Do current stem size distributions predict future population changes? An empirical test of intraspecific patterns in tropical trees at two spatial scales

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Abstract: It is critical to understand the responses of tropical tree species to ongoing anthropogenic disturbances. Given the longevity of large trees and the scarcity of appropriately long-term demographic data, standing size distributions are a potential tool for predicting species' responses to disturbances and resultant changes in population structure. Here we test the utility of several different measures of size distribution for predicting subsequent population changes at the intraspecific level using demographic records from two subsampled 50-ha tree plots in Malaysia (Pasoh and Lambir). Most measures of size distribution failed to successfully predict population change better than random; however, the 'coefficient of skewness' (a measure of the relative proportion of small vs. large stems in a population) was able to correctly predict the direction of population change for approximately three-quarters of species at both sites. At Pasoh, the magnitude of this relationship decreased with adult stature and rate of turnover, but was unrelated to sapling growth rates at either site. Finally, using data for species common at both forests, we found that size distributions were generally uninformative of subsequent differences in population change between sites (only median dbh correctly predicted the direction of change for more species than random). Based on these results we conclude that some measures of intraspecific differences in size distribution are potentially informative of population trends within forests but have limited utility across broader spatial scales.

Key Words: coefficient of skewness, forest dynamics, Malaysia, population dynamics, Weibull distribution

INTRODUCTION

Tropical forests face an increasing onslaught of human disturbances at both global and local scales due to climate change, increasing atmospheric CO_2, habitat fragmentation and hunting, as well as the associated losses of seed predators/dispersers and herbivores (Lewis *et al.* 2004a, Wright 2005). All of these disturbances are predicted to disproportionately affect certain tree species within forests (Laurance *et al.* 2002, 2004a, 2006; Phillips *et al.* 2002, 2004; Terborgh 1992) which in turn may ameliorate or exacerbate the magnitude of disturbance (Bunker *et al.* 2005, Laurance *et al.* 2006). For example, fast-growing tree species may be increasing

in relative abundance throughout the tropics due to rising atmospheric CO_2 (Laurance *et al.* 2004a). Since these species have less-dense wood than slower-growing species (Alder *et al.* 2002, Muller-Landau 2004), their increased predominance may lead to a reduction in the total carbon storage capacity of tropical forests.

Unfortunately, investigating the response of tropical tree populations to disturbance has proven extremely difficult due to their longevity (Chambers *et al.* 1998, Laurance *et al.* 2004b) and the paucity of correspondingly long-term mortality, recruitment and growth rate data (Condit *et al.* 1998). In order to circumvent the lack of adequate demographic data, some studies rely on the assumption that current size distributions predict future population changes such that species/populations with many immature stems in relation to larger stems are believed to be self-replacing or increasing, while

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Table 1 Location and general characteristics of the study plots. A dry month is defined as having < 100 mm of rain.

Site	Location (latitude, longitude)	Mean annual percipitation (mm)	Number of dry months	Number of species	Number of species per ha	Census years
Pasoh	2°58′N, 102°18′E	1788	0-1 (January)	817	495	1986, 1990, 1995, 2001
Lambir	4°10′N, 114°01′E	2664	0	1180	1180	1991, 1997, 2002

species/populations with relatively few small stems are believed to be declining in abundance (Baker *et al.* 2005, Bunyavejchewin *et al.* 2003, Foster *et al.* 1996, Franklin *et al.* 1993, Hart *et al.* 1989, Knowles & Grant 1983, Lorimer 1980, Read *et al.* 1995).

The one study to directly test this hypothesis in tropical forests compared population changes of species with relatively high numbers of saplings to species with relatively few saplings within a single plot; no significant relationship between size distribution and population change was found (Condit *et al.* 1998). This lack of relationship is not surprising given the large inter-specific variations in life history strategies of the species included. Even at equilibrium, fast-growing species or species that rely on episodic disturbances for recruitment are expected to have very different size distributions than slower-growing, advanced-recruitment species (Muller-Landau *et al.* 2006, Niklas *et al.* 2003, Wright *et al.* 2003).

In many studies the question of interest is not at the species level, but rather at the population level (i.e. is species *x* declining at sites with high levels of disturbance relative to less-disturbed sites?). Since differences in life history are not a concern, it is perhaps more reasonable to expect a relationship between size distribution and population change at the intraspecific level. However, this hypothesis remains untested.

Here we test the relationship between several different indices describing standing stem size distributions and subsequent population changes for tropical trees using long-term records of tree demography from two 50-ha forest plots in Pasoh and Lambir, Malaysia (Lee *et al.* 2004, Manokaran *et al.* 2004). Using individual hectares within these plots as the sampling units, we test intraspecific patterns at the local scale. Furthermore, we investigate if the strength of the size-distribution/population-change relationship is associated with differences in several species traits which serve as proxies for life history and reproductive strategies; including adult stature, sapling growth rate, and rate of turnover (Muller-Landau 2004, Wright *et al.* 2003). Finally, using data for 100 species occurring at sufficient densities within both forests, we also test if intraspecific differences in standing size distributions predict subsequent population changes across a larger spatial scale for disparate populations experiencing different local disturbance regimes.

METHODS

Study sites

This study was conducted using long-term tree census data from the Pasoh and Lambir 50-ha Forest Dynamic Plots located in the Malaysian states of Negeri Sembilan and Sarawak, respectively. At each site, all trees ≥ 1 cm in dbh were identified to species, mapped, tagged and measured to the nearest mm approximately every 5 y. The Pasoh plot was established in 1986 and includes a total of 817 species. The Lambir plot was established in 1991 and includes 1180 species (the Lambir plot actually covers an area of 52 ha but to facilitate cross-plot comparisons only the easternmost 50 ha were used in this study). The distance between plots is approximately 1300 km. Basic geographic, climatic and diversity information are presented in Table 1. Both plots are administered in conjunction with the Center for Tropical Forest Science which ensures strict standardization of censuses.

Relationship between size distribution and population change within forests

In order to look at intraspecific patterns in size distribution and population change within Pasoh and Lambir, we divided all plot data into non-overlapping 1-ha (100 × 100 m) subplots. Analyses of local patterns within forests were restricted to tree species with an adult stature of ≥ 10 cm dbh. Adult stature was defined as the 95% quantile of the standing dbh distribution (Alder *et al.* 2002, King *et al.* 2006). Analyses were further restricted to species occurring at abundances of ≥ 25 individuals per ha in at least 10 of the subplots. It has previously been deemed that 25 individuals is an adequate number for estimating size distributions (Wright *et al.* 2003). To ensure that results were not biased by selection criteria, we repeated all analyses using a range of abundance cutoffs (≥ 10, 25, 50, 100 ind ha^{-1} in ≥ 5, 10, 25 subplots). Patterns did not differ qualitatively, so here we only report results calculated for species at ≥ 25 ind ha^{-1} in ≥ 10 subplots.

Using the initial dbh measurements from each plot, we calculated several different indices to describe the standing size distribution for each of the included species in each of the 1-ha subplots for which there were ≥ 25 individuals (most species did not occur at sufficient

densities in all subplots and thus had sample sizes < 50). Indices used to characterize size distributions included the median dbh, the ratio of large (dbh > 10 cm) to small (dbh ≤ 10 cm) stems, the coefficient of skewness (g_1), and the shape and scale parameters of the Weibull distribution (a and b, respectively).

The coefficient of skewness describes the evenness of truncated distributions (Bendel *et al.* 1989) and is defined as:

$$-g_1 = \frac{n \sum\limits_i (x_i - \bar{x})^3}{(n - 1)(n - 2)s^3}$$

where n is the number of stems and x_i, $\bar{x}$ and s are the log(dbh) of stem i, the mean of x_i, and the standard deviation of x_i, respectively. $g_1 > 0$ for size distributions with relatively few small stems and many large stems; $g_1 < 0$ for distributions with relatively few large stems and many smaller sized stems (Bendel *et al.* 1989).

The parameters a and b were calculated by fitting the Weibull probability function to the distribution of stem diameters through optimization of the log-likelihood. The Weibull probability distribution function is defined as:

$$f(x) = \frac{a}{b} \left(\frac{x}{b}\right)^{a-1} e^{-\left(\frac{x}{b}\right)^a}$$

For each subplot 'population', the rate of change in abundance (P) was calculated as:

$$P_{jk} = \frac{\log(n2_{jk}) - \log(n1_{jk})}{t_{jk}}$$

where $n1_{jk}$ and $n2_{jk}$ are the number of stems for species j in subplot k recorded in the initial and final censuses, respectively (Pasoh: 1985, 2000; Lambir:1992, 2002), and t_{jk} is the mean time (recorded in days) between censuses for species j in subplot k (Condit *et al.* 1999, Lewis *et al.* 2004b).

For each species, we calculated the relationship between initial size distribution and P as the linear least-squares regression between the standardized size distribution indices and the standardized rate of population change (P) using the 1-ha subplots as the sampling units (standardizations performed within species by centring population values on the mean and dividing the centred values by their root-mean-square). The slope of the standardized regression, M, is an indicator of the direction and magnitude of the relationship between the standing size distribution and subsequent population change such that $M < 0$ indicates a more positive population change in populations with relatively more small stems.

In order to determine if M was associated with species traits we compiled a database of adult stature,

sapling growth rate and turnover rate for each of the species analysed at Pasoh and Lambir. Adult stature was calculated as described above. Sapling growth rate was calculated as the mean exponential growth rate (log(dbh at final census)–log(dbh at initial census))/time) of stems 1–5 cm initial dbh. Turnover rate was calculated as the mean of the logarithmic annual mortality and recruitment (Condit *et al.* 1999, Phillips & Gentry 1994, Phillips *et al.* 2004). The relationships between each of these traits and M were determined through linear least-squares regression.

Relationship between size distribution and population change between forests

For the 100 species occurring at sufficiently high densities (≥ 2 individuals ha^{-1}) within both Pasoh and Lambir, we calculated all measures of size distribution and population change at the whole-plot level. For this analysis, the 1990–2001 data were used for calculations in Pasoh and the 1991–2002 data in Lambir. The direction of the relationship (M) for each species was determined and compared to the expectations of the null hypothesis (i.e. equal numbers of positive and negative M). Since there were only two pairs of values per species, data were not standardized.

In order to determine the significance of the M values as calculated across Pasoh and Lambir, we divided both plots into 6.25 ha (250×250 m) subplots. For species with ≥ 25 stems in ≥ 5 subplots at each site (n = 30 species), we then calculated M for all possible pairs of subplots drawn from each site (i.e. subplot i from Lambir vs. subplot j from Pasoh) and compared the distribution of values to the null expectation of $M = 0$.

All analyses were conducted in R 2.2.1 (http://www.R-project.org/) using custom-written functions and routines. Weibull distributions were fitted to dbh data using functions available through the R MASS package.

RESULTS

Within forest

The only index to successfully predict the direction of population change for more species than random at both Pasoh and Lambir was the coefficient of skewness (g_1). The distributions of M values based on all indices used to describe stem size distributions are presented in Table 2. Here we describe in detail the results based on the within-forest analyses using g_1.

Despite the very low overlap in the identity of species analysed, $M < 0$ for 72–73% of species at both Pasoh and Lambir (Pasoh: 43 of 58 species, Binomial test:

Table 2 Within-plot distributions of *M* (standardized regression coefficients between the size distribution and population change (*P*)) as calculated using various indices to describe stem size distributions and the binomial probability of the number of species with *M* < 0 (indicating that populations with greater proportions of small stems increased in abundance).

Index	Number of species with $M < 0$ (No. significant)	Number of species with $M > 0$ (No. significant)	Binomial P-value (one-tailed)
Pasoh			
Median dbh	36 (7)	22 (2)	0.04
Ratio of large to small stems	26 (4)	32 (6)	0.82
Skewness (g_1)	42 (4)	16 (1)	0.00
Weibull shape	35 (6)	23 (3)	0.07
Weibull scale	38 (4)	20 (1)	0.01
Lambir			
Median dbh	25 (7)	23 (6)	0.44
Ratio of large to small stems	22 (3)	26 (9)	0.76
Skewness (g_1)	35 (10)	13 (1)	0.00
Weibull shape	27 (11)	21 (1)	0.24
Weibull scale	30 (3)	18 (2)	0.06

$P < 0.0005$; Lambir 35 of 48 species, Binomial test: $P = 0.001$) indicating that at both sites, right-skewed populations (i.e. with many saplings relative to adults; low g_1) tended to have more positive rates of population change than populations with relatively few saplings (Figure 1).

The mean *M* of all species analysed within Pasoh was −0.068. This is significantly less than zero (95% CI = 0.032–0.104; CIs based on 10 000 bootstrapped resamples). However, when analysed individually through least-squares regression, the relationship was statistically significant for only a few species at the $P = 0.05$ cutoff (4 species (6.8%) significant according to one-tailed tests). Likewise, at Lambir, *M* averaged −0.111 (95% CI = 0.54–0.172) but for only 10 species (20.8%) was the relationship significantly different from zero.

At Pasoh, there was a significant positive relationship between *M* and adult stature ($F_{1,56} = 6.88$, $R = 0.034$, $P < 0.01$) such that for larger species, standing size distribution was less predictive of subsequent population change (Table 3). There was also a positive relationship between *M* and annual turnover ($F_{1,56} = 6.01$, $R = 0.32$, $P < 0.05$). There was no significant relationship between *M* and sapling growth rates ($F_{1,56} = 2.42$, $P = 0.11$). At Lambir, the magnitude of *M* was not related to any of the species traits included (adult stature: $F_{1,46} < 0.01$, $P = 0.97$; turnover: $F_{1,46} = 0.71$, $P = 0.40$; sapling growth rate: $F_{1,46} = 2.21$, $P = 0.14$; Table 3).

Between forests

In the cross-plot comparison, the only measure of stem size distribution to correctly predict the direction of population changes for more species than random was the median dbh (Table 4). The relationship between median dbh and *P* was negative (i.e. *M* < 0) for 63% of species co-occurring in Pasoh and Lambir (Binomial test: P = 0.006). However, for no size distribution index was the mean of *M* significantly distinguishable from zero (significance

Table 3 Correlation coefficients between species traits and *M* (standardized regression coefficients between the size distribution and population change (*P*)) as calculated for various indices describing stem size distributions.

Index	Correlation coefficient (two-tailed P-value)		
	Sapling growth rate	Adult stature	Turnover
Pasoh			
Median dbh	0.09 (0.49)	0.21 (0.12)	0.09 (0.49)
Ratio of large to small stems	0.44 (0.00)	0.23 (0.08)	0.41 (0.00)
Skewness (g_1)	0.21 (0.11)	0.34 (0.01)	0.32 (0.02)
Weibull shape	−0.07 (0.60)	0.08 (0.53)	0.02 (0.90)
Weibull scale	0.25 (0.05)	0.26 (0.05)	0.24 (0.07)
Lambir			
Median dbh	0.02 (0.89)	−0.15 (0.31)	0.26 (0.08)
Ratio of large to small stems	0.10 (0.48)	−0.26 (0.08)	0.28 (0.05)
Skewness (g_1)	0.21 (0.14)	0.01 (0.97)	0.12 (0.40)
Weibull shape	0.00 (0.99)	0.03 (0.83)	0.08 (0.60)
Weibull scale	0.18 (0.21)	0.01 (0.95)	0.09 (0.56)
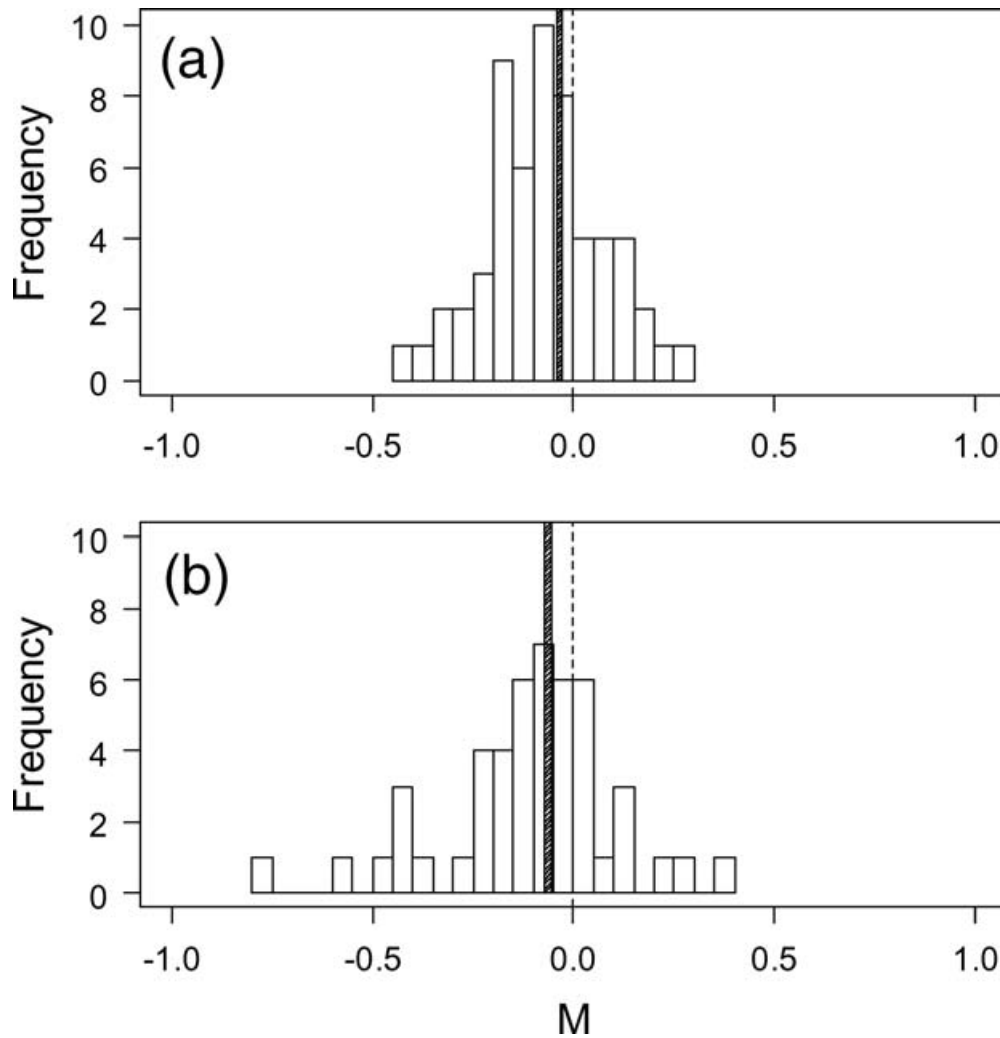
Figure 1 The distribution of M (standardized regression coefficients between the size distribution (g_1) and population change (P)) calculated using 1-ha subsample plots within Pasoh (a) and Lambir (b). Negative values indicate that populations with many small stems had more positive changes in abundance than populations with relatively few small stems. The dashed vertical lines indicate 0; the shaded boxes indicate the 95% confidence intervals around the means as determined through bootstrapping (Pasoh: mean $M = 0.068$, 95% CI = 0.032–0.104, Lambir: mean $M = 0.111$, 95% CI = 0.54–0.172).

based on 10 000 bootstrapped resamples). Additionally, for 30 species analysed individually through subplot comparisons, M was only statistically distinct from null in two cases (1%; Table 4).

DISCUSSION

In order to understand the effects of human disturbances on forested ecosystems, it is imperative that we be able

Table 4 Between-forest distributions of M (regression coefficients between the size distribution and population change (P)) as calculated using various indices to describe stem size distributions and the number of species (out of 30 tested) with M values significantly different from zero.

Index	Number of species with $M < 0$	Number of species with $M > 0$	Binomial P-value (one-tailed)	Number of species with significant M
Median dbh	63	37	0.01	0
Ratio of large to small stems	50	50	0.54	0
Skewness (g_1)	56	44	0.14	1
Weibull shape	54	46	0.24	1
Weibull scale	55	45	0.18	0

to predict how these disturbances will affect individual species (Bunker *et al.* 2005). This is of added importance since these species-specific responses may in turn feed back to affect the magnitude of the original disturbance (as in the case of rising CO_2) and/or result in further disturbances of an entirely different nature (such as increased treefalls and gap creation following droughts). Since most large trees are prohibitively long-lived, studies have often relied on the assumption that standing size distributions reflect future population changes. However, there are many reasons why differences in the abundance of small stems may not actually result in long-term population changes. For example, due to strong density-dependent mortality, populations with many small stems may not produce any more reproductive adults than populations with few small stems. Likewise, in species with pulsed recruitment, either due to masting or reliance on temporally patchy resources (i.e. gaps), the density of small stems may fluctuate greatly through time and will not be accurately represented by any single census (Wright *et al.* 2003).

In this study, we analysed the utility of several different indices characterizing standing size distributions for predicting subsequent population changes within and between two different lowland tropical rain forests. The only index to successfully predict the direction of population change within both forests more often than random was the coefficient of skewness (g_1). Using g_1, approximately three-quarters of species analysed within each forest had $M < 0$, indicating that at the local scale this measure of stem size distribution was in fact reflective of population changes over the subsequent 10–15 y such that populations with relatively large numbers of saplings (low g_1) tended to increase in abundance while those with fewer saplings tended to either decrease or increase more slowly than other populations. However, for most individual species the relationship between g_1 and population change was not statistically distinguishable from zero. It is probable that this lack of significance can be attributed at least in part to the 'short' duration of the study. While this is a comparatively long-term study of forest dynamics (especially for tropical forests), one to two decades may simply not be a long enough period for differences in sapling abundances to result in significant changes in the population-level dynamics of long-lived species. If this study were continued over a longer period, we expect that the magnitude of population changes and the significance of M would increase.

Assuming that larger trees take longer to reach maturity than do smaller trees, the short duration of the study may also help explain why M (as based on g_1) increased with adult stature at Pasoh. In contrast, the duration of the study cannot explain the positive relationship between M and turnover. One possible explanation for this relationship is that species with rapid turnover may have highly ephemeral sapling abundances that are not well captured by standard censuses (Wright *et al.* 2003).

When calculated by comparing populations at Pasoh with those at Lambir, the only measure of size distribution to predict differences in population change for more species than random was the median dbh. Within 63% of shared species, the population with the lower median dbh (i.e. relatively more small stems) tended to increase in abundance more rapidly than at the other site (in 72% of shared species, abundances increased more rapidly at Lambir than at Pasoh over the 10-y interval). However, the strengths of the relationships were all relatively weak such that the mean M never differed from the null expectation regardless of the measure of size distribution.

CONCLUSIONS

Based on the results of this study, we conclude that within forests, intraspecific differences in sapling abundances as characterized by the coefficient of skewness are a potentially useful tool for predicting future trends in population change. In contrast, other measures of size distribution failed to correctly predict directions of change better than random. Even using g_1, the relationship between stem size distribution and subsequent population change was not statistically significant except for a very small number of species and thus is inadequate to predict actual rates of change. For large canopy trees, such as the ones included in this study, many decades may be required before effects at the sapling stage propagate through larger size classes to eventually result in overall changes in population dynamics, and thus the relatively weak association between size distributions and population change, especially in the larger species, is not surprising. In addition, there are many factors that may uncouple relative sapling abundances and rates of population change including the action of density-dependent forces, pulsed recruitment, and/or stochastic events such as droughts, windstorms, fires etc. (Coomes *et al.* 2003). When comparing disparate populations, the role of these factors will become increasing important as populations respond to independent local disturbance/climatic events. As a result, size distributions had only a very weak association with rates of population change when analysed across a broad spatial scale. Therefore, while size distributions may be informative of population trends at the local scale, we recommend against their use for investigating patterns across broader spatial scales, such as the effects of global change on population dynamics (Wright 2005).

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