

Evaluating Turnover in Tropical Forests

O. L. Phillips and A. H. Gentry report an increased rate of forest turnover throughout the tropics (1). However, a significant statistical problem arises from the use of standard methods to estimate turnover, as these estimates can be affected by the length of the census interval. Such analysis can also be confounded by short-term climatic events and other factors.

In their first analysis, Phillips and Gentry (1) combine estimates of turnover from different permanent plot studies and show that higher values correlate to more recent periods of observation. From the data summary in the report [table 1 in (1)], it appears that older data are generally derived from long-term studies, while more recent data come from studies that tend to be of short duration. For heterogeneous populations it can be shown theoretically that count-derived mortality and recruitment rates estimated

over short periods will be higher on average than those derived over longer census intervals. The magnitude of this effect depends on the size and life expectancies of the subpopulations (2) and can be acute when one fraction of the population has a much higher mortality than the rest. This phenomenon may explain some previously published observations (3). A long-term data series from Budongo Forest, Uganda (4), suggests that this effect is marked even within a relatively uniform population of large timber trees (Fig. 1). Thus, an apparent increase in forest turnover may be a result, at least in part, of a decrease in periods of time between census measurements.

In their second analysis Phillips and Gentry use data from permanent plots measured over successive periods and demonstrate that turnover rates are generally increasing [table 2 in (1)]. Usable data are rare, mostly short term, and of recent origin. Turnover rates are vulnerable to diverse environmental factors and are liable to fluctuate. The increase in turnover (1) shown by the selected neotropical data (mean rising from 1.7 to 2.65% per year, $n = 8$, all data showing an increase) indicates a causal "event." The severe El Niño during 1982–83 had a major impact in the neotropics and globally (5), and many anomalous meteorological events occurred (6). The impact on forests was not restricted to the increased mortality specifically identified at Barro Colorado Island, Panama (7). The high turnover observations cover the 1982–83 period and its aftermath, as do all the neotropical data covered in the report. Five of the 11 paleotropical studies discussed in the report show a decreasing turnover rate, even though the El Niño had a severe impact on many Asian forests (8). In those few observations not spanning the El Niño period, the mean turnover value decreases (1.32 to 1.19% per year, $n = 3$). An "El Niño event" hypothesis suggests that we should observe a period of increased stem mortality, and subsequently of recruitment, to occur in 1982 and 1983 and its aftermath, and that these variations are related to the death, or die-back (that is, reduced vigor), of less drought-tolerant stems.

Phillips and Gentry's study is unquestionably important and has implications for policy-makers, but their observations remain open to alternative interpretations. Difficulties in assessing turnover are compounded by other biases such as those they have acknowledged (1). Biases in site selection, inconsistent definitions of the populations being measured, and the impact of research activity itself are each problematic

and their potential implications remain unclear, but these difficulties should be addressed. Techniques for calculating and comparing turnover values can be improved to reduce likely artifacts. More robust methods should be sought to assess global changes in forest turnover and metabolism.

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24 October 1994; revised 6 February 1995; accepted 8 March 1995

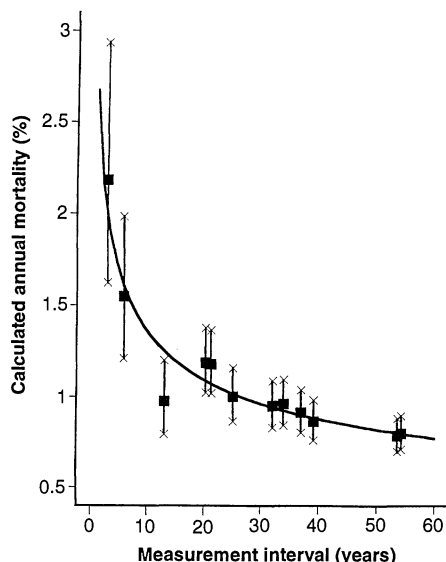
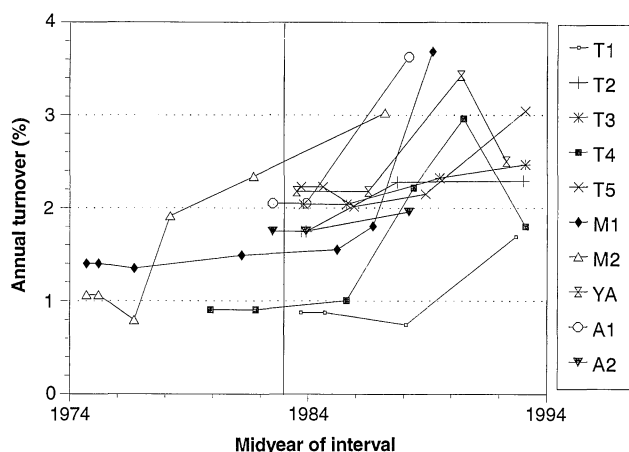


Fig. 1. Calculated mortality rate (%) against measurement interval for a population of trees from Budongo Forest, Uganda (plot 7, see 4). Stems were defined in 1939 as belonging to selected "timber" species having stem sizes greater than 25 cm diameter at reference height ($n = 125$ in 1939 and 81 in 1993). In this analysis only survivors from 1939 are included. Total time elapsed and total number of stems lost are used in the calculation of mortality (m) according to a cumulative model: $m\%/100 = 1 - (N_t/N_0)^{1/\Delta t}$ where $m\%$ is percent annual mortality; N_0 and N_t are population counts at first and later evaluations, respectively; and Δt is census interval. Error bars represent 75% confidence limits according to the F distribution (autocorrelation between observations were not considered). A power relation was fitted by multiplicative regression and provides a model of the relationship: $m\% = 1.11 \Delta t^{-0.33}$, $R^2 = 90.36\%$.

Response: Sheil raises the possibility that a change in sampling frequency might affect the rate of tree turnover in tropical forests calculated. The hypothesized artifact may well have implications for turnover studies, but it is difficult to gauge from the cited data how substantial it will be. No two tropical forests are alike, so it is not correct to extrapolate results from a single plot to the rest of the tropics. Moreover, the Budongo dataset cited by Sheil is extremely small and therefore highly influenced by chance events. The initial population is smaller than are those of each of the 40 sites we analyzed (1) and the mean number of tree deaths per year is typically much less than one. Assembling data from enough large population multi-inventory monitoring sites to test for the hypothesized effect would be a challenge. In any event, it seems unlikely that an artifact in calculating turnover rates could affect our conclusion that "there has been a significant upward trend in ... turnover of tropical forest trees" (1, p. 954). The mean length of individual

Fig. 1. Turnover rates in West Amazon forests 1974–94. All known monitored mature forests in west Amazonia with ≥ 2 measurement intervals are plotted. Turnover rate in a particular interval is plotted at the mid-point of the interval; however, the turnover rate in the first interval is also plotted at the start date to show the timespan of the first interval relative to the 1982–83 El Niño. Vertical line corresponds to 1 January 1983. The slope of all ± 10 is positive. For details of the sites (denoted in the key) and sampling protocols see table 1 in (7).



measurement intervals is not tightly correlated with the mid-year of our sites (2): Censuses were not performed at younger sites more frequently than at older sites. More critically, we find no relationship between a site's overall turnover rate and the mean length of the measurement intervals, between inventories, over which that turnover was calculated (3). More frequently sampled sites did not have higher turnover values.

Sheil suggests that the 1982–83 El Niño event could be responsible for the observed increase in turnover. But the data we presented in our report do not seem to support this. Better time-resolved data than were available at the time of our study indicate no surge in mortality rates during inventory intervals spanning the event.

We pointed out in our report that the meteorological data needed to test for weather effects on turnover are largely unavailable, but other than the Barro Colorado Island site (omitted a priori from our analysis) we know of no reports of drought-induced mortality in the early 1980s suggesting that most monitored forests were not seriously affected. Moreover, on balance, table 2 in our report does not shed much light on whether El Niño events affected the results of our second analysis. For example,

the few multi-interval studies initiated at about the time of the 1982–83 El Niño event [A1, A2, YA] had greater turnover rates 5 to 10 years after the event than during or immediately after it. Better time-resolved data from Peru has now raised the number of these forests to seven (Fig. 1) (4). Of the three west Amazonian forests monitored since the 1970s, two (M1 and T4) did not experience appreciably increased turnover until 3 to 5 years later, and the other (M2) experienced increased turnover 5 years before the El Niño. The peak mortality interval varied from site-to-site and did not coincide with the El Niño at any of the 10 sites (1, 4, 5). These data show the value of regular recensusing and demonstrate, so far at least, that the event has had no discernible impact on tree turnover in west Amazonia, the most densely sampled region.

In general, I have greater confidence that work by different ecologists is broadly comparable. For example, 34 of the 40 sites we analyzed considered all trees with diameter ≥ 10 cm, and most investigators published raw data and nuances of their protocols, or have made these available. Moreover, as Sheil indicates, it is not clear what any effect of the biases he suggests might be (had we discovered “decreasing turnover” several plausible artifact explanations could

be invoked). By illustration, research and collection activities are often concentrated when the plot is being set up, with subsequent activity often limited only to occasional recensuses. Over a 5-, 10-, 20-, or 30-year period would this activity tend to enhance early mortality (and recruitment?) rates, late mortality (and recruitment?) rates, both, or neither?

I agree that the dataset is not flawless. Improvements in the baseline data and further analysis will help us to interpret spatial and temporal patterns of tree turnover and its impact on plants and animals. However, the existing data do not support the suggestions that the trend to increasing turnover is an artifact either of changing measurement intervals or of one extreme climatic event. The improvements in the database since we submitted our report further confirm the conclusion that turnover rates have increased.

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6. I thank S. Pimm for comments and J. Terborgh and T. Erwin for permission to use their unpublished data. Additional unpublished results from Peru were recorded in 1984–85 by A. Gentry, C. Diaz, and R. Vásquez and in September 1994 by a team from Missouri Botanical Garden (Proyecto Flora del Perú), Biodiversidad Amazonica, Universidad Nacional San Antonio Abad del Cusco, Harvard University, and Leeds University. The American Philosophical Society, Peruvian Safaris S.A., Leeds University, the Pew Charitable Trust, the Winslow, MacArthur, Mellon, Geraldine R. Dodge, and Wallace Genetic Foundations all gave financial support.

16 November 1994; accepted 8 March 1995