

Assessing the response of plant functional types to climatic change in tropical forests

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Abstract. We propose and test a classification of plant functional types for tropical trees based on demography, growth form, phenology, and moisture requirements, using data from a 50-ha forest dynamics plot in Panama. Correlations among demographic variables for individual species - mortality, growth, and the tendency to colonize light gaps - were strong, and a single principal component (PC) accounted for a large fraction of the demographic variability. Most species - shade-tolerants - were clustered at the low end of the PC axis (low growth, low mortality), while the rest were continuously distributed over a wide range. Three demographic guilds could be defined from scores on this axis: we call these pioneer, building phase, and shade-tolerant trees, following earlier terminology.

Leaf lifetime correlated negatively with the demographic axis, and there was a weak relationship between demography and moisture-preference: no species with high demographic scores also had high moisture requirements. There was no significant relationship between deciduousness and the demographic axis, but deciduousness was negatively correlated with leaf lifetime and moisture index. Altogether, 11 different combinations of demographic variables, deciduousness, moisture needs, and growth form (canopy vs. understory species) were identified.

We evaluated how these functional types changed in abundance between 1982 and 1995. Because of a recent run of dry years and long dry seasons, we predicted that deciduous species, canopy species, pioneers, and drought-tolerant species would be increasing at the expense of their counterparts. Only one aspect of this prediction was borne out: moisture-demanding species declined sharply in abundance relative to drought-tolerant species. Neither deciduousness nor growth form was associated with population change, and pioneer species declined in abundance more often than shade-tolerants. The overall structure of the forest - the density of deciduous, pioneer, and understory species - did not change much, but the decline of the moisture-demanding guild indicates that a change in composition is preceding a structural change.

Keywords: Demography; Growth form; Moisture requirement; Phenology; Tropical tree.

Nomenclature: Croat (1978); Condit et al. (1996).

Introduction

If global climates change in the next century by as much as some models predict, there will be pronounced impacts on the world's vegetation. In the tropics, it is likely that shifts in precipitation will have a greater impact on vegetation than rising temperature (Foster 1982a, b; Hartshorn 1992; Bawa & Markham 1995), and no one knows how much effect increasing CO₂ will have. Predicting how forests respond to various climate scenarios requires detailed information about the demography and physiology of forest trees, sophisticated vegetation modeling, and knowledge about historical changes. Detailed predictions about temperate forest change have been made using these approaches (Solomon 1986; Pastor & Post 1988; Overpeck et al. 1990; Botkin & Nisbet 1992; Shugart & Smith 1992; Cramer in press), but information on the impact of climate change - past or present - in the tropics is rare (Bush & Colinvaux 1990; Foster 1982a; Condit et al. 1996; O'Brien et al. 1992).

The approach for modeling global vegetation endorsed by the GCTE* is that of 'plant functional types' (Steffen et al. 1992; Cramer in press). The goal is to model functional guilds - collections of species with similar impacts on their ecosystem, similar demographics, and similar responses to perturbations - rather than to model individual plant species (Boutin & Keddy 1993). Although this approach begs the question of what is 'similar', it seems inevitable that broad-scale vegetation modeling will not deal with individual plant species, and that some sort of grouping will be necessary. This does not obviate the need nor the importance of individual-species models for predicting vegetation responses, it simply justifies the exploration of models based on plant functional types.

Our purpose here is to examine functional characteristics of tropical trees based on data from over 200 species in a long-term census plot on Barro Colorado Island in Panama (Hubbell & Foster 1983; Condit et al. 1992b). We propose to group species using four sets of

variables: growth form, demography, moisture requirement, and phenology. For growth form, we consider canopy and understory trees, the groups most important to overall forest structure. For demography, we test for associations among mortality, growth, and the tendency to colonize canopy openings, examining the pioneer/shade-tolerant paradigm of tropical tree biology (Swaine & Whitmore 1988; Whitmore 1989) and the ruderal/climax paradigm of general plant ecology (Grime 1977, 1988). For moisture requirement, we develop a quantitative index based on the relative abundance of a species in wetter and drier regions of the 50-ha plot. Finally, we consider two phenological variables: deciduousness, because of its importance to drought-resistance, and leaf lifetime, which is often related to plant growth rate (Coley 1988; Körner 1991; Chapin 1993).

We evaluate the usefulness of these proposed plant functional types in modeling how tropical forests respond to climate change. Does a single pioneer/shade-tolerant axis account for most variation in growth, mortality, and gap preference? Are there relationships between functional characteristics - deciduousness, growth form, leaf turnover, and moisture preference - and the demographic axis? The point of plant functional groupings is to reduce demographic and morphological variation into a few key axes, which we attempt with a proposed classification of functional types for tropical trees.

We also examine how plant functional types have actually responded to climatic change. Barro Colorado suffered an abrupt decline in rainfall around 1966 and an unusually severe dry season in 1983 (the 50-ha census began in 1981), and effects of this drying trend on tree growth, mortality, and population trends of various species in the plot have been documented (Condit et al. 1992a, 1995a, 1996). Most interesting, species with high moisture demands declined sharply in abundance between 1982 and 1990 (Condit et al. 1996). Here, we re-examine those relationships using newly defined functional categories and more recent census data from 1995, profiting from the unusual opportunity to observe which plant traits are predictors of forest change under climatic variation.

Material and Methods

The forest and the climate

The forest-dynamics plot is on Barro Colorado Island (BCI) in the Panama Canal, at the Smithsonian Tropical Research Institute reserve. The island has 1500 ha of diverse, moist, lowland tropical forest, and has been completely protected from human disturbance

(other than research) for 70 years. Most of the island, including 48 ha of the 50-ha plot, has seen no human disturbance for over 500 years. Detailed descriptions of the flora and fauna can be found in Croat (1978) and Leigh et al. (1982).

The climate on BCI is warm all year, but rainfall is seasonal. Most of the 2500 mm of precipitation falls during the eight-month wet season, with almost none coming from December through April (Windsor 1990; Windsor et al. 1990). Of particular interest from the climate change perspective is that there was an abrupt, 14% decline in total rainfall at BCI around 1966 (Windsor 1990; Windsor et al. 1990), and a concomitant increase in the frequency of severe dry seasons (Condit et al. 1992a). This dry period was punctuated by an extremely severe drought in 1983, associated with a strong El Niño event. During early 1983, just 3 mm of rain fell over a 12-week period and temperatures were 2 °C above normal (Leigh et al. 1990).

This drought caused immediate tree death (Leigh et al. 1990). In the 50-ha plot, forest-wide mortality was 3% per year during 1982-1985 but 2% per year during 1985-1990 (Condit et al. 1995a). Condit et al. (1996) published the population densities of all 313 species found in the 50-ha plot (a 314th species was added in 1995), and evaluated changes in abundance in relation to the drought. Here, we re-evaluate these results from the perspective of plant functional types.

Plot census

Censuses of the 50-ha plot were carried out in 1981-1983, 1985, 1990, and 1995 (Hubbell & Foster 1983, 1986a, b; Condit et al. 1992a, b; we refer to the first census, which lasted two years, as the 1982 census). All free-standing, woody stems ≥ 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 lower point where the stem was cylindrical. DBH of buttressed trees were taken above the buttresses.

Plant functional types

We analyzed seven characteristics of each tree species: three demographic, two phenological, one indicator of drought-tolerance, and one structural. The first demographic character was mortality rate, which was listed in Condit et al. (1995a) for each species, in two DBH classes (10-99 and ≥ 100 mm DBH) and two time intervals (1982-1985 and 1985-1990). Here, we used data for both size classes, but only the second interval, since the first was strongly influenced by the 1983 drought. The second

character was growth rate, defined as:

$$\frac{\ln(dbh_t) - \ln(dbh_0)}{t} \quad (1)$$

where *dbh* is a tree's DBH and \ln its natural logarithm, measured at time *t* and at time 0 (Condit et al. 1993a, b). We calculated growth over 1985-1990 - to avoid the drought's influence (Condit et al. 1992b) - in two DBH classes: 10-19 and 100-199 mm. The DBH classes were narrower than those used for mortality because growth changes more with DBH than mortality: growth, as given by Eq. 1, declines continuously with DBH for all species we have examined, reaching (or nearly reaching) a plateau at DBHs > 100 mm (Condit et al. 1993a, b). The two size classes represent the intercept (growth at 10 mm DBH) and the plateau of this curve. The third demographic variable measured for each species was colonizing status, defined as the fraction of recruits in the 50-ha plot found in light gaps, given in Welden et al. (1991); we call this the 'colonizing index'.

The phenological indices were mean leaf lifetime in forest light gaps, as given by Coley (1988), and deciduousness. Deciduous species were defined as those that are completely leafless for at least four consecutive weeks during most years. We identified 34 of 314 species in the 50-ha plot as deciduous, using our own observations and a brief discussion in Croat (1978), and consulting other scientists at BCI (J. Wright and R. Pérez, unpubl. data; there are no published records on deciduousness for most BCI tree species). 32 of these species lose their leaves during part or all of the dry season, but *Cordia alliodora* (*Boraginaceae*) is leafless from the end of the dry season until about two months into the wet season, and *Erythrina costaricana* (*Fabaceae*) is leafless only during part of the wet season. Our definition of deciduousness does not include several species which drop all their leaves but promptly develop them again, usually during the dry season. These species are effectively evergreen, since their leaf loss has essentially no effect on the forest's leaf area or productivity.

Moisture preference was defined by a tendency to occur on moister soils within the 50-ha plot. This was based on each species' distribution relative to the 7° to 30° slopes that surround the central plateau of the plot. The slopes are wetter during the dry season than the plateau itself, due to a water table on a basalt cap beneath the plateau (Becker et al. 1988; Condit et al. 1995a, 1996). Several species have distributions that clearly follow these slopes (Hubbell & Foster 1986a), and some of these slope-specialists are commonly observed along streams outside the plot.

In Condit et al. (1995a, 1996), we used the ratio of density on the slopes to density on the plateau as an index of moisture demands for a species. Here we use a

derivation of this index aimed at removing a bias caused by spatial autocorrelation in species' distributions (Harms 1996). The technique is similar to a bootstrap analysis. First, 500 random slope and plateau habitats were created by assembling 20 m × 20 m quadrats within a simulated 50-ha plot; each artificial habitat had the same area as the true slope or plateau, and each was contiguous (that is, every quadrat bordered another quadrat of the same habitat). Within each (of 500) habitats, the ratio of density on the artificial slope to the artificial plateau was calculated for each species (based on the species' distribution in the real plot), and the proportion of random ratios (of 500) which were smaller than the observed ratio (in the real plot) was the index. The index is thus the probability that the observed habitat association is stronger than a chance association. A probability ≥ 97.5% indicates a statistically significant slope association (5% level, two-tailed test). A low probability means the distribution is no more associated with the slopes than would be expected by chance (see Harms 1996 for details).

The final functional variable was growth form, referring to a species' maximum height (Hubbell & Foster 1986b). In previous papers, we used four groups - shrubs, treelets, mid-size trees, and large trees - but here we collapsed the first two and the second two, referring to the resulting groups as understory and canopy trees. This is partly for simplicity and partly because prior results showed similar population responses of the two understory groups on the one hand and two canopy groups on the other (Condit et al. 1996). Understory trees are those with a maximum height on BCI shorter than 20 m, seldom reaching the canopy, while canopy trees have maximum heights ≥ 20 m.

Species evaluated

Many of the 314 species in the 50-ha plot species were too rare to analyze. Demographic variables were calculated for 142 species: 85 canopy and 57 understory, including only species with ≥ 5 stems in the required DBH classes for growth rates. Colonizing index and mortality rates have been published for all 142. The moisture preference index was calculated for 297 species, including all 142 whose demography was examined (Harms 1996). Deciduousness and growth form are known for nearly all 314 species, but just 12 deciduous species were among the 142 with demographic variables. Leaf lifetimes for 39 species have been published (Coley 1988), 31 of which were among the 142 used in the demographic analysis. Certain combinations were unavailable for testing: only two deciduous species and only one species with a published leaf lifetime were understory species. Tests involving these two characters

were thus possible for canopy trees only. Tests involving the demographic data were restricted to the 142 main species, but other correlations were examined with larger samples.

Species names were taken from Condit et al. (1996). Authorities can be found in Croat (1978), and all species whose names have changed since Croat's monograph are listed in an appendix in Condit et al. (1996).

Analyses

Our first goal was to define plant functional types according to demography. A principal components analysis (PCA) was carried out using the five demographic variables (colonizing index, growth and mortality in two DBH classes) in 85 canopy species, and three variables (without the larger DBH class) in 57 understory species. PCA has been widely used to define plant functional types (Golluscio & Sala 1993; Fernández Alés et al. 1993; Franklin et al. 1995). Based on the paradigm of pioneer vs. shade-tolerant tree species in tropical forests, we predicted a high correlation among the variables, with the first principle component reflecting pioneer status.

We then evaluated how other plant characteristics correlated with pioneer status. We predicted that species with higher growth rates would have shorter leaf lifespan, and that deciduousness would be correlated positively with pioneer status. We also predicted that moisture-preference would correlate negatively with pioneer status, that is, that shade-tolerant species would be more restricted to moist soils than pioneers.

Our final goal was to evaluate the usefulness of functional types in predicting the response of the forest as a whole and of individual species to climatic change. The rate of population change between 1982 and 1990 (the change in the natural logarithm of population size divided by time) has been published for 313 species in the plot (Condit et al. 1996); here we update this by using the recently completed 1995 census and recalculate a 1982-1995 rate of change. We evaluated first whether the demographic variables - as condensed by principal components - predicted population change, then whether deciduous species changed in abundance relative to evergreen species, whether understory species declined in abundance, and whether moisture preference was correlated with population change. Non-parametric statistical tests were used: correlations were done using Spearman's ρ and associations between continuous and nominal variables with the Mann-Whitney U-test. All analyses were carried out separately for canopy and understory species.

Results

Demographic variables

There were significant correlations among the five demographic variables, as predicted. For canopy species, there were significant positive correlations among all pairs of four of the variables - colonizing index, growth in two DBH classes, and mortality in the small DBH class (Spearman's rank correlation, $p < 0.05$). This means that species with high colonizing indices tended to have high growth rates in both DBH classes and high mortality in the small DBH class. The fifth variable was mortality rate in the large DBH class, which was not significantly correlated with colonizing index nor growth rates, but was correlated with mortality in the small DBH class. All non-significant associations were positive, though. For understory species, the colonizing index was significantly and positively associated with growth and mortality, but growth and mortality were not significantly associated with each other (although the association was positive).

Principal components analyses (PCA) reflected these correlations. In canopy species, the first axis accounted for 55% of all variation, with the following eigenvalues: 0.46 for colonizing index, 0.54 for growth at small DBH, 0.41 for growth at large DBH, 0.54 for mortality at small DBH, and 0.19 for mortality at large DBH. The second axis accounted for 20% more of the variance, and was dominated by mortality at the large DBH (eigenvalue 0.93); other eigenvalues had absolute values < 0.33 (some were negative). Thus, a species' score on the first axis is a composite of the four correlated demographic variables, and reflects the predicted axis of pioneer status: high scores indicate a strong tendency to recruit into gaps, high growth, and high mortality. The second axis reflects the fifth variable - mortality at large DBH - which was mostly uncorrelated with the others (Figs. 1, 2).

For understory species, the overall picture was similar. The first PC axis had eigenvalues of 0.62 for colonizing index, 0.55 for growth, and 0.56 for mortality; it accounted for 65% of the variation. The second axis had eigenvalues of 0.70 for mortality, -0.71 for growth, and 0.003 for colonizing index, accounting for 22% more of the variance (Fig. 1). The first axis reflects pioneer status, as it does for canopy species, and the second axis separates species with high mortality and low growth from those with low mortality and high growth. Scores based on the canopy PCA and the understory PCA, when calculated for the same species, were almost perfectly correlated: $PCA_{can} = 0.89 PCA_{und}$, $r^2 = 0.997$ (PCA_{can} is the score on the first axis of the canopy PCA and PCA_{und} that for the understory PCA; both could be

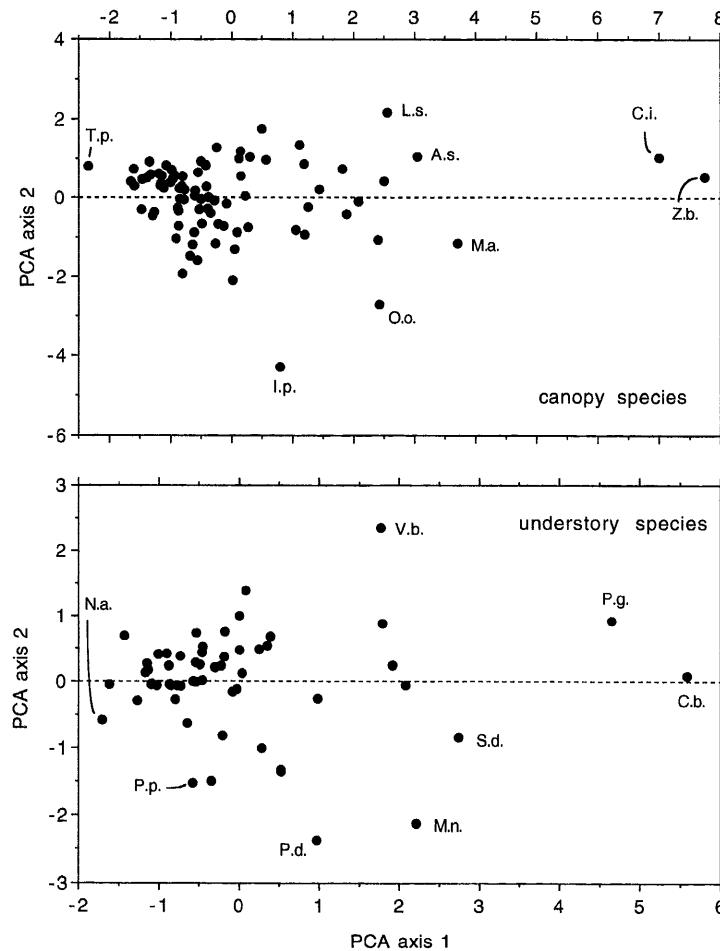


Fig. 1. Principal components for demographic variables, each point representing data for a single species. PCA was done separately for canopy and understory species. Species abbreviations, canopy trees: T.i., *Talisia princeps* (Sapindaceae); I.p., *Inga pezizifera*, (Fabaceae); O.o., *Ocotea oblonga* (Lauraceae); L.s., *Luehea seemannii* (Tiliaceae); A.s., *Annona spraguei* (Annonaceae); M.a., *Miconia argentea* (Melastomataceae); C.i., *Cecropia insignis* (Moraceae); Z.b., *Zanthoxylum belizense* (Rutaceae). Species abbreviations, understory trees: N.a., *Neea amplifolia* (Nyctaginaceae); P.p., *Piper perlasense*, (Piperaceae); P.d., *Psychotria deflexa* (Rubiaceae); V.b., *Vismia baccifera* (Hypericaceae); M.n., *Miconia nervosa* (Melastomataceae); S.d., *Senna dariensis* (Fabaceae); P.g., *Palicourea guianensis* (Rubiaceae); C.b., *Croton billbergianus* (Euphorbiaceae).

calculated for canopy species, but not understory, which were missing the large DBH class). This high correlation is convenient, since it means that the first PC axis score of canopy and understory species can be directly compared; for example, a score of 5 for a canopy species is equivalent to 5.6 in an understory species.

Fig. 1 locates all 142 species in demographic space, showing the considerable extent to which a single axis explains demographic variability. *Cecropia insignis*, *Zanthoxylum belizense*, *Palicourea guianensis*, and *Croton billbergianus* stand out as extremes on the first PC axis; all are well-known pioneers. Two canopy species, *Inga pezizifera* and *Ocotea oblonga*, were well off the first axis, both having very high mortality in the large DBH class (Fig. 2). Among understory species,

Piper perlasense, *Psychotria deflexa*, and *Miconia nervosa* were well off the first axis, having high mortality rates but low or moderate growth, and *Vismia baccifera* had very high growth but low mortality. We subsequently refer to this first PC axis as the 'demographic axis' and its value as for a species as the 'demographic score'.

Figs. 1 and 2 also show how a majority of species are compressed in a fairly small demographic space, relative to the total variation: a tight knot of species having growth rates < 8% per year in the small DBH class, < 4% per year in the large, mortality rates < 4% per year in the small DBH class, and colonizing indices < 30; 61% of all species (87 of 142) fell in this range. This knot of species generally had demographic scores < 1, and in

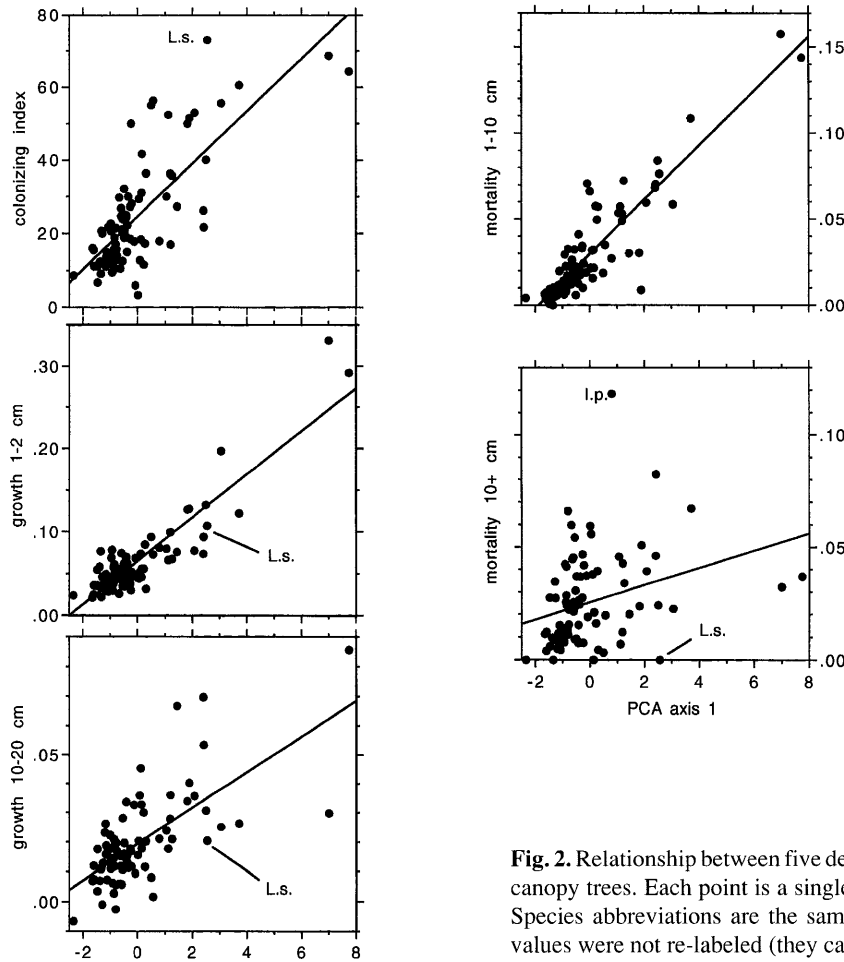


Fig. 2. Relationship between five demographic variables and the first PCA axis, canopy trees. Each point is a single species. Lines are from linear regression. Species abbreviations are the same as for Fig. 1, but the four highest PCA values were not re-labeled (they can be identified by comparing with Fig. 1).

further analyses, we classified species with scores > 1 as 'pioneers' and those with scores < 1 as 'shade-tolerant'. (In the discussion, we propose that the wide range of pioneer scores be divided into two groups.)

Phenology

Leaf lifetime was strongly correlated with the demographic axis (Fig. 3; Spearman rank correlation, $p < 0.0001$). All pioneers had leaf lifetimes < 1 year, whereas most shade-tolerants had leaf lifetimes > 1 year. Leaf lifetime was significantly and negatively associated with growth in both DBH classes, mortality in the small DBH class, but not mortality in the larger DBH class (Spearman's rank correlation).

Deciduous species had a shorter mean leaf lifetime than evergreen species, 6.1 months vs. 17.3 months (12 and 27 species, respectively, $p = 0.0004$, Mann-Whitney U-test). We could not prove that deciduous species had higher demographic indices than evergreen species, but the trend was as predicted: 12 deciduous had a mean

demographic score of 0.90, whereas 73 evergreen canopy species had a mean of -0.15 ($p = 0.2$, Mann-Whitney U-test). Five of 12 deciduous species were pioneers, compared to 12 of 73 evergreen species.

Moisture index

There was no significant relation between the moisture index and demographic score for either growth form (Spearman rank correlation), however, there were no pioneer species with high moisture affinities (of 25 pioneer species, none had a moisture index ≥ 97.5 ; 15 of 117 shade-tolerant species did). Thus, there was a deficit of species with high values of both indices, but over the whole range of variation, there was no relationship. Condit et al. (1995a, 1996) noted a similar association between our earlier slope index (slope to plateau density ratio) and the colonizing index.

Deciduous species had a significantly lower moisture index than evergreen species (32 deciduous species, mean index 41.3; 149 evergreen canopy trees,

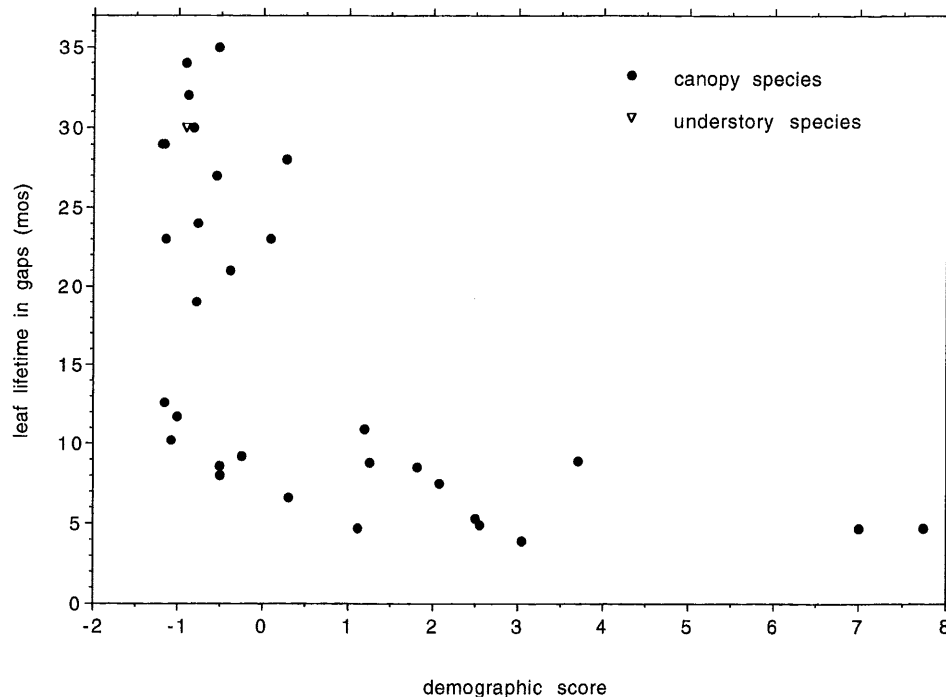


Fig. 3. Relationship between leaf lifetime and the demographic score (first PCA axis). Each point is a single species.

mean 55.1; $p < 0.01$, Mann-Whitney U-test). Leaf lifetime was positively associated with moisture index, but not quite reaching statistical significance ($p = 0.07$, Spearman rank correlation, 38 canopy species).

Population changes

Contrary to prediction, there was a negative association between the demographic score of a species and its rate of population change from 1982 to 1995. In both canopy and understory species, the correlation was significant (Spearman's rank correlation: $p < 0.0001$ for 85 canopy species; $p = 0.03$ for 57 understory species). This matches the result reported by Condit et al. (1996), but the latter was based only on colonizing index, not the entire demographic axis. Thus, more pioneers had declining populations than shade-tolerant species. There were striking exceptions to this overall relationship, indeed some of the fastest growing populations were pioneers (Condit et al. 1996). Among understory species, the two most extreme pioneers (*Palicourea guianensis*, *Croton billbergianus*) had the fastest growing populations, and among canopy species, the fastest growing populations were also pioneers (*Annona spraguei*, *Miconia argentea*).

Moisture index was negatively associated with 1982-

1995 population change in both canopy and understory species (Fig. 4; Spearman's rank correlation: $p < 0.0001$ for 103 understory species; $p = 0.04$ for 173 canopy species). Condit et al. (1996) drew similar conclusions based on the older slope index (slope to plateau density ratio), but the effect in canopy species was not significant (that analysis included fewer species and population changes from 1982 to 1990).

Growth form did not correlate with 1982-1995 population change. The mean population change of 178 canopy species was -0.79% per year, while for 103 understory species it was -1.6% per year ($p = 0.5$, Mann-Whitney U-test). Nor did deciduousness correlate with population change: 32 deciduous species had a mean change of -0.62% per year, while 146 evergreen canopy species had a mean of -0.83% per year ($p = 0.7$, Mann-Whitney U-test).

Overall change in the forest

The above conclusions were based on testing population changes of individual species. We can also look at population changes of entire guilds, ignoring species. Understory trees and canopy trees remained a near-constant fraction of the forest, paralleling the trend found for individual species. Pioneer individuals

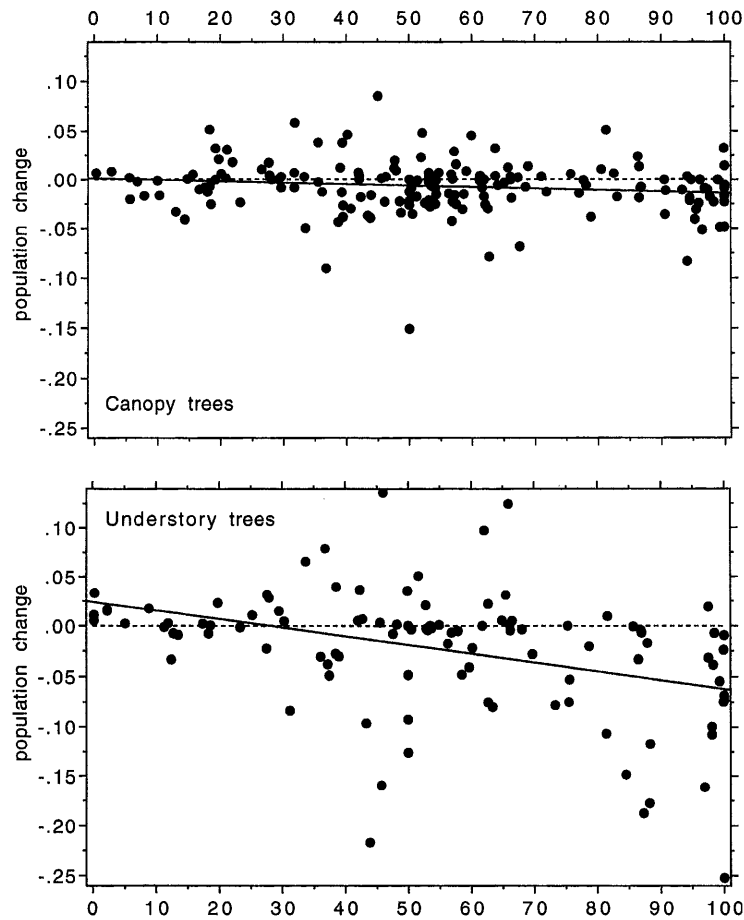


Fig. 4. Relationship between moisture index and annual population change. Each point represents data for a single species. The dashed lines are at zero population change.

declined in abundance, particularly among understory species, paralleling the results for individual species (Table 1). However, there was an increase in the pioneer population among canopy individuals (all stems ≥ 300 mm DBH; Table 1). Deciduous species also declined in abundance overall but increased in representation among canopy individuals (Table 1). The changes in total abundance of pioneer and deciduous species were not consistent trends: among all stems ≥ 10 mm DBH, both groups first decreased in abundance from 1982-1985, then increased, then decreased again.

The most dramatic change was a 47% decline in the total population of understory slope-specialists (Table 1). The change in slope-specialist density was consistent through time, declining with each census.

Total density in the 50-ha plot rose 3.7% between 1982 and 1990 (235 349 to 244 072 individuals), then fell 6.1% by 1995 (to 229 071). We originally thought that the 1982-1990 change was caused by stems missed in 1982 (Condit et al. 1992b), but it now appears that these are real fluctuations in density.

Discussion

There are two main sets of conclusions to draw. First, we will summarize observed changes in the BCI forest over eight years, particularly with regards to plant functional types and the observed decline in precipitation. These changes have been discussed elsewhere (Condit et al. 1992b, 1995a, 1996), so we will be brief here. Our second and more important conclusions concern the usefulness of functional types in models of tropical forest dynamics, again focusing on the impact of climatic change. This is a particularly useful dataset for defining and assessing functional types, for we have a quantitative classification of tree species along with the opportunity to observe actual climate-driven changes in functional groups.

There have not been detectable changes in the overall structure of the BCI forest: neither total stem density, wood volume (Condit et al. 1995b), proportion of deciduous species, nor proportion of understory species have changed by any appreciable amount over 13 years. Pioneers have declined somewhat in total density, but

Table 1. Changes in the total population of functional groups. Pioneer species are those species with a score on the first PCA axis > 1; slope species are those with a moisture index ≥ 97.5 . Indented groups (preceded by -) refer to subgroups of the prior, non-indented group. Most figures are the percentage of the total number of individuals of all 314 species in 50 ha: 235 349 in 1982 and 229 071 in 1995; or when indicated, of individuals ≥ 300 mm in DBH: 4267 in 1982 and 4135 in 1995. For pioneer species, though, the percentage is of the total number of individuals for the 142 species included in the demographic analysis: 224 827 in 1982 and 220 599 in 1995; or for individuals ≥ 300 mm DBH: 3281 in 1982 and 3129 in 1995. Note that when numbers are given for 'canopy species', this refers to all individuals of species which grow to the canopy, including saplings (and likewise for understory species), but when numbers are given for DBH ≥ 300 mm, it includes only individuals above that size. The percent change is the 1995 percent minus the 1982 percent, divided by the latter, times 100.

Species group	% of 1982 total	% of 1995 total	% change
Canopy species	44.6	45.4	+ 1.8
Understory species	55.4	54.6	- 1.5
Deciduous species	2.8	2.7	- 6.3
Deciduous ≥ 300 mm	18.3	18.7	+ 2.7
Pioneer species	4.7	4.2	- 9.6
- canopy species	2.9	2.8	- 4.7
- understory species	1.7	1.4	- 17.9
Pioneer ≥ 300 mm	16.6	18.2	+ 9.5
Slope species	6.9	5.8	- 17.4
- canopy species	5.5	4.9	- 9.9
- understory species	1.4	0.7	- 46.9

this change has not been consistent through time. The only sharp change in abundance was the decline of the moisture-dependent guild. This guild is a fairly minor component of the forest - 6.9% of stems in 1982 - but represents 24 of 314 species, or 8% of the diversity. Thus, a change in species composition is preceding any change in the overall structure of this forest.

We had predicted that deciduous species would increase in abundance during the drying trend, and that understory species would decline. These predictions were not borne out, despite the fact that drier forests in central Panama have more deciduous and fewer understory individuals (Condit et al. unpubl. data). Perhaps there has not been enough time to observe these trends, after all, forest change is likely to be slow. It is thus all the more remarkable that we detected the decline of the moisture-demanding guild.

The difficulty of observing forest change illustrates the need for predictive models, and our most important

conclusions concern functional types and how they might be used in modeling exercises. We found that a simple paradigm - the pioneer/shade-tolerant dichotomy (Swaine & Whitmore 1988; Whitmore 1989) - worked quite well to describe the demography of 142 tree species. Growth and mortality rates of saplings were strongly correlated with each other, and with the tendency to recruit into light gaps. A majority of species - the shade-tolerant ones - fell in a narrow range of demographic variables. Outside this narrow range was a wide scatter of a rather small number of species, ending with four extreme pioneers. Our data support other studies in finding that the pioneer/shade-tolerant dichotomy is really a continuum of demography (Alvarez-Buylla & Martínez-Ramos 1992; Osunkoya et al. 1994).

It is interesting and useful that leaf lifetime correlated strongly with demography. Leaf lifetime may prove to be a simple index for predicting demography (Körner 1991; Chapin 1993; Coley 1988), and it in turn may be easy to predict from physiological and morphological characteristics of leaves (King 1994). In addition, we found a tendency for high demographic scores and short leaf lifespans to associate - negatively - with the moisture-preference index. We had insufficient data to show associations between deciduousness and demography or moisture index, but the trends observed did point in the predicted direction, with deciduous species tending to be pioneers and tending to have broad drought tolerance. All of these associations, however, had a similar pattern that limits their predictive power: pioneer species had short leaf lifespans and were not moisture-demanding, however, shade-tolerant species included the whole range of variation (Table 2).

Pioneers are a simple functional group: fast-growing, light-demanding, insensitive to moisture variation, with high leaf turnover. But shade-tolerant species form

Table 2. Summary of functional and demographic associations observed in tree species in the BCI 50-ha plot. The arrow is meant as a reminder that the demographic axis reflects a continuum, summarized here by just two discrete groups.

Plant character	Demographic axis	
	Pioneer \longrightarrow	Shade-tolerant
Recruitment	mostly in gaps	everywhere
Growth, small DBH	high	low
Mortality, small DBH	high	low
Growth, large DBH	high	low
Mortality, large DBH	wide range	wide range
Leaf lifetime	short	long or short
Deciduousness	many	some
Moisture-demanding	few	some
Growth form	canopy/understory	canopy/understory

Table 3. Proposed functional types for tropical trees at Barro Colorado Island. An 'X' in a cell means that a given combination of characters exists, representing a functional type. Demographic traits were here divided into three groups, with pioneers divided into two because of their broad range of demographic scores; building phase trees would have a demographic score between 1 and 3. Slope species (moisture index ≥ 97.5) are indicated here as those tolerant of dry seasons of 3-4 months; the remaining species in the 50-ha plot are tolerant of > 4 month drought.

Demographic character	Growth form	Leaf phenology	Drought tolerance	
			long (> 4 months)	medium (3-4 months)
Extreme pioneer	Canopy tree	Deciduous	X	
Extreme pioneer	Canopy tree	Evergreen	X	
Extreme pioneer	Understory tree	Evergreen	X	
Building phase	Canopy tree	Deciduous	X	
Building phase	Canopy tree	Evergreen	X	
Building phase	Understory tree	Evergreen	X	
Shade-tolerant	Canopy tree	Deciduous	X	
Shade-tolerant	Canopy tree	Evergreen	X	X
Shade-tolerant	Understory tree	Evergreen	X	X

a more complex group: some have long-lived leaves, but others short-lived, some are moisture-demanding, others not, and some are deciduous, but most not (Table 2). Thus it appears that while the demographic data could be collapsed fairly successfully into a single axis, the structural, phenological, and moisture information axes were largely perpendicular to one another and to demography.

Table 3 presents a proposed set of functional types that capture these results. We recognize that this classification is incomplete, in that there are some important features not yet considered. For example, total fecundity, seed dispersal distances, and response to disturbances might be crucial for certain aspects of a forest model (Westoby & Leishman in press). Moreover, we should be cautious about collapsing all demographic information into one axis. Clark & Clark (1992) point out that among shade-tolerant species, the paradigm of a single demographic axis is inadequate to describe life-history differences, and there certainly was variation within the cluster of shade-tolerant species in our dataset: some species had mortality rates well below 1% per year, and others 2-3% per year. Such differences may not be trivial from the perspective of forest dynamics.

To model forests over wider areas, we would also have to consider a much broader range of climatic tolerance. Many tropical trees never experience dry seasons, and others tolerate six months of drought. Species could be assigned climatic guilds based on distributions, just like we did within the 50-ha plot, but with wider-scale information [precise modeling techniques have been developed for temperate forests (Lenihan 1993; Brzeziecki et al. 1993), but few tropical tree distributions are known well enough to apply them]. Distributional data should then be augmented with physi-

ological and morphological information (Mulkey et al. 1992; Borchert 1994) to refine classifications. Borchert (1994), for example, developed a classification of climatic guilds based on wood structure and deciduousness, which could extend our proposal. This interplay between top-down (distributional data) and bottom-up (morphological and physiological data) is the approach to climate modeling advocated by Root & Schneider (1995).

From the perspective of global models of vegetation, atmosphere, or biogeochemistry (Cramer in press), we are probably not far from a prototype model of tropical tree functional types. Augmenting the categories described in Table 3 with information on dispersal, disturbance response, and broader climate tolerances would yield 40-50 functional types, and a model describing their dynamics could be based on demographic parameters we have from the BCI plot. The model might do an adequate job predicting forest response to climate change, and would be a starting point.

There are major issues, however, which such a model would not address, particularly how community composition and diversity - at the species level - would be affected by climate. The basic functional-type model would provide a framework for a more detailed, species-specific approach, but new questions arise. How do animals and fungi affect tree dynamics (Condit et al. 1992a, b; Leigh et al. 1993; Gilbert et al. 1994)? Do individual tree species directly affect each other's demography? How important is variation in soil chemistry to tree demography, and how will climate change alter this? Models that incorporate such detail are, unfortunately, a long way off.

Acknowledgements. This paper was stimulated by the 1994 GCTE workshop held at the Potsdam Institute for Climatology, Germany, and many thanks are owed to the organizers and participants. The workshop was sponsored by the German Federal Ministry of Research and Technology (BMFT), project number 01 LK 9328/6. Research at BCI was made possible by The Smithsonian Tropical Research Institute in Panama, and we thank I. Rubinoff for his consistent support of the project, R. Pérez and S. Loo de Lao for maintaining the plot and its database, and more than 100 people from 10 countries for field work. The project has been supported by grants from the National Science Foundation, the Smithsonian Scholarly Studies Program, the Smithsonian Tropical Research Institute, the John D. and Catherine T. MacArthur Foundation, the World Wildlife Fund, the Earthwatch Center for Field Studies, the Geraldine R. Dodge Foundation, and the Alton Jones Foundation. This article is a scientific contribution from the Center for Tropical Forest Science, which is supported by the John D. and Catherine T. MacArthur Foundation.

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Received 3 February 1995;

Revision received 3 October 1995;

Final revision received 4 April 1996;

Accepted 10 April 1996.