yet we do not know whether this is typical for tropical forests because no other large-scale censuses exist for comparison.

KEY WORDS: demography. population dynamics, tropical populations

INTRODUCTION

The myth that tropical climates provide a stable environment for tropical forest organisms has long been buried. We know that annual shifts in moisture availability can stress vegetation and limit the distribution of many species

(Hartshorn 1992, Wright 1992). Now, thanks to long-term weather records kept by the Panama Canal Commission, we also know that the vegetation of Barro Colorado Island (BCI) must face supra-annual shifts in moisture availability (Windsor 1990, Windsor *et al.* 1990). Total precipitation at BCI underwent an abrupt decline around 1965, averaging 2740 mm prior to 1965 and 2430 mm since, paralleling a worldwide reduction in rainfall in the northern tropics (Bradley *et al.* 1987, Diaz *et al.* 1989). Moreover, associated with a strong El Niño event, the annual dry season of 1983 was unusually long and severe, causing elevated tree mortality (Condit *et al.* 1992b, Condit *et al.* 1995, Leigh *et al.* 1990). The 1983 drought and the long-term drop in rainfall are undoubtedly part of the same phenomenon, as the frequency of dry seasons (15 December to 15 April) receiving less than 100 mm of rain increased from once every 6.2 years prior to 1965 to once every 3.5 years since (Windsor 1990).

How does the composition of a tropical forest change when precipitation patterns shift? Unusual droughts and variation in rainfall are recognized more and more as important in tropical forests (Foster 1982a, Hartshorn 1992, Leigh *et al.* 1990, Woods 1989), but we know little about how populations of individual species change as a result. Certainly we know that past climate changes have led to shifts in species' distributions (Bush & Colinvaux 1990, Bush *et al.* 1990, Hamilton & Taylor 1991, Sukumar *et al.* 1993), and in temperate forests, detailed descriptions of range shifts that accompany past climate changes are so well documented (Davis 1981, Delcourt & Delcourt, 1987) that precise predictions on the impact of future climate scenarios can be made (Botkin & Nisbet 1992, Dale & Franklin 1989, Franklin *et al.* 1992, Overpeck *et al.* 1990, Pastor & Post 1988, Shugart & Smith 1992, Solomon 1986, Urban *et al.* 1993). The species-specific information behind these predictions is not available for most tropical forests. Only for the Luquillo forest in Puerto Rico has a species-specific model been used to predict the impact of climate change; O'Brien *et al.* (1992) assessed the potential impact of increasing hurricane frequency.

To gather information on many individual species of tropical trees in one community, we established a large-scale and long-term population survey of forest at Barro Colorado Island in Panama. In order to include substantive information on populations of many species, a large plot was mapped: 50 ha of forest, with all stems above 10 mm in diameter included (Condit 1995, Hubbell & Foster 1983). This dataset provides detailed information on change in forest composition and its relation to climate change. Similar large plots in natural forest are now being censused in India, Malaysia, Thailand, Sri Lanka, Puerto Rico, Ecuador, Cameroon and Zaïre (Condit 1995, Manokaran *et al.* 1992, Sukumar *et al.* 1992, Zimmerman *et al.* 1994), so we will soon be able to make a worldwide assessment on the lability of the species composition of tropical forests.

Here we provide population estimates for 313 species of tropical trees found in the 50 ha plot in Panama between 1982 and 1990. We address specific hypotheses about how the community is changing, in particular, how it might be

affected by long-term reduction in rainfall (Condit *et al.* 1992b, Hubbell & Foster 1990a, 1992). First, we consider species whose distributions within the plot are associated with moist microhabitats: a seasonal swamp and the moderately sloping terrain that drops off from the plateau in the centre of the plot (Becker *et al.* 1988, Hubbell & Foster 1983, 1986a). These areas remain wet throughout most dry seasons because a basalt cap below the plateau accumulates water during the wet season and drains slowly into the swamp and slopes throughout the dry season. Our prediction is that species associated with the moist microsites should be especially sensitive to the overall drying trend and will have suffered disproportionate losses in population.

In addition, we consider population changes of species that preferentially colonize light gaps within the forest. There are two different predictions about colonizing species. First, Hubbell & Foster (1990a, 1992) suggested that the plot is undergoing a slow loss of weedy species, because the region just north of the plot (plus 2 ha within the plot) was cleared of forest about 90 years ago, and has since regrown. Colonizing species probably gained abundance within the old forest because of their large populations just outside, and are now declining. If this is the case, we should be able to detect disporportionate population declines among colonizing species. The second prediction on colonizers is just the opposite, and is based on the observation that the drought opened the forest canopy briefly during 1983 (Becker & Smith 1990). With more light reaching the ground, colonizing species should increase in abundance. Population changes of species preferring gaps can tell us which of the potentially opposing forces is more important.

MATERIALS AND METHODS

Study site

Barro Colorado (BCI) is a 1500 ha island that was a hilltop until the Panama Canal was finished in 1914. The island is part of the Barro Colorado Nature Monument and has been operated as a research reserve since 1923. It is entirely forested, most in old-growth forest with no signs of human disturbance for over 500 years: 48 ha of the 50 ha plot are in old-growth, with 2 ha in an area cleared until about 1900 as part of a French settlement. Temperatures are uniform year-round at BCI, but rainfall is seasonal, with almost none falling between mid-December and mid-April. Details on climate, flora and fauna can be found in Croat (1978) and Leigh *et al.* (1982).

Census

A 50 ha plot on the top of the island was fully censused in 1981–1983, 1985 and 1990 (Condit *et al.* 1992a,b, 1993a,b, Hubbell & Foster 1983, 1986a,b, 1987, 1990a,b, 1992); we refer to the first census, which lasted two years, as the 1982 census. All free-standing, woody stems $\geqslant$10 mm diameter at breast height (dbh) were identified, tagged and mapped. The diameter of each stem

was measured at breast height (1.3 m) unless there were irregularities in the trunk there, in which case the measurement was taken at the nearest point downward where the stem was cylindrical. Dbhs of buttressed trees were taken above the buttresses. There were about 242,000 living stems in each census (Hubbell & Foster 1990a), and 305,875 stems over all three censuses; 28 have not been identified to species. A total of 313 species have been identified: 304, 306 and 303 in successive censuses. (Three new species have been added since Condit *et al.* 1992b, all rare plants that had been misidentified as more common species.) Included in the list of 313 is a single tree that appeared to be a hybrid between *Apeiba membranacea* and *A. tibourbou*, and two distinct varieties of *Swartzia simplex* (Croat 1978).

Analyses

Species included. Abundances for all 313 species are reported. Species' names match those from Croat (1978) and D'Arcy (1987), except for species which were discovered, or whose names have been changed, since. An Appendix lists all cases where names do not match those found in Croat (1978) or D'Arcy (1987), and allows any species listed here to be located in those floras or in our previous publications on the 50 ha plot. Authorities for all species can be found via these references.

Tests of hypotheses about changes in abundance included only those species that had at least 20 individuals ⩾10 mm dbh in at least one of the censuses. We used this cutoff because large percentage changes in abundance of very rare species could be caused by minor, chance events. Four species of *Bactris* palms were also eliminated from analyses because we changed methods for counting individuals of these species. This left 219 species for analyses of all stems ⩾10 mm dbh. Analyses were then repeated for changes in the number of individuals ⩾100 mm dbh, including the 136 species that had at least 20 stems in at least one census. We included an analysis with this larger cutoff because many other studies of tropical forest use the 100 mm limit (Phillips & Gentry 1994, Phillips *et al.* 1994).

Species characteristics. We analysed changes in abundance as they correlated with three species characteristics – growth form, moisture preference and tendency to recruit into light gaps. Species were divided into four growth forms – large trees (⩾20 m tall), mid-sized trees (10–20 m), treelets (4–10 m) and shrubs (1–4 m) – based on the maximum height attained at BCI (Hubbell & Foster 1986a). Moisture regime was defined using the slopes in the 50 ha plot, which have higher soil moisture content during the dry season than the plateau above them (Becker *et al.* 1988), and the swamp, which is flooded throughout the wet season and remains moist in the dry season (Hubbell & Foster 1986a).

Many species have distributions clearly demarcated by the slopes and the swamp (Hubbell & Foster 1986a), and we calculated the density of all species in the different habitats (unpublished data). We used the ratio of density on

the slopes (all 20 m × 20 m quadrats inclined ⩾7°) to density on the lower part of the plateau (quadrats with slope <7° and elevation <152 m, excluding the swamp) as an index of 'slope-specialization', and the ratio of density in the swamp (all 20 m × 20 m quadrats holding standing water through most of the wet season) to density on the lower plateau as an index for 'swamp-specialization'. We considered 'slope-specialists' and 'swamp-specialists' species with ratios ⩾1.5; this cutoff was chosen because chi-squared tests showed that nearly all higher ratios were significantly different from 1.0 ($P<0.01$), while most below did not (unpublished data). This index was preferable to a definition based on statistical significance, because the latter is sensitive to sample size. Finally, as a 'colonizing index' for each species, we used the fraction of recruits in light gaps given in Welden *et al.* (1991): Hubbell & Foster (1986b) used a similar but not identical 'index of heliophily'. Colonizers were defined as those species with an index ⩾30; again, this corresponds roughly with a statistically significant preference for recruiting in gaps (Welden *et al.* 1991) but does not depend on sample size. Most colonizers are probably 'pioneers' as defined by Swaine & Whitmore (1988), but they emphasized seed germination characteristics, which we do not consider here. Species for which information was lacking were omitted from all analyses requiring that information. The slope and swamp indices were calculated for all but 27 of the very rare species, but the colonizing index was available for only the 156 species listed in Welden *et al.* (1991).

Statistical tests. In order to determine whether certain groups of species suffered disproportionate losses, the number of species that increased or decreased in abundance between 1982 and 1990 was tallied as a function of the four categorical variables. For statistical tests, a standard ANOVA was not possible because the design was unbalanced, with many empty cells. Instead, chi-squared tests were used on each of the variables: for example, a 2 × 2 contingency table for slope-specialization category and for population change provided a chi-squared statistic with one degree of freedom. To determine effects of each variable separately, we proceeded as follows. Swamp effect was assessed by contingency tables for swamp and non-swamp species; since swamp status was not associated with colonizing nor slope status, the latter two categories were simply ignored when swamp effect was tested. But slope and colonizing variables were associated – there were fewer slope-colonizer species than expected by chance – so we segregated species simultaneously by both categories. All tests were carried out on the four growth forms separately.

For each species, we calculated the annualized rate of population change (r) using a standard model of exponential population growth:

$$r = \frac{ln\ N_t - ln\ N_0}{t}$$

where N_t and N_0 are population sizes at time t and time 0 and *ln* means the natural logarithm. The time interval, t, for each species was defined as the

arithmetic mean time elapsed between censuses for individuals of that species (based on the census data of each 20 m × 20 m quadrat in the plot).

Earlier publications

Hubbell & Foster (1990a, 1992) described population changes based on the 1982–1985 interval, and Condit *et al.* (1992b) updated this with 1990 data, but this is the first presentation on abundance for all 313 species. Discrepancies between the numbers reported here and those from earlier reports are slight and are due solely to corrections of old errors. Since this is an on-going process, future reports might give figures slightly different from those reported here.

Access to data

We hope that the table of abundances for 313 species provided here will be useful for many future studies, and we will provide computer versions of the table to anyone interested. Please send us a diskette and indicate preferred formats.

RESULTS

Changes in abundance for stems ⩾10 mm dbh

Of the 219 more common species considered here, 105 had increases in stem number between 1982 and 1990, 108 had decreases and six did not change. For all 313 species in the plot, 136 increased, 154 decreased and 23 did not change. As previously noted (Condit *et al.* 1992b, Hubbell & Foster 1990a, 1992), rare species – in this case the 94 having fewer than 20 stems in all censuses – suffered proportionally more declines than common species. Table 1 gives the abundance in all three censuses for all 313 species.

Many populations did not change by much (Figure 1). Of 219 species, 88 (40%) had population changes <1% per year between 1982 and 1990. But some species had dramatic changes in abundance: 27 species (12%) changed at rates more than 5% per year, 18 declining and nine increasing (Table 2). Some common species underwent substantial declines. *Poulsenia armata* fell from 3430 to 2126 stems, and *Acalypha diversifolia* from 1568 to 827. The most rapid rate of decline was *Piper aequale*, which had 219 stems in 1982 and 83 in 1990 (Table 2). On the other hand, the population of *Palicourea guianensis* rose from 377 to 1475 stems, while the much less common *Psychotria graciflora* had the biggest rate of increase, from 10 to 44 stems over eight years (Table 2). The mean rate of change for the 219 species was −0.29% per year, while the mean rate of absolute change was 2.25% (the mean of the absolute values of rates of change).

Changes in abundance for stems ⩾100 mm dbh

The range of population change among larger stems was no different than for smaller (Figure 1B). Of the 136 species considered, 66 increased in abundance from 1982 to 1990, 61 decreased and seven stayed the same. Fifty-one

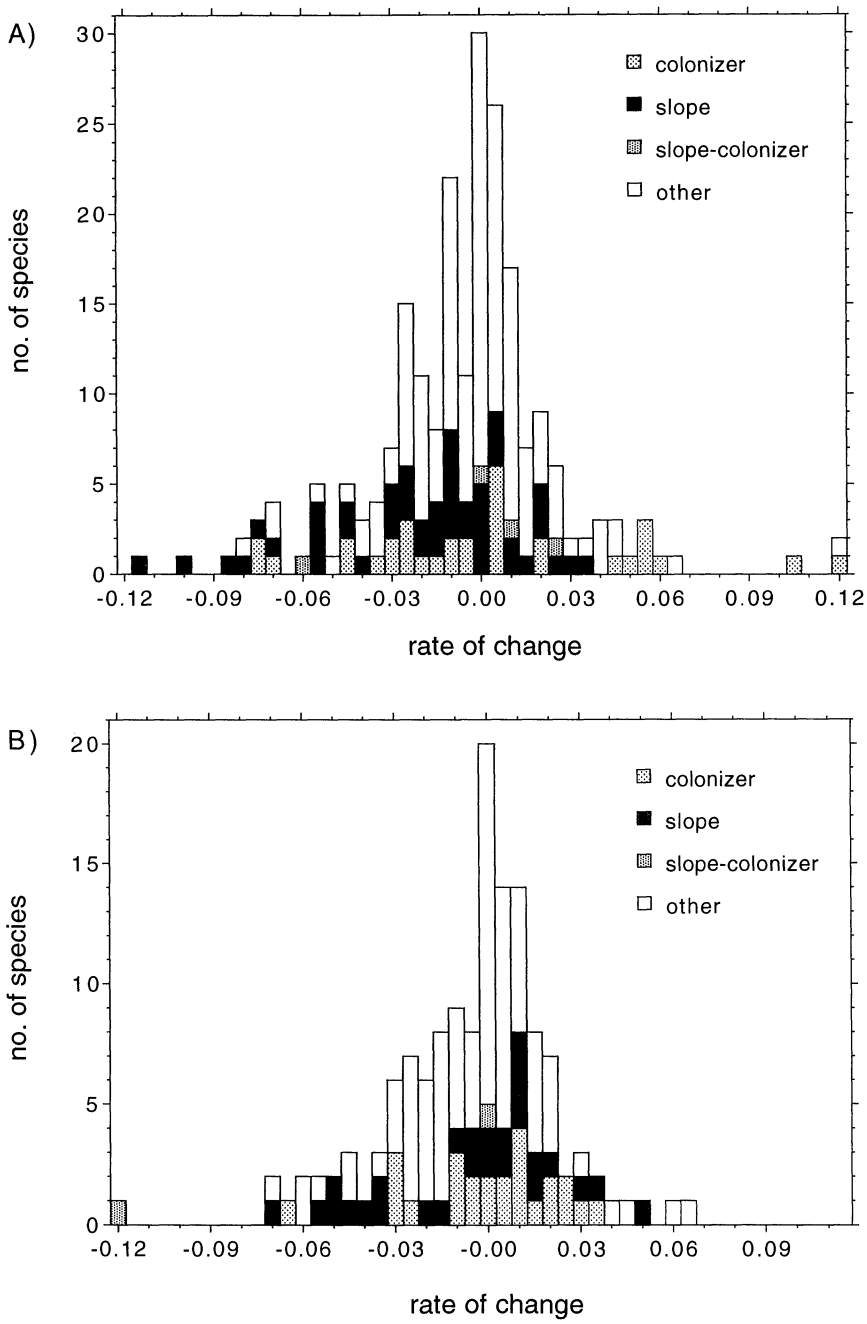

Figure 1. Distribution of population growth rates. The 'colonizer' category includes all colonizing species that were not slope-specialists, and the 'slope' category includes slope species that were non-colonizing; 'slope-colonizers' are the four specializing in both areas. 'Other' includes all species that were neither slope nor colonizing plus all species that were missing information on one or both categories. (A) Rate of change of populations of stems ≥10 mm dbh, including 219 species (see text). (B) Rate of change of populations of stems ≥100 mm dbh, including 136 species (see text).

Table 1. Total populations of all 313 species recorded in the 50 ha plot on Barro Colorado Island, above two dbh cutoffs. Following each species name are four codes: a column headed G (for growth form), with T = large tree, M = mid-sized tree, U = treelet, S = shrub, H = hemi-epiphyte and ... = unknown; column headed C (colonizing status), W (swamp status) and S (slope status), under which, the letters C, W and S indicate specialists, species that were substantially more abundant in the given habitat (see text), the letter n indicates non-specialists, or species equally abundant inside or outside the given habitat (or more abundant outside), and ... indicates that information was not available (see text). The columns headed 'rate' give the exponential rate of population change between 1982 and 1990, first for stems ≥10 mm and then for stems ≥100 mm dbh.

	Codes					Stems ≥10 mm dbh				Stems ≥100 mm dbh			
Species	G	C	W	S	Family	1982	1985	1990	Rate 1982–1990	1982	1985	1990	Rate 1982–1990
Acacia melanoceras	U	...	W	n	Leguminosae	5	6	11	0.092	2	1	2	0.000
Acalypha diversifolia	S	C	W	n	Euphorbiaceae	1568	1208	827	−0.072	2	3	3	0.044
Acalypha macrostachya	U	C	n	n	Euphorbiaceae	80	67	45	−0.071	2	0	2	0.000
Adelia triloba	U	C	n	n	Euphorbiaceae	345	314	279	−0.024	115	114	106	−0.009
Aegiphila panamensis	M	n	n	n	Verbenaceae	134	125	93	−0.043	23	21	24	0.004
Alchornea costaricensis	T	C	n	n	Euphorbiaceae	384	313	265	−0.043	160	158	157	−0.002
Alchornea latifolia	M	...	n	n	Euphorbiaceae	2	2	3	0.052	2	2	2	0.000
Alibertia edulis	U	n	W	n	Rubiaceae	305	342	377	0.024	2	2	3	0.046
Allophylus psilospermus	M	n	n	n	Sapindaceae	175	171	153	−0.015	30	32	27	−0.012
Alseis blackiana	T	n	n	n	Rubiaceae	7595	8057	8424	0.012	847	858	940	0.011
Amaioua corymbosa	U	...	n	n	Rubiaceae	31	32	32	0.003	2	3	4	0.074
Anacardium excelsum	T	...	W	S	Anacardiaceae	28	26	24	−0.016	23	23	22	−0.004
Anaxagorea panamensis	S	C	n	S	Annonaceae	472	473	588	0.028	0	0	0	...
Andira inermis	T	n	n	n	Leguminosae	318	307	306	−0.004	42	36	33	−0.027
Annona acuminata	S	n	W	n	Annonaceae	509	526	568	0.012	0	0	0	...
Annona hayesii	U	...	n	n	Annonaceae	1	1	1	0.000	0	0	0	...
Annona spraguei	M	C	n	n	Annonaceae	57	71	143	0.108	18	18	22	0.023
Apeiba hybrid	T	...	...	...	Tiliaceae	1	1	0	...	1	1	0	...
Apeiba membranacea	T	...	n	n	Tiliaceae	389	342	330	−0.019	238	226	238	0.000
Apeiba tibourbou	M	...	n	n	Tiliaceae	46	39	33	−0.039	26	23	22	−0.019
Aphelandra sinclairiana	S	...	W	S	Acanthaceae	13	10	7	−0.077	0	0	0	...
Appunia seibertii	S	...	...	...	Rubiaceae	1	1	4	0.146	0	0	0	...
Ardisia bartlettii	S	...	n	n	Myrsinaceae	3	3	1	−0.115	0	0	0	...
Ardisia fendleri	U	...	n	S	Myrsinaceae	77	80	85	0.011	1	1	0	...
Ardisia guianensis	S	...	W	n	Myrsinaceae	21	15	17	−0.026	0	0	0	...
Aspidosperma cruenta	T	n	n	S	Apocynaceae	451	471	485	0.008	48	53	55	0.015
Astrocaryum standleyanum	M	...	W	n	Palmae	248	232	221	−0.013	233	225	217	−0.008
Astronium graveolens	T	...	n	n	Anacardiaceae	65	59	66	0.001	35	35	35	0.000
Bactris barronis	U	...	n	n	Palmae	112	57	23	−0.184	0	0	0	...
Bactris coloniata	S	...	n	S	Palmae	240	83	23	−0.267	0	0	...	
Bactris coloradonis	U	...	n	n	Palmae	40	18	6	−0.222	0	0	0	...

Bactris major	U	n	W	n	Palmae	476	362	224	−0.090	0	0	0	...
Banara guianensis	U	...	W	S	Flacourtiaceae	0	0	4	...	0	0	0	...
Beilschmiedia pendula	T	n	n	n	Lauraceae	2376	2671	2750	0.017	308	303	295	−0.004
Bertiera guianensis	S	...	n	n	Rubiaceae	2	2	1	−0.072	0	0	0	...
Brosimum alicastrum	T	n	n	n	Moraceae	865	897	925	0.007	183	179	183	0.000
Brosimum guianense	T	...	...	...	Moraceae	1	1	1	0.000	1	1	1	0.000
Calophyllum longifolium	T	n	n	S	Guttiferae	649	722	893	0.037	55	54	60	0.010
Capparis frondosa	S	n	n	n	Capparidaceae	3536	3676	3550	0.000	0	2	1	...
Casearia aculeata	U	n	n	n	Flacourtiaceae	467	476	480	0.003	24	26	23	−0.004
Casearia arborea	T	C	n	n	Flacourtiaceae	21	23	21	0000	2	3	3	0.052
Casearia guianensis	U	...	n	n	Flacourtiaceae	12	14	16	0.032	0	0	0	...
Casearia sylvestris	M	n	n	n	Flacourtiaceae	248	232	211	−0.019	72	67	58	−0.024
Cassipourea elliptica	M	n	W	n	Rhizophoraceae	765	850	945	0.025	67	72	78	0.018
Cavanillesia platanifolia	T	...	n	S	Bombacaceae	22	21	22	0.000	21	21	21	0.000
Cecropia insignis	T	C	n	n	Moraceae	517	447	405	−0.028	280	249	261	−0.008
Cecropia obtusifolia	M	C	W	n	Moraceae	61	38	48	−0.028	38	24	22	−0.064
Cedrela odorata	T	...	n	S	Meliaceae	5	2	9	0.068	2	2	2	0.000
Ceiba pentandra	T	...	n	n	Bombacaceae	72	67	61	−0.019	42	40	37	−0.014
Celtis schippii	M	...	n	S	Ulmaceae	182	166	148	−0.023	42	38	32	−0.031
Cespedezia macrophylla	T	n	...	...	Ochnaceae	7	5	5	−0.037	3	2	2	−0.046
Cestrum megalophyllum	S	...	W	S	Solanaceae	309	237	157	−0.077	0	0	0	...
Chamaedorea tepejilote	S	...	n	S	Palmae	32	22	16	−0.080	0	0	0	...
Chamguava schippii	U	n	n	n	Myrtaceae	195	240	289	0.048	1	1	2	0.085
Chimarrhis parviflora	T	...	n	n	Rubiaceae	2	2	1	−0.086	0	0	1	...
Chrysochlamys eclipes	S	n	n	S	Guttiferae	460	438	423	−0.009	2	5	3	0.043
Chrysophyllum argenteum	T	C	n	n	Sapotaceae	423	477	683	0.056	75	84	84	0.013
Chrysophyllum cainito	T	C	W	n	Sapotaceae	70	80	109	0.051	21	23	25	0.019
Clidemia dentata	S	...	W	n	Melastomataceae	8	14	17	0.094	0	0	0	...
Clidemia octona	S	...	n	n	Melastomataceae	3	6	9	0.124	0	0	0	...
Clidemia septuplinervia	S	...	...	...	Melastomataceae	1	2	0	...	0	0	0	...
Cnemidaria petiolata	S	...	...	...	Cyatheaceae	8	3	1	−0.252	0	0	0	...
Coccoloba coronata	M	n	n	n	Polygonaceae	181	191	185	0.002	22	21	20	−0.011
Coccoloba manzanillensis	U	n	n	n	Polygonaceae	445	448	473	0.007	8	9	12	0.047
Colubrina glandulosa	T	...	n	n	Rhamnaceae	2	1	1	−0.074	2	1	1	−0.074
Conostegia bracteata	S	...	n	n	Melastomataceae	4	4	3	−0.030	0	0	0	...
Conostegia cinnamomea	S	n	W	S	Melastomataceae	391	281	209	−0.071	0	0	0	...
Cordia alliodora	T	C	n	n	Boraginaceae	111	108	119	0.008	61	60	60	−0.001
Cordia bicolor	M	C	n	n	Boraginaceae	715	758	1042	0.046	255	258	283	0.012
Cordia lasiocalyx	M	n	n	S	Boraginaceae	1698	1665	1688	0.000	420	442	441	0.005
Coussarea curvigemmia	U	n	n	n	Rubiaceae	1502	1663	1963	0.032	40	46	57	0.042
Coutaria hexandra	U	...	...	...	Rubiaceae	1	1	1	0.000	0	0	0	...
Croton billbergianus	U	C	W	n	Euphorbiaceae	620	619	1012	0.059	67	67	75	0.013
Cupania cinerea	M	...	n	n	Sapindaceae	6	7	12	0.083	1	1	1	0.000

Table 1. (*cont.*)

Species	Codes G	C	W	S	Family	Stems ≥10 mm dbh 1982	1985	1990	Rate 1982–1990	Stems ≥100 mm dbh 1982	1985	1990	Rate 1982–1990
Cupania latifolia	T	...	n	S	Sapindaceae	54	48	51	−0.006	8	9	10	0.025
Cupania rufescens	T	n	W	n	Sapindaceae	55	71	96	0.065	5	6	6	0.022
Cupania sylvatica	U	n	n	n	Sapindaceae	962	1040	1146	0.020	28	30	41	0.045
Cyphomandra hartwegii	S	...	n	n	Solanaceae	5	4	3	−0.062	0	0	0	...
Dendropanax arboreus	T	...	n	n	Araliaceae	18	18	16	−0.013	11	11	11	0.000
Dendropanax stenodontus	T	...	n	n	Araliaceae	159	144	121	−0.033	96	93	84	−0.016
Desmopsis panamensis	U	n	n	n	Annonaceae	11735	12141	12167	0.004	17	15	12	−0.040
Diospyros artanthifolia	M	n	n	n	Ebenaceae	48	54	70	0.045	9	12	14	0.052
Dipteryx panamensis	T	...	n	n	Leguminosae	56	52	53	−0.006	33	33	34	0.003
Drypetes standleyi	T	n	n	S	Euphorbiaceae	2173	2266	2279	0.005	196	227	262	0.031
Elaeis oleifera	M	...	W	...	Palmae	22	21	21	−0.005	22	21	21	−0.005
Enterolobium schomburgkii	T	...	n	n	Leguminosae	13	12	13	0.000	2	2	2	0.000
Erythrina costaricensis	U	...	n	S	Leguminosae	289	236	185	−0.052	47	46	30	−0.051
Erythroxylum macrophyllum	M	n	n	n	Erythroxylaceae	327	308	300	−0.010	18	20	16	−0.013
Erythroxylum panamense	U	n	W	n	Erythroxylaceae	104	105	111	0.007	0	0	0	...
Eugenia coloradensis	T	n	n	n	Myrtaceae	803	840	832	0.004	78	79	83	0.007
Eugenia galalonensis	U	n	n	n	Myrtaceae	961	1157	1379	0.041	21	25	16	−0.031
Eugenia nesiotica	M	n	n	n	Myrtaceae	509	529	539	0.006	48	48	53	0.011
Eugenia oerstedeana	M	n	n	n	Myrtaceae	2088	2208	2346	0.013	133	140	159	0.020
Faramea occidentalis	U	n	n	n	Rubiaceae	23460	25154	26912	0.016	1228	1402	1652	0.034
Ficus bullenei	...	...	...	...	Moraceae	1	1	1	0.000	1	1	1	0.000
Ficus citrifolia	H	...	n	n	Moraceae	0	0	1	...	0	0	0	...
Ficus colubrinae	...	...	n	n	Moraceae	1	1	1	0.000	1	1	1	0.000
Ficus costaricana	H	...	W	n	Moraceae	16	11	7	−0.090	8	7	7	−0.014
Ficus insipida	T	...	W	n	Moraceae	9	8	7	−0.027	3	3	3	0.000
Ficus maxima	T	...	W	S	Moraceae	11	11	10	−0.011	5	6	3	−0.059
Ficus obtusifulia	H	...	W	n	Moraceae	12	10	8	−0.043	10	8	8	−0.023
Ficus pertusa	H	...	n	n	Moraceae	0	0	1	...	0	0	0	...
Ficus popenoei	H	...	W	n	Moraceae	9	8	7	−0.030	7	6	5	−0.039
Ficus tonduzii	M	...	n	S	Moraceae	66	61	45	−0.044	42	37	30	−0.039
Ficus trigonta	H	...	n	S	Moraceae	8	5	5	−0.050	6	4	5	−0.019
Ficus yoponensis	T	...	n	n	Moraceae	6	6	6	0.000	6	6	6	0.000
Garcinia intermedia	M	n	n	n	Guttiferae	3654	4023	4300	0.018	77	75	81	0.005
Garcinia madruno	M	n	n	n	Guttiferae	652	682	524	−0.025	23	26	24	
Genipa americana	T	...	W	n	Rubiaceae	91	88	84	−0.009	20	20	21	0.005
Geonoma interrupta	U	...	...	...	Palmae	19	14	3	−0.203	0	0	0	...
Guapira standleyanum	T	...	n	n	Nyctaginaceae	230	208	191	−0.021	90	91	99	0.010

Guarea grandifolia	T	...	n	n	Meliaceae	55	57	62	0.014	10	10	10	0.000
Guarea guidonia	M	n	W	S	Meliaceae	1781	1829	1968	0.011	370	363	376	0.001
Guarea sp. nov.	M	n	n	n	Meliaceae	1558	1492	1378	−0.014	105	95	83	−0.026
Guatteria dumetorum	T	n	n	S	Annonaceae	1587	1529	1472	−0.008	285	280	277	−0.003
Guazuma ulmifolia	T	...	W	n	Sterculiaceae	55	50	52	−0.006	28	30	34	0.021
Guettarda foliacea	U	n	n	n	Rubiaceae	382	382	369	−0.004	78	83	80	0.002
Gustavia superba	M	C	n	n	Leythidaceae	881	821	828	−0.007	637	642	650	0.002
Hamelia axillaris	S	n	W	n	Rubiaceae	114	92	107	−0.007	1	0	0	...
Hamelia patens	...	...	n	n	Malvaceae	0	2	2	...	0	0	0	...
Hampea appendiculata	M	...	n	n	Malvaceae	76	49	40	−0.076	41	33	25	−0.058
Hasseltia floribunda	M	n	W	n	Flacourtiaceae	1147	1019	866	−0.033	262	256	249	−0.006
Heisteria acuminata	U	n	n	n	Olacaceae	105	107	108	0.003	5	6	7	0.039
Heisteria concinna	M	n	n	n	Olacaceae	888	964	988	0.012	246	256	275	0.012
Herrania purpurea	U	C	n	n	Sterculiaceae	522	531	548	0.005	0	0	0	...
Hirtella americana	T	...	n	n	Chrysobalanaceae	50	47	47	−0.006	8	8	6	−0.031
Hirtella triandra	M	n	n	S	Chrysobalanaceae	4144	4661	5025	0.022	516	554	616	0.020
Hura crepitans	T	...	W	n	Euphorbiaceae	127	119	117	−0.009	100	97	100	0.000
Hybanthus prunifolius	S	n	n	n	Violaceae	39872	41154	40511	0.001	3	3	1	−0.125
Hyeronima alcheornoides	T	C	W	n	Euphorbiaceae	101	100	99	−0.002	44	42	42	−0.005
Inga acuminata	U	n	n	n	Leguminosae	07	250	300	0.042	11	14	20	0.068
Inga cocleensis	M	C	n	n	Leguminosae	219	219	232	0.007	39	39	46	0.020
Inga fagifolia	T	...	W	n	Leguminosae	58	60	70	0.022	8	7	6	−0.031
Inga goldmanii	T	n	n	n	Leguminosae	498	468	462	−0.008	62	51	51	−0.022
Inga marginata	T	n	n	S	Leguminosae	913	810	741	−0.023	81	74	91	0.013
Inga minutula	T	...	n	S	Leguminosae	12	12	11	−0.010	4	3	2	−0.081
Inga mucuna	T	...	n	n	Leguminosae	1	1	1	0.000	0	0	0	...
Inga pezizifera	T	n	n	S	Leguminosae	208	202	184	−0.013	25	15	13	−0.068
Inga punctata	T	...	W	S	Leguminosae	17	18	20	0.018	8	7	7	−0.015
Inga quaternata	M	n	n	S	Leguminosae	735	742	731	0.000	34	40	48	0.038
Inga ruiziana	T	...	n	n	Leguminosae	80	70	62	−0.030	10	6	10	0.000
Inga sapindoides	M	C	n	n	Leguminosae	391	354	327	−0.021	67	67	75	0.013
Inga spectabilis	T	...	n	n	Leguminosae	22	24	25	0.015	12	12	14	0.018
Inga umbellifera	M	n	n	n	Leguminosae	942	997	1040	0.011	21	17	12	−0.065
Jacaranda copaia	T	C	n	n	Bignoniaceae	342	319	298	−0.016	224	230	240	0.008
Koanophyllon wetmorei	S	...	n	S	Asteraceae	15	12	12	−0.029	0	0	0	...
Lacistema aggregatum	U	n	n	n	Lacistemaceae	1557	1661	1694	0.010	43	40	37	−0.017
Lacmellea panamensis	M	...	W	n	Apocynaceae	91	91	98	0.008	36	37	42	0.018
Laetia procera	T	...	n	n	Flacourtiaceae	24	23	30	0.027	9	9	11	0.024
Laetia thamnia	U	n	n	n	Flacourtiaceae	514	519	542	0.006	15	17	25	0.061
Lafoensia punicifolia	T	...	W	n	Lythraceae	8	7	6	−0.035	4	4	5	0.027
Leandra dichotoma	S	...	n	n	Melastomataceae	0	1	1	...	0	0	0	...
Licania hypoleuca	M	n	n	n	Chrysobalanaceae	120	121	133	0.012	19	16	15	−0.027
Licania platypus	T	n	n	S	Chrysobalanaceae	253	293	315	0.024	9	9	10	0.011

Table 1. (*cont.*)

Species	Codes G	C	W	S	Family	Stems ≥10 mm dbh 1982	1985	1990	Rate 1982–1990	Stems ≥100 mm dbh 1982	1985	1990	Rate 1982–1990
Lindackeria laurina	M	...	W	n	Flacourtiaceae	109	97	89	−0.023	85	78	69	−0.023
Lonchocarpus latifolia	T	C	n	n	Leguminosae	842	846	889	0.006	147	137	124	−0.020
Lopimia dasypetala	S	...	...	...	Malvaceae	1	1	0	...	0	0	0	...
Lozania pittieri	U	...	...	...	Lacistemaceae	18	15	7	−0.117	3	2	0	...
Luehea seemannii	T	C	W	n	Tiliaceae	188	190	225	0.020	87	93	94	0.008
Lycianthes maxonii	S	...	...	...	Solanaceae	1	1	0	...	0	0	0	...
Maclura tinctoria	T	...	...	...	Moraceae	2	2	1	−0.086	0	1	1	...
Macrocnemum glabrescens	M	C	n	S	Rubiaceae	96	101	106	0.010	24	25	25	0.004
Malmea sp. nov.	M	n	n	n	Annonaceae	276	320	372	0.035	14	15	17	0.023
Malpighia romeroana	S	n	n	n	Malpighiaceae	54	64	60	0.012	0	0	0	...
Maquira costaricana	M	n	n	n	Moraceae	1418	1445	1503	0.006	223	200	176	−0.027
Margaritaria nobilis	U	...	n	n	Euphorbiaceae	1	2	4	0.144	1	1	1	0.000
Marila laxiflora	M	...	n	S	Guttiferae	22	26	22	0.000	10	11	11	0.010
Maytenus schippii	M	...	n	n	Celastraceae	82	82	88	0.008	20	19	20	0.000
Miconia affinis	U	C	n	n	Melastomataceae	371	394	439	0.020	4	2	9	0.098
Miconia argentea	M	C	W	n	Melastomataceae	531	678	902	0.062	45	50	56	0.025
Miconia elata	U	...	n	n	Melastomataceae	34	31	30	−0.015	2	3	2	0.000
Miconia hondurensis	U	...	W	n	Melastomataceae	30	29	37	0.025	7	4	6	−0.018
Miconia impetiolaris	U	...	W	S	Melastomataceae	6	5	8	0.031	0	0	0	...
Miconia nervosa	S	C	n	n	Melastomataceae	359	294	320	−0.014	0	0	0	...
Miconia prasina	U	...	n	n	Melastomataceae	0	0	2	...	0	0	0	...
Mouriri myrtilloides	S	n	n	n	Melastomataceae	6948	7712	7618	0.011	0	1	0	...
Myrcia gatunensis	U	n	n	n	Myrtaceae	40	49	56	0.040	2	2	4	0.082
Myrospermum frutescens	T	...	n	n	Leguminosae	28	24	23	−0.021	9	9	10	0.011
Nectandra cissiflora	T	n	n	n	Lauraceae	349	339	314	−0.013	23	20	27	0.019
Nectandra globosa	M	C	W	S	Lauraceae	117	113	119	0.001	12	10	13	0.009
Nectandra purpurea	M	n	n	n	Lauraceae	80	77	81	0.001	4	2	3	−0.035
Nectandra sp. nov. 1	T	...	n	S	Lauraceae	9	9	6	−0.044	1	0	0	...
Nectandra sp. nov. 3	...	...	...	...	Lauraceae	1	1	0	...	0	0	0	...
Neea amplifolia	S	n	n	n	Nyctaginaceae	62	71	68	0.011	0	0	0	...
Ochroma pyramidale	M	...	n	n	Bombacaceae	5	9	7	0.040	3	5	6	0.082
Ocotea cernua	M	n	n	n	Lauraceae	346	337	332	−0.004	24	28	26	0.009
Ocotea oblonga	T	n	n	n	Lauraceae	215	184	190	−0.014	33	31	27	−0.022
Ocotea puberula	T	n	n	n	Lauraceae	269	243	222	−0.023	9	10	16	0.069
Ocotea whitei	T	n	n	S	Lauraceae	1130	941	769	−0.042	167	170	176	0.005
Oenocarpus mapoura	M	...	n	n	Palmae	1790	1712	1802	0.000	752	746	754	0.000
Olmedia aspera	U	n	n	S	Moraceae	442	376	279	−0.051	50	42	33	−0.046

Ormosia amazonica	T	…	…	…	Leguminosae	1	2	2	0.078	1	1	1	0.0000
Ormosia croatii	T	n	n	S	Leguminosae	52	56	71	0.034	4	3	4	0.000
Ormosia macrocalyx	T	…	n	n	Leguminosae	4	4	4	0.000	4	4	4	0.000
Ouratea lucens	S	n	n	n	Ochnaceae	1122	1240	1266	0.014	0	0	0	…
Palicourea guianensis	S	C	W	n	Rubiaceae	377	663	1475	0.165	0	0	0	…
Pentagonia macrophylla	U	n	n	S	Rubiaceae	568	513	453	−0.026	2	2	2	0.000
Perebea xanthochyma	M	n	n	n	Moraceae	268	268	273	0.002	13	13	19	0.047
Phoebe cinnamomifolia	T	C	n	n	Lauraceae	88	83	87	−0.001	18	18	19	0.006
Picramnia latifolia	U	n	n	S	Simaroubaceae	1169	1177	1174	0.000	38	39	42	0.011
Piper aequale	S	n	n	S	Piperaceae	219	158	83	−0.113	0	0	0	…
Piper arboreum	U	…	n	S	Piperaceae	107	83	60	−0.069	0	0	0	…
Piper carrilloanum	S	…	…	…	Piperaceae	12	10	4	−0.121	0	0	0	…
Piper cordulatum	S	n	n	n	Piperaceae	3149	3713	1777	−0.069	1	0	0	…
Piper culebranum	S	…	W	S	Piperaceae	120	65	53	−0.099	0	0	0	…
Piper imperiale	U	…	…	…	Piperaceae	9	3	3	−0.126	0	0	0	…
Piper perlasense	S	n	n	S	Piperaceae	110	117	68	−0.052	0	0	0	…
Piper reticulatum	U	n	W	S	Piperaceae	180	169	149	−0.022	9	9	9	0.000
Pithecellobium macradenium	T	…	n	n	Leguminosae	1	1	1	0.000	1	1	1	0.000
Pithecellobium rufescens	M	…	n	n	Leguminosae	2	2	2	0.000	0	0	0	…
Platymiscium pinnatum	T	n	n	n	Leguminosae	256	248	266	0.004	71	69	64	−0.012
Platypodium elegans	R	C	n	n	Leguminosae	170	157	159	−0.007	58	49	45	−0.029
Pochota quinta	T	…	n	n	Bombacaceae	2	1	1	−0.083	2	1	1	−0.083
Pochota sessilis	T	…	…	…	Bombacaceae	25	24	23	−0.009	9	11	11	0.022
Posoqueria latifolia	M	…	n	n	Rubiaceae	77	80	77	0.000	14	15	14	0.000
Poulsenia armata	T	n	n	S	Moraceae	3430	2686	2126	−0.054	923	857	801	−0.016
Pourouma bicolor	T	…	n	S	Moraceae	40	43	43	0.009	11	12	15	0.039
Pouteria fossicola	T	…	n	S	Sapotaceae	3	3	3	0.000	2	2	2	0.000
Pouteria reticulata	T	n	n	n	Sapotaceae	1652	1718	1766	0.007	157	170	192	0.023
Pouteria stipitata	M	…	n	n	Sapotaceae	61	61	62	0.001	33	31	29	−0.015
Prioria copaifera	T	n	n	n	Leguminosae	1356	1408	1442	0.007	279	309	336	0.022
Protium costaricense	M	n	n	S	Burseraceae	913	860	870	−0.005	110	101	105	−0.005
Protium panamense	M	n	n	n	Burseraceae	2715	2844	3029	0.013	65	51	57	−0.015
Protium sp. nov.	M	…	n	S	Burseraceae	0	1	3	…	0	0	0	…
Protium tenuifolium	M	n	n	n	Burseraceae	2664	2905	3081	0.016	354	353	362	0.002
Pseudobombax septenatum	T	…	W	n	Bombacaceae	22	15	18	−0.022	11	9	8	−0.035
Psidium friedrichsthalianum	U	…	W	S	Myrtaceae	39	42	47	0.020	4	4	4	0.000
Psychotria acuminata	S	…	W	n	Rubiaceae	8	11	16	0.086	0	0	0	…
Psychotria brachiata	S	…	…	…	Rubiaceae	0	0	1	…	0	0	0	…
Psychotria chagrensis	S	…	n	S	Rubiaceae	13	17	15	0.017	0	0	0	…
Psychotria deflexa	S	n	n	n	Rubiaceae	88	77	60	−0.047	0	0	0	…
Psychotria furcata	S	…	W	n	Rubiaceae	5	1	2	0.000	0	0	0	…
Psychotria graciliflora	S	…	W	n	Rubiaceae	10	14	44	0.185	0	0	0	…
Psychotria granadensis	S	…	n	n	Rubiaceae	7	5	4	−0.065	0	0	0	…

Table 1. (*cont.*)

Species	Codes G	C	W	S	Family	Stems ≥10 mm dbh 1982	1985	1990	Rate 1982–1990	Stems ≥100 mm dbh 1982	1985	1990	Rate 1982–1990
Psychotria grandis	U	n	W	S	Rubiaceae	104	97	81	−0.027	2	2	2	0.000
Psychotria horizontalis	S	n	n	n	Rubiaceae	6168	6446	5920	−0.004	0	2	0	...
Psychotria limonensis	S	...	n	n	Rubiaceae	15	17	19	0.027	0	0	0	...
Psychotria marginata	S	n	n	n	Rubiaceae	582	691	696	0.021	0	0	0	...
Psychotria pittieri	S	...	n	S	Rubiaceae	4	3	3	−0.031	0	0	0	...
Psychotria racemosa	S	...	n	n	Rubiaceae	1	2	2	0.086	0	0	0	...
Pterocarpus belizensis	T	...	n	n	Leguminosae	9	8	3	−0.125	1	1	0	...
Pterocarpus rohrii	T	n	n	n	Leguminosae	1577	1629	1705	0.009	136	103	88	−0.056
Quararibea asterolepis	T	n	n	n	Bombacaceae	2394	2379	2348	−0.002	703	694	699	0.000
Quassia amara	U	...	n	n	Simaroubaceae	155	151	147	−0.005	7	8	8	0.014
Randia armata	U	n	n	n	Rubiaceae	1128	1155	1143	0.001	228	234	241	0.006
Randia formosa	U	...	n	n	Rubiaceae	4	4	4	0.000	0	0	0	...
Rinorea sylvatica	S	n	n	n	Violaceae	2571	2615	2596	0.001	1	0	0	...
Sapium aucuparium	T	...	W	n	Euphorbiaceae	47	41	40	−0.018	23	20	16	−0.040
Sapium sp. nov.	T	...	...	...	Euphorbiaceae	3	3	3	0.000	3	3	3	0.000
Scheelea zonensis	M	...	W	n	Palmae	44	40	36	−0.023	44	40	36	−0.023
Schefflera morototoni	T	...	...	...	Araliaceae	1	1	0	...	1	1	0	...
Schizolobium parahybum	T	...	n	n	Leguminosae	13	13	16	0.026	1	1	1	0.000
Senna dariensis	S	C	n	n	Leguminosae	205	138	116	−0.065	1	2	2	0.080
Simarouba amara	T	n	n	n	Simaroubaceae	1240	1250	1292	0.004	247	255	269	0.010
Siparuna guianensis	M	...	n	S	Monimiaceae	37	34	32	−0.018	16	15	15	−0.008
Siparuna pauciflora	U	n	n	S	Monimiaceae	431	354	316	−0.035	24	26	18	−0.033
Sloanea terniflora	T	n	n	n	Elaeocarpaceae	601	591	575	−0.005	85	85	80	−0.006
Socratea exorrhiza	M	n	n	n	Palmae	812	737	684	−0.021	374	357	336	−0.013
Solanum arboreum	S	...	...	...	Solanaceae	1	1	0	...	0	0	0	...
Solanum asperum	S	...	W	n	Solanaceae	0	0	4	...	0	0	0	...
Solanum hayesii	M	C	n	S	Solanaceae	125	89	77	−0.058	40	25	13	−0.136
Solanum steyemarkii	S	...	n	n	Solanaceae	7	6	2	−0.145	0	0	0	...
Sorocea affinis	S	n	n	n	Moraceae	3302	3371	3302	0.000	47	44	30	−0.051
Spachea membranacea	U	...	n	n	Malpighiaceae	19	17	15	−0.028	8	8	7	−0.015
Spondias mombin	T	C	W	n	Anacardiaceae	63	67	101	0.057	24	23	30	0.026
Spondias radlkoferi	T	C	n	n	Anacardiaceae	192	164	202	0.006	55	56	57	0.004
Stemmadenia grandiflora	U	...	...	...	Apocynaceae	1	1	0	...	1	1	0	...
Sterculia apetala	T	...	W	n	Sterculiaceae	68	53	65	−0.005	25	24	27	0.008
Stylogyne standleyi	S	n	W	n	Myrsinaceae	713	735	751	0.006	1	1	0	...
Swartzia simplex (var. *grandiflora*)	U	n	n	n	Leguminosae	2255	2422	2574	0.015	198	203	212	0.007

Swartzia simplex (var. *ochnacea*)	U	n	n	n	Leguminosae	2701	2821	2857	0.006	104	112	123	0.019
Symphonia globulifera	T	n	n	S	Guttiferae	188	178	175	−0.008	46	38	30	−0.048
Tabebuia guayacan	T	...	n	n	Bignoniaceae	76	74	73	−0.004	30	28	28	−0.007
Tabebuia rosea	T	n	W	n	Bignoniaceae	316	300	318	0.000	81	75	71	−0.014
Tabernaemontana arborea	T	n	W	n	Apocynaceae	1287	1328	1421	0.011	293	302	303	0.004
Tachigali versicolor	T	n	n	n	Leguminosae	2923	2980	3095	0.006	86	82	88	0.002
Talisia nervosa	U	n	n	n	Sapindaceae	813	819	802	−0.001	0	0	0	...
Talisia princeps	M	n	n	n	Sapindaceae	623	638	673	0.008	7	9	5	−0.038
Terminalia amazonica	T	...	W	n	Combretaceae	62	60	59	−0.005	28	28	28	0.000
Terminalia oblonga	T	...	n	n	Combretaceae	92	90	98	0.007	43	42	46	0.007
Ternstroemia tepezapote	U	...	n	n	Theaceae	1	1	1	0.000	0	0	1	...
Tetragastris panamensis	T	n	n	n	Burseraceae	3253	3699	4085	0.026	318	323	353	0.012
Tetrathylacium johansensii	T	...	W	n	Flacourtiaceae	10	7	7	−0.039	8	7	6	−0.032
Theobroma cacao	U	...	n	S	Sterculiaceae	22	20	21	−0.005	12	14	13	0.009
Thevetia ahouai	U	n	W	S	Apocynaceae	107	97	97	−0.011	2	1	1	−0.078
Tocoyena pittieri	M	...	W	S	Rubiaceae	6	8	7	0.017	4	5	5	0.026
Trattinickinia aspera	T	...	n	n	Burseraceae	112	96	82	−0.036	50	47	48	−0.004
Trema micrantha	M	...	n	n	Ulmaceae	32	23	21	−0.051	21	18	15	−0.041
Trichanthera gigantea	U	...	n	n	Acanthaceae	12	9	8	−0.048	3	3	2	−0.047
Trichilia pallida	M	n	W	n	Meliaceae	567	574	591	0.004	76	75	80	0.006
Trichilia tuberculata	T	n	n	n	Meliaceae	12927	13166	13298	0.003	2022	1902	1783	−0.014
Trichospermum galeottii	M	...	n	n	Tiliaceae	7	4	2	−0.154	6	4	2	−0.135
Triplaris cumingiana	M	n	W	n	Polygonaceae	371	342	319	−0.016	125	127	145	0.016
Trophis racemosa	M	n	n	S	Moraceae	312	323	325	0.004	54	48	38	−0.040
Turpinia occidentalis	T	...	n	n	Staphyleaceae	153	113	85	−0.069	69	56	57	−0.022
Unonopsis pittieri	M	n	n	S	Annonaceae	771	785	787	0.002	136	148	160	0.019
Urera baccifera	S	...	n	S	Urticaceae	2	5	17	0.240	0	0	0	...
Virola sebifera	M	n	n	n	Myristicaceae	2406	2276	2086	−0.016	607	588	607	0.000
Virola sp. nov.	T	...	n	S	Myristicaceae	58	53	53	−0.010	21	20	23	0.010
Virola surinamensis	T	...	n	S	Myristicaceae	300	259	239	−0.025	174	163	158	−0.010
Vismia baccifera	U	n	W	n	Guttiferae	75	77	80	0.007	1	3	2	0.075
Vismia billbergiana	U	...	...	...	Guttiferae	3	4	3	0.000	0	0	0	...
Vismia macrophylla	M	...	...	...	Guttiferae	1	0	0	...	1	0	0	...
Vochysia ferruginea	T	...	W	n	Vochysiaceae	35	29	29	−0.022	10	11	11	0.011
Xylopia macrantha	M	n	n	S	Annonaceae	817	916	1044	0.027	79	99	128	0.054
Xylosma chloranthum	U	...	...	...	Flacourtiaceae	1	1	0	...	0	0	0	...
Xylosma oligandrum	S	n	n	n	Flacourtiaceae	183	169	149	−0.024	1	1	1	0.000
Zanthoxylum belizense	T	C	n	n	Rutaceae	220	252	237	0.008	103	108	140	0.036
Zanthoxylum panamense	T	C	n	n	Rutaceae	297	238	227	−0.031	83	70	66	−0.027
Zanthoxylum procerum	M	C	n	n	Rutaceae	207	212	170	−0.023	26	28	35	0.034
Zanthoxylum setulosum	M	...	...	...	Rutaceae	1	1	1	0.000	1	1	1	0.000
Zuelania guidonia	M	...	W	n	Flacourtiaceae	40	41	40	0.000	13	14	11	−0.018

Table 2. Species whose population of stems ≥10 mm changed at a rate ≥5% per year. The four columns of species characteristics are the same as those given in Table 1 (growth form, colonizing, swamp and slope status). Species are ordered from those with the fastest shrinking populations to the fastest growing; the line separates growing from shrinking populations.

					Population		Rate of population change		
Species	G	C	W	S	1982	1990	1982–1985	1985–1990	1982–1990
Piper aequale	S	n	n	S	219	83	−0.0984	−0.1223	−0.1131
Piper culebranum	S	...	W	S	120	53	−0.2036	−0.0391	−0.0992
Chamaedorea tepejilote	S	...	n	S	32	16	−0.1128	−0.0600	−0.0803
Cestrum megalophyllum	S	...	W	S	309	157	−0.0769	−0.0783	−0.0777
Hampea appendiculata	M	...	n	n	76	40	−0.1363	−0.0388	−0.0760
Acalypha diversifolia	S	C	W	n	1568	827	−0.0742	−0.0717	−0.0727
Acalyphya macrostachya	U	C	n	n	80	45	−0.0626	−0.0762	−0.0714
Conostegia bracteata	S	n	W	S	391	209	−0.0931	−0.0563	−0.0711
Piper cordulatum	S	n	n	n	3149	1777	0.0545	−0.1407	−0.0693
Turpinia occidentalis	T	...	n	n	153	85	−0.0937	−0.0539	−0.0690
Piper arboreum	U	...	n	S	107	60	−0.0798	−0.0624	−0.0690
Senna dariensis	S	S	n	n	205	116	−0.1171	−0.0328	−0.0657
Solanum hayesii	M	C	n	S	125	77	−0.1121	−0.0273	−0.0582
Poulsenia armata	T	n	n	S	3430	2126	−0.0703	−0.0441	−0.0545
Piper perlasense	S	n	n	S	110	68	0.0162	−0.1029	−0.0529
Erythrina costaricana	U	...	n	S	289	185	−0.0622	−0.0464	−0.0525
Trema micrantha	M	...	n	n	32	21	−0.1167	−0.0172	−0.0519
Olmedia aspera	U	n	n	S	442	279	−0.0434	−0.0564	−0.0510
Chrysophyllum cainito	T	C	W	n	70	109	0.0399	0.0579	0.0510
Chrysophyllum argenteum	T	C	n	n	423	683	0.0366	0.0681	0.0560
Spondias mombin	T	C	W	n	63	101	0.0207	0.0785	0.0575
Croton billbergianus	U	C	W	n	620	1012	−0.0005	0.0944	0.0590
Miconia argentea	M	C	W	n	531	902	0.0764	0.0542	0.0626
Cupania refescens	T	n	W	n	55	96	0.0775	0.0578	0.0654
Annona spraguei	M	C	n	n	55	143	0.0680	0.1328	0.1082
Palicourea guianensis	S	C	w	n	377	1475	0.1861	0.1533	0.1654
Psychotria graciliflora	S	...	W	n	10	44	0.1231	0.2176	0.1853

(38%) changed by <1% per year, and 11 (8%) changed by more than 5% per year (eight of the latter were declines and three increases). The fastest rate of change in the larger size class was *Inga acuminata*, which increased from 11 to 20 stems; a more common species increasing nearly as rapidly was *Xylopia macrantha*, whose population rose from 79 to 128 stems. The greatest decline was in *Solanum hayesii*, which had 40 stems in 1982 but just 13 in 1990. A more abundant species, *Pterocarpus rohrii*, fell from 136 to 83 stems. The mean rate of population change among 136 species in the large size class was −0.32%, and the mean rate of absolute change was 1.93%. These are not significantly different from rates for stems ≥10 mm (t-test).

Within-species consistency in population change

Rates of change during 1982–1985 and 1985–1990 were consistent within species (Figure 2A; the correlation is highly significant: $r^2 = 0.266$, $P < 0.0001$ for stems ≥10 mm dbh; $r^2 = 0.246$, $P < 0.0001$ for stems ≥100 mm). There were

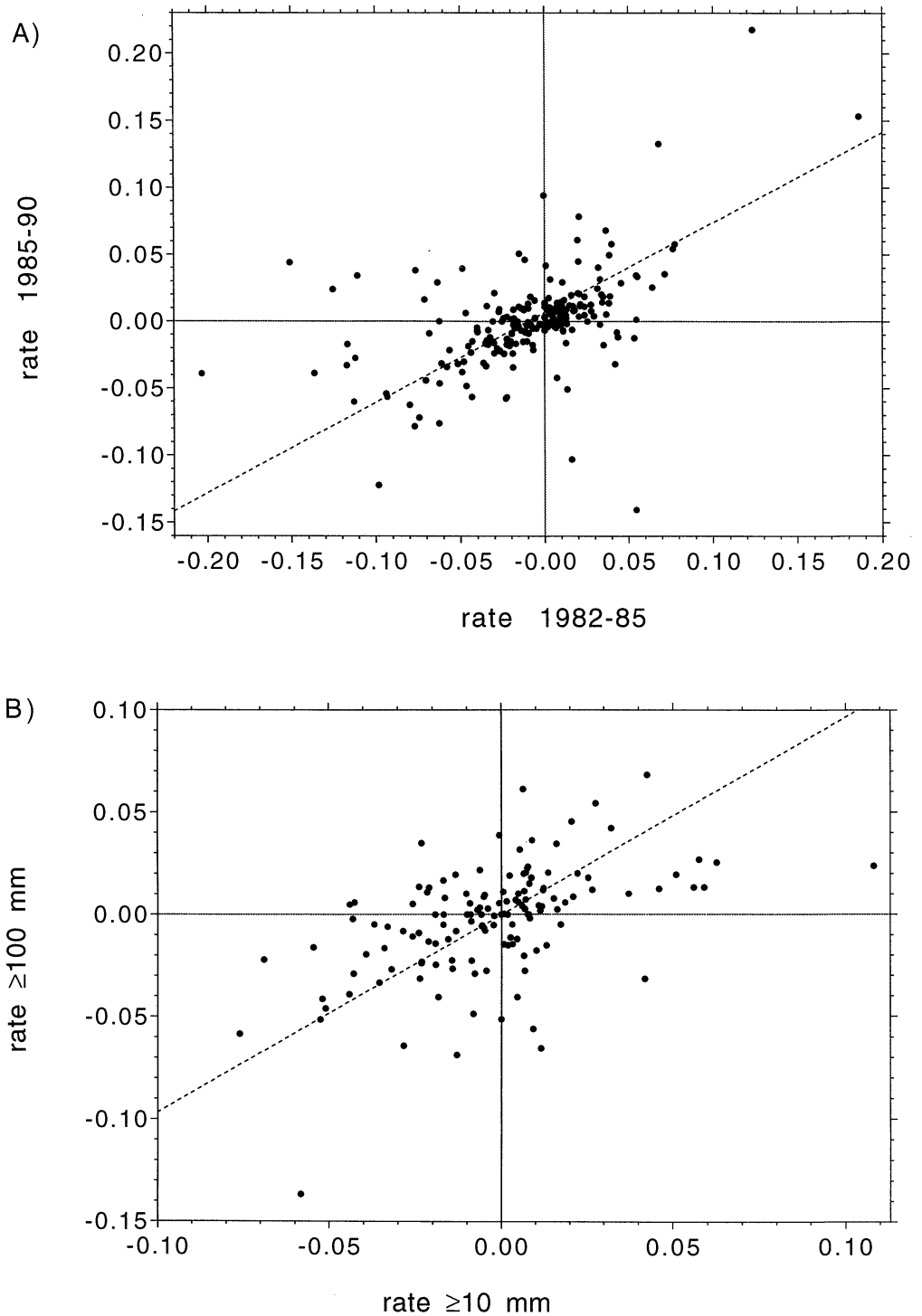

Figure 2. Scatter plots of population change, with one point plotted for each species. The dotted lines are diagonal regressions, shown only to indicate the direction of trends. (A) Population change for stems ⩾10 mm dbh, plotting 1985–1990 rate *vs* 1982–1985; 219 species included. (B) Population change over 1982–1990, plotting rate for stems ⩾100 mm dbh *vs* rate for stems ⩾10 mm dbh; 136 species included.

Table 3. Numbers of species with increasing and decreasing populations, by colonizing status, slope status and growth form. 'Slope' means slope-specialists that were not colonizers, 'colonizer' means colonizing species that were not slope-specialists and 'neither' means species that were neither slope-specialists nor colonizers (unlike Figure 1, this latter category does not include species for which information was missing). The four slope-colonizer species are not included. Asterisks between the increasing and decreasing columns indicate a significant difference in the fraction of species increasing between a given group and the 'neither group' (** indicating $P<0.01$ and * $P<0.05$). The final column gives the mean rate of population change for each species group.

		Number of populations				
Growth form	Status	Increasing		Decreasing	No change	Mean rate of change
Large trees	Slope	5		6	0	−0.004 ±0.030
	Neither	15		7	0	0.005 ±0.017
	Colonizer	8		8	0	0.003 ±0.032
Mid-sized trees	Slope	5		3	0	0.008 ±0.012
	Neither	17		11	0	0.001 ±0.020
	Colonizer	4		4	0	0.018 ±0.049
Understorey trees	Slope	1	**	6	0	−0.025 ±0.016
	Neither	19		2	0	0.016 ±0.016
	Colonizer	3		2	0	−0.002 ±0.049
Shrubs	Slope	0	*	4	0	−0.062 ±0.043
	Neither	10		5	1	−0.004 ±0.024
	Colonizer	1		3	0	0.003 ±0.011
All species	Slope	11	**	19	0	−0.013 ±0.033
	Neither	61		25	1	0.005 ±0.020
	Colonizer	16	*	17	0	0.006 ±0.050

cases, though, where populations increased dramatically prior to 1985 then declined afterwards, or vice versa. For example, *Piper cordulatum* increased from 3149 to 3713 stems, then declined to 1777 (Table 1). Rate of change was also fairly consistent between the two size classes ($r^2=0.265$, $P<0.0001$ for the 1982–1990 rate), but again there were exceptions (Figure 2B). For example, *Trichilia tuberculata*, the most abundant large tree in the plot, suffered a rather considerable decline among stems ≥100 mm dbh, but its population ≥10 mm dbh increased (Table 1).

Population change as a function of species characteristics

Slope status. Slope status was clearly associated with a species' probability of declining in abundance. Excluding all colonizing species (in order to separate the effect of that variable) there were 30 slope-specialists, 19 declining in abundance and 11 increasing. Of 87 non-slope species, 25 declined and 61 increased (Table 3). Thus, 29% of non-slope but 63% of slope-species declined in abundance ($\chi^2=11.1$, df = 1, $P<0.01$). Sample sizes were augmented if colonizers were included, and the pattern remained: 63% of 52 slope species but 42% of 165 non-slope species declined in abundance.

The pattern did not hold for all growth forms, though, in fact the distinction between slope and non-slope species was due entirely to species of smaller stature – shrubs and treelets. Of this group, 91% of slope-species and only 19%

of non-slope species declined in abundance, with the difference statistically significant in both growth forms (Table 3). But in large and mid-sized trees, there was no such distinction, with 47% of slope and 36% of non-slope species declining in abundance and no significant difference in either growth form (Table 3).

Slope-specialists suffered the most impressive population declines. Of the 18 species declining more than 5% per year, 11 were slope-specialists (Figure 1A, Table 2). The four most rapid declines were slope-specialist shrubs (Table 2). Conversely, none of the nine species increasing more than 5% per year were slope-specialists (Table 2).

The poor performance of slope-specialists was not evident when considering stems above 100 mm dbh, because there were few treelets and shrubs included in this size class. For large and mid-sized trees, slope-specialists performed no worse than non-slope: six of 17 slope species decreased in abundance, whereas of non-slope species, 20 of 40 declined. Among treelets and shrubs, slope-specialists did suffer more declines than non-slope species (two out of three *vs* four out of 13) but the sample was far too small to evaluate statistically.

Colonizing species. Species designated as gap-colonizers performed somewhat worse than non-colonizing species, although not as poorly as slope species. Excluding slope-specialists (to isolate the effect of the colonization variable), 52% of 33 colonizing species and 29% of 87 non-colonizers declined in abundance ($\chi^2 = 5.3$, $P < 0.05$, Table 3). Each of the four growth forms showed a comparable pattern, with colonizers doing slightly worse than non-colonizers, but none was statistically significant by itself (Table 3).

Despite the fact that colonizers on average performed poorly, they were over-represented among rapidly increasing populations. Seven of the nine species increasing faster than 5% per year were colonizers, and only one was not (the other had an unknown colonization index). In contrast, of the 18 species decreasing faster than 5% per year, four were colonizers and six were not.

When considering abundance changes in stems $\geqslant$100 mm dbh, there was no indication that colonizers performed differently than non-colonizers. Excluding slope-specialists, 10 of 25 colonizing species decreased in abundance, while 24 of 53 non-colonizers declined. The four growth forms did not differ.

Swamp status. Swamp status was unrelated to population change. Considering stems $\geqslant$10 mm dbh, 26 of 51 swamp species declined in abundance (51%), whereas 78 of 167 non-swamp species declined (47%). For stems $\geqslant$100 mm dbh, 10 of 26 swamp species (38%) and 51 of 110 non-swamp (46%) declined. Neither difference, nor any for individual growth forms, reached statistical significance. Like colonizing species, though, swamp-specialists were over-represented among rapid increasers: seven of nine species increasing $\geqslant$5% per year were swamp species, but only four of 18 species declining by $\geqslant$5% per year were.

DISCUSSION

Nearly all shrubs and treelets that occur preferentially on the slopes of the 50 ha plot declined in abundance. We know the slopes around the side of the plateau are a wetter microhabitat during the dry season (Becker *et al.* 1988), and we assume that species more abundant there are less able to tolerate drought stress. We can support this assumption by casual observations on species distributions: some of the familiar slope-specialists at BCI – *Poulsenia armata*, *Olmedia aspera*, *Erythrina costaricana* and *Acalypha diversifolia* – are common along permanent streams in forests near BCI (there are no permanent streams on BCI). Further casual support comes from the genus *Piper*, which is particularly abundant in wet forests; five of its eight species in the 50 ha plot species are slope-specialists (all eight declined in abundance).

It seems certain that this group of shrubs and treelets that cannot tolerate long drought invaded the plateau forest at BCI during the wetter periods prior to 1966 but is now being eliminated by the increased severity of the dry season. It is possible that the extreme dry season of 1983 is solely responsible; alternatively, it may be a continuing problem caused by recurring severe dry seasons. We cannot distinguish between the two alternatives now, but future censuses will. If the only problem for drought-intolerant species was 1983, then populations should level off and perhaps even climb by 1995 or 2000, when the plot will be censused anew. We are certain, however, that dry season length and severity is the crucial edaphic variable affecting population success and limiting species' ranges at BCI (Wright 1992, Wright & van Schaik 1994). Reduction of rainfall during the wet season is probably inconsequential (at least for trees) since water is never limiting then.

Why have moisture-demanding trees of larger stature not suffered population declines as consistently as shrubs and treelets? We anticipated that they would, largely because of two prominent canopy trees and strong slope-specialists that suffered severe declines in abundance: *Poulsenia armata* and *Ocotea whitei*. But other slope-specialists in the canopy, such as *Calophyllum longifolium*, have healthy populations. We suggest the following hypothesis to account for this division and the general decline of shrubs and treelets. As adults, some trees, like *Calophyllum*, have longer roots than others, like *Poulsenia*, long enough to reach water below the slopes during the dry season, but not from the plateau (which is higher and thus further from the water table, see Wright & van Schaik 1994); *Poulsenia* thus suffered high mortality at all sizes during the 1983 El Niño drought, whereas *Calophyllum* did not. But both species have drought-sensitive seedlings, and are thus largely restricted to the wetter areas within the plot. Likewise, there are shrubs and treelets with drought-sensitive seedlings that are restricted to moist regions, but nearly all have short root systems as adults (Becker & Castillo 1990, Wright 1992) and suffer from long dry seasons at BCI. (Some shrubs have other drought-adaptations and are widespread in the plot.)

During moderate dry seasons, there is presumably enough water near the surface of the slopes for these drought-intolerant plants, and this allowed their spread into the plot prior to 1966, when dry seasons were less severe. The swamp may remain wet even during the most severe dry seasons, so that swamp-specialists can persist despite the drying trend.

Are the slope-specialists becoming extinct on BCI, or will they persist in locally wet sites? It appears not – all shrubs and treelets that declined throughout the plot declined on both the slopes and the plateau; in fact, most species had similar rates of change in both regions. Thus, it seems that there is a group of drought-intolerant species headed for extinction at BCI, at least 16 treelets and shrubs, and perhaps as many as 30–40 including the large, drought-sensitive trees like *Poulsenia* and *Ocotea whitei*. Howe (1990) has already predicted that *Virola surinamensis*, a large, slope-specialist tree, will go extinct on BCI due to its inability to tolerate long dry seasons. He based his conclusion on seedling survival data, not having seen the 1982–1990 population data which bears out his prediction – a decline from 300 to 239 stems.

Species which preferentially invade light gaps in the 50 ha plot – what we called colonizing species – had an almost bimodal distribution of population change. A few species had very rapid increases, but the rest did worse than average. Condit *et al.* (1992b) and Hubbell & Foster (1990a) have stated two different hypotheses about factors affecting the populations of gap-colonizers. One is that the more open canopy caused by drought-induced mortality in 1983 (Becker & Smith 1990) created more recruitment opportunities for species that demand light gaps, leading to a population burst in the 10 mm size class by 1985 or 1990. The other hypothesis is that the 50 ha plot is undergoing succession because the area just north of the plot (plus 2 ha within the plot) was cleared around the turn of the century but has matured since. Ruderal species abundant in the near-by farmland maintained high sink populations within the old forest because of the large number of seeds entering, but these populations are now declining. Both factors may in fact be at work at the same time. There are some colonizing species which can obviously maintain high populations within gaps of old forest (all seven of the rapidly rising species would be examples), but other species such as *Apeiba tibourbou* and *Schefflera morototoni* which are abundant only in large clearings may not persist in the old forest and are now in decline (indeed, the latter dropped out of the plot between 1982 and 1985).

An obvious concern with these conclusions is the method for identifying edaphic preferences of individual species. Some associations with topographic regions may be due to factors having nothing to do with moisture or light preference. Artefactual correlations weaken our power to detect effects of moisture preference, but the trends we did detect should be robust with respect to this error and ought to appear even stronger if species with accidental associations were segregated. We eventually hope to get physiological information on

some species to define independently those that are drought-tolerant (Mulkey *et al.* 1994, Wright & van Schaik 1994).

The mean rate of absolute population change in the plot was 2.25% per year, a 20% increase or 16% decrease after eight years. About 10% of the populations in the plot are changing >5% per year (a 49% increase or 33% decrease over eight years). These seem like substantial rates for trees, which ought to have rather lethargic population trajectories due to their long life spans and slow growth (Condit *et al.* 1992b, Hubbell & Foster 1990a). Are such changes typical for tropical forests, or is BCI unusual because of the climatic shift taking place? In a study of 50 ha of dry forest in India, several tree and shrub species underwent severe declines in abundance – in just three years – due to elephant herbivory (R. Sukumar, unpublished data). Other studies in the tropics have been on much smaller areas with irregular censuses, and are very difficult to compare. For example, Manokaran & Kochummen (1987) documented some abrupt declines and increases in a 34-year record of tropical forest in Malaysia: *Shorea parvifolia* declined from 26 to 16 individuals in 16 years, and *Dacryodes puberula* from 14 to four in 34 years, both consistent declines of about 5% per year, but both are based on small samples. The empirical issue of stability in tree populations and community composition of tropical forests must be resolved by more large datasets, and large-scale plots are now under way at 11 sites in Africa, Asia and America (Condit 1995). Results from these will settle the matter.

These plots will offer a baseline for assessing the impact of global climate change on tropical forests. Long-term changes in precipitation can have tremendous effects on forests (Foster 1982a,b, Hartshorn 1992), and if Phillips & Gentry (1994) are correct, CO_2-fertilization may be changing forest-wide dynamics. We see perhaps 10% of the species at BCI headed for extinction because of a 25-year decline in precipitation. Understanding and even anticipating climatic effects on tropical forests will be crucial for their long-range conservation.

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APPENDIX

The 48 species names that have been changed since the 50 ha plot was initiated in 1981 or which do not appear in Croat (1978). The current name is the one appearing in Table 1. The eight species listed as *sp. nov.* were newly discovered in the 50 ha plot and remain undescribed.

Current name	Name in D'Arcy (1987)	Name in Croat (1978)
Appunia seibertii	*Appunia seibertii*	not appearing
Ardisia guianensis	*Ardisia guianensis*	not appearing
Brosimum guinense	*Brosimum guinense*	not appearing
Chamaedorea tepejilote	*Chamaedorea tepejilote*	*Chamaedorea wenlandiana*
Chamguava schippii	*Psidium anglohondurensis*	*Psidium anglohondurensis*
Chrysochlamys eclipes	*Tovomitopsis nicaraguensis*	*Tovomitopsis nicaraguensis*
Chrysophyllum argenteum	*Cynodendron panamense*	*Cynodendron panamense*
Erythroxylum macrophyllum	*Erthroxylum macrophyllum*	not appearing
Garcinia intermedia	*Garcinia intermedia*	*Rheedia edulis*
Garcinia madruno	*Garcinia madruno*	*Rheedia acuminata*
Guarea grandifolia	*Guarea grandifolia*	*Guarea multiflora*
Guarea sp. nov.	not appearing	not appearing
Heisteria acuminata	*Heisteria acuminata*	*Heisteria longipes*
Hyeronima alcheornoides	*Hyeronima laxiflora*	*Hyeronima laxiflora*
Inga acuminata	not appearing	not appearing
Lonchocarpus latifolia	*Lonchocarpus latifolia*	*Lonchocarpus pentaphyllus*
Lopimia dasypetala	*Lopimia dasypetala*	*Pavonia dasypetala*
Maclura tinctoria	*Chlorophora tinctoria*	not appearing
Malmea sp. nov.	not appearing	*Crematosperma sp.*
Myrospermum frutescens	*Myrospermum frutescens*	not appearing
Nectandra purpurea	*Nectandra purpurea*	*Nectandra purpurescens*
Nectandra sp. nov. 1	not appearing	not appearing
Nectandra sp. nov. 3	not appearing	not appearing
Ocotea puberula	*Ocotea puberula*	*Ocotea pyramidata*
Ocotea whitei	*Ocotea whitei*	*Ocotea skutchii*
Oenocarpus mapoura	*Oenocarpus mapoura*	*Oenocarpus panamanus*
Ormosia amazonica	*Ormosia amazonica*	not appearing
Osmosia croatii	*Ormosia coccinea*	*Ormosia coccinea*
Phoebe cinnamomifolia	*Phoebe cinnamomifolia*	*Phoebe mexicana*
Pochota quinata	*Bombacopsis quinata*	*Bombacopsis quinata*
Pochota sessilis	*Bombacopsis sessilis*	*Bombacopsis sessilis*
Pourouma bicolor	*Pourouma guianensis*	*Pourouma guianensis*
Pouteria reticulata	*Pouteria unilocularis*	*Pouteria unilocularis*
Protium sp. nov.	not appearing	not appearing

APPENDIX 1. (*cont.*)

Current name	Name in D'Arcy (1987)	Name in Croat (1978)
Psychotria graciflora	*Psychotria graciflora*	not appearing
Pterocarpus belizensis	*Pterocarpus belizensis*	not appearing
Sapium aucuparium	*Sapium caudatum*	both (now considered synonyms)
Sapium sp. nov.	not appearing	not appearing
Schefflera morototoni	*Didymopanax morototoni*	*Didymopanax morototoni*
Senna dariensis	*Senna dariensis*	*Cassia fruticosa*
Socratea exorrhiza	*Socratea exorrhiza*	*Socratea durissima*
Solanum steyemarkii	*Solanum argenteum*	*Solanum argenteum*
Terminalia oblonga	*Terminalia oblonga*	*Terminalia chiriquensis*
Trichilia pallida	*Trichilia pallida*	*Trichilia montana*
Trichilia tuberculata	*Trichilia tuberculata*	*Trichilia cipo*
Trichospermum galeottii	*Trichospermum galeottii*	*Trichospermum mexicanum*
Urera baccifera	*Urera baccifera*	not appering
Virola sp. nov.	not appearing	not appearing