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Increasing Turnover through Time in Tropical Forests

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Tree turnover rates were assessed at 40 tropical forest sites. Averaged across inventoried forests, turnover, as measured by tree mortality and recruitment, has increased since the 1950's, with an apparent pantropical acceleration since 1980. Among 22 mature forest sites with two or more inventory periods, forest turnover also increased. The trend in forest dynamics may have profound effects on biological diversity.

Since the mid 20th-century, a substantial body of data has been gathered on rates of tree mortality and recruitment ("turnover") in humid tropical forests. Turnover rates in mature tropical forests correlate with estimates of net productivity, as gauged by rates of basal area increment and mortality ([i], [ii], [iii]). Humid tropical forests are highly productive ([iv], [v]), so proportional increases should be easier to detect than in temperate systems. Tropical forest study-sites are also relatively secure from certain forms of anthropogenic atmospheric change such as acid precipitation ([vi]), and their diversity buffers them against pathogen epidemics that can afflict temperate forests ([vii]). Also, tropical forest inventory plots typically have no history of clear-felling or extractive logging; few temperate forests are old-growth. Therefore, tropical forest turnover data may provide a novel test of the hypothesis that global forest productivity is increasing ([viii]).

We compiled data on rates of tree turnover in tropical forests using logarithmic models to estimate annual mortality and recruitment rates (2). The evidence for directional change through time in tropical forest dynamics was evaluated by two methods. First, we used all forest dynamics data with $\geq$4 yrs of continuous measurement (mean 13.3; median 11.0; range 4-38 yrs) and an area of $\geq$0.2 ha (mean 2.7; median 1.2; range 0.2-23.5 ha) (Table 1 ([ix])). Only forests known to have suffered mass-mortality by deforestation, cyclones, drought, or flooding were excluded. The first long-term inventory that satisfied the criteria began in 1934, and measurements from the last were made as recently as 1993. The time between successive inventories of each plot was always >1 year; therefore, within each monitoring period we allocated the period's annualized turnover rate to each of the years included in the monitoring period. Using these estimates, we then compared turnover rates across all mature tropical forests through time, and then separately for neotropical and paleotropical forests. Then, individual sites that have two or more successive inventory periods were used to test for temporal change within individual forests.

There has been a significant upward trend in average measured rates of turnover of

tropical forest trees $\geq$10 cm diameter since at least 1960 ([x]). One possible confounding factor is the tendency for early sites to be mostly paleotropical, and for recent sites to be mostly neotropical. Within our data set, neotropical sites are more dynamic than paleotropical ones ([xi]). Yet, when graphed separately both neotropical and paleotropical data sets continue to show significant increases in turnover through time, with marked accelerations in turnover in the 1980's (Fig. 1) ([xii]). Although highly suggestive, this does not prove that turnover rates have increased since unequal sampling of forest types across time could skew the results.

Mature forests inventoried for two or more successive periods (equal to at least three successive inventories) provide a more rigorous test of the hypothesis that tropical forests have become more dynamic since they permit analysis of change *within* sites (Table 2). They have also been followed for longer (mean 17.0; median 15.0; range 6.25-38 yrs; n = 22). Three candidate sites were excluded from statistical analyses - two that may have been affected by drought or other severe conditions prior to establishment (BA, Q5), and one that was heavily affected by drought during the inventory period (BC) ([xiii]). The remaining 19 sites are well-distributed geographically (eight neotropical, eight South-East Asian, two Australian, one African), were established as early as 1947 and reinventoried as recently as 1993, and span most of the range of the climatic and substrate variation within the humid tropical forest biome.

We scored sites by whether annual averaged mortality and recruitment rates were higher or lower during the second inventory period than during the first. When investigators reported three or more inventory periods, we combined results from successive periods to create just two periods with as similar length as possible. Overall, forests experienced significantly more turnover during the second inventory period than during the first ([xiv]). Of the 19 sites, turnover increased in 14 and decreased in five; the magnitude of change in four of the decreasing sites was very small. New inventory data for large lianas and stranglers hint of a recent trend in tropical forest structure and a possible mechanism to explain the

increase in turnover: in five out of six forests liana and strangler density has increased since 1983 (Table 3, [xv]); lianas are known to contribute to host tree mortality ([xvi]).

Humid tropical forest plots have clearly become more dynamic, suggesting a world-wide causative factor. Below, we briefly explore some candidates, related to inventory methodology and environmental change. This exploration is preliminary and speculative, but the strong signal justifies some discussion.

One methodological cause of the trend might be adverse effects on tree survival from tree tagging and collecting and soil compaction. We would expect similar time periods to elapse before any such effects were manifested; therefore, given the wide range in plot start dates, the monotonic nature of the trend implies that this is not decisive. Some plots were deliberately located in "good looking" forest, and an unusual predominance of large trees might be expected to show increasing turnover through time. Yet, small plots explicitly chosen to avoid gaps ([xvii]) actually slowed slightly (LA, ME); and almost all sites that were sampled randomly accelerated (for example, A1-2, M1-2, SC).

Environmental change is a more likely cause. Candidates include progressively more extreme weather (e.g., drought, strong wind, temperature changes), adjacent deforestation altering local environmental conditions, and elevated productivity as a result of increased atmospheric CO_2. Although detailed site-by-site meteorological data needed to test for weather effects on turnover are unavailable, current trends in deforestation and atmospheric change may lead to lower precipitation, increased seasonality, and more frequent extreme weather events in the tropics ([xviii]). Therefore the possibility exists that tropical climate change contributed to the trend, although sites with known severe weather perturbations were dropped prior to analysis. Forest microclimates are also sensitive to adjacent deforestation ([xix]), but short-term data only show direct biological consequences at <1 km ([xx]). In contrast, ≥ 5 sites with accelerating turnover are >50 km from major deforestation fronts (SC, A1-2,

M1-2). Furthermore, it is unclear if average distances between forest plots and deforestation fronts are less now than before: study sites have always combined primary forest status with accessibility. Therefore, edge-effect environmental change appears to be an unlikely cause of the turnover increase.

The accelerating increase in turnover coincides with an accelerating buildup of CO_2 ([xxi]). Increasing CO_2 concentrations may have already altered plant morphology and raised growth rates ([xxii]), but ecosystem effects are hard to predict. Experiments on the effects of controlled environmental change at cellular, physiological, and whole plant levels cannot be easily extrapolated to higher level phenomena like forest dynamics ([xxiii]). For example, any effect on tree turnover of rising atmospheric [CO_2] could result as much from stimulated liana growth as tree growth. Thus, vines show greatly enhanced growth with elevated [CO_2] ([xxiv]), and are highly productive ([xxv]) "structural parasites" ([xxvi]) known to affect tree-fall rates (16, [xxvii]); most tropical forests have a high liana density ([xxviii]).

Whichever factor is most critical, the evidence suggests that even "intact" tropical forest has been affected by recent climatic and atmospheric changes. The trend to accelerated turnover has implications for global change, with likely effects on tropical biodiversity and possible unexpected links between the global carbon cycle and tropical forests. If forest turnover rates continue to increase, primary forests may become more characterized by climbing plants and gap-dependent tree species, best positioned to benefit from increased disturbance and atmospheric CO_2. Accelerating dynamics in western Amazonia (A1-2, M1-2, SC, T1, YA) imply that even the largest areas of tropical forest could become inadequate to conserve samples of the biome without rapid progress on reducing carbon emissions. While faster turnover may create a more heterogeneous forest environment, and hence enhance species richness at local scales, large-scale biodiversity levels could decline. Eventually, extinctions are possible among the slowest growing shade tolerant tree species, and among tropical forest organisms with life-cycles tied to these trees. Lianas and fast

growing trees have less dense wood than shade tolerant species ([xxix]). Therefore, if populations of gap-dependent species increase, primary tropical forests may increasingly become a net carbon source, rather than a sink as assumed in most recent global circulation models ([xxx]). Such a process would constitute an unexpected synergism between CO_2 emissions from industrialized and tropical countries ([xxxi]).

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x.. This is confirmed by a $\underline{t}$-test comparison of estimated 1990 turnover rates versus estimated 1960 turnover rates ($\underline{t}$ = 3.87, d.f. = 19, $\underline{P}$ <0.001 (one-tailed test)).

xi.. $\underline{t}$ = 1.96, d.f. = 36, $\underline{P}$ = 0.059, two-tailed test.

xii.. Within-hemisphere t-test comparisons of estimated annual turnover confirm that forest plots in both hemispheres have become more dynamic (paleotropical: $\underline{t}$ = 2.69, 1985 versus 1960, d.f. = 13, $\underline{P}$ = 0.009 (one-tailed test); neotropical: $\underline{t}$ = 2.64, 1990 versus 1975, d.f. = 17, $\underline{P}$ = 0.008 (one-tailed test)).

xiii.. This procedure was conservative: forest turnover at all three sites accelerated, especially at BC and BA (Table 2).

xiv.. Wilcoxon matched-pair signed-rank test, $\underline{z}$ = 2.31, d.f. = 18, $\underline{P}$ = 0.010 (one-tailed test). At the only site with a marked decrease in turnover (S1) it appears likely that recruitment in the final inventory period was incompletely recorded. If this site is discounted, $\underline{z}$ = 2.87, d.f. = 17, $\underline{P}$ = 0.004 (one-tailed test). If sites last recorded before 1980 are discounted, $\underline{z}$ = 2.52, d.f. = 16, $\underline{P}$ = 0.006 (one-tailed test).

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