Tropical Diversity and Global Change

Stuart L. Pimm and Andrew M. Sugden

Two of the scientific challenges with far-reaching consequences that face society today are the rapid loss of Earth's biological diversity and the recent changes in global atmosphere and climate. We hardly understand the effects of the atmospheric changes. Complex feedback makes linking the well-documented changes in chemistry—increasing atmospheric CO_2—to the physics—global warming—difficult enough (*1*). But linking either to the biology of diversity is an even greater challenge (*2*). No two plant species (out of a possible ~5×10^5) need respond the same way to laboratory-controlled increases in temperature and CO_2, and mixtures of plants respond differently still (*3*). Laboratory studies must eventually be extended to the field, but examination of vegetation on a global scale requires global surveys, and detecting change requires long-term global surveys. On page 954 in this issue of *Science*, Phillips and Gentry surmount the obvious practical difficulties of this approach (*4*). They compile many independent surveys of tropical forests and find that they are changing more rapidly now than in the past. The extent of the changes implicates global processes. Their existence in species-rich forests predicts associated changes in biological diversity. Phillips and Gentry move us considerably nearer to understanding the suspected links between global change and the loss of diversity (*5*).

Phillips and Gentry have discovered a worldwide increase in forest turnover, a measure of the recruitment of individuals into, and the death of individuals from, an area. Turnover measures how fast individuals are moving through the population, not just how fast they die. (The total number of individuals may remain more or less constant, even though the turnover increases.) Trees are not counted until they are sufficiently large—in this case, until their bole diameters are 10 cm or greater. Ideally, the turnover would be determined in many suitably selected areas at fixed, regular intervals for long periods. But tropical surveys rarely have the funds to continue for decades, and such surveys are rare in old-growth temperate forests. Because surveys are established for various reasons, trees are actually counted at very different intervals. But who can fault the originators of these surveys for design problems, apparent only decades later, when we try to put the survey to a use for which it was not designed?

Phillips and Gentry tackle the problem of the varying intervals between species counts in much the same way that one compares financial interest rates. The nervous investor frequently inspecting his account finds it recruited new money at 5.7% per quarter, while his more relaxed colleague finds her account grew 303% in 5 years. Both accounts grow at the same rate, of course—25% per year. Phillips and Gentry report turnovers as annualized rates and interpolate these rates to 5-year intervals. Their figure shows that these rates increased, particularly over the last 25 years.

Their composite value for turnover does not reveal that the particular sites contributing to that value change from one time period to the next. Given a large enough random sample, this site switching would not matter. With a small sample, however, there is always the possibility that the most recent sites are areas that even in the past would have had high turnovers. Consider the large increase in turnover from 1980 to 1985 in their New World sites. Only 6 of the 15 sites contributing to the 1985 turnover estimates are among the 8 sites contributing to the 1980 estimates. (The overlap is greater for the Old World sites—and for other intervals.) Ecological analyses suffer from a surfeit of hypotheses. No ecologist would have difficulty in proposing ad hoc explanations for why the 9 new sites in 1985 had high turnovers because of their special and local conditions.

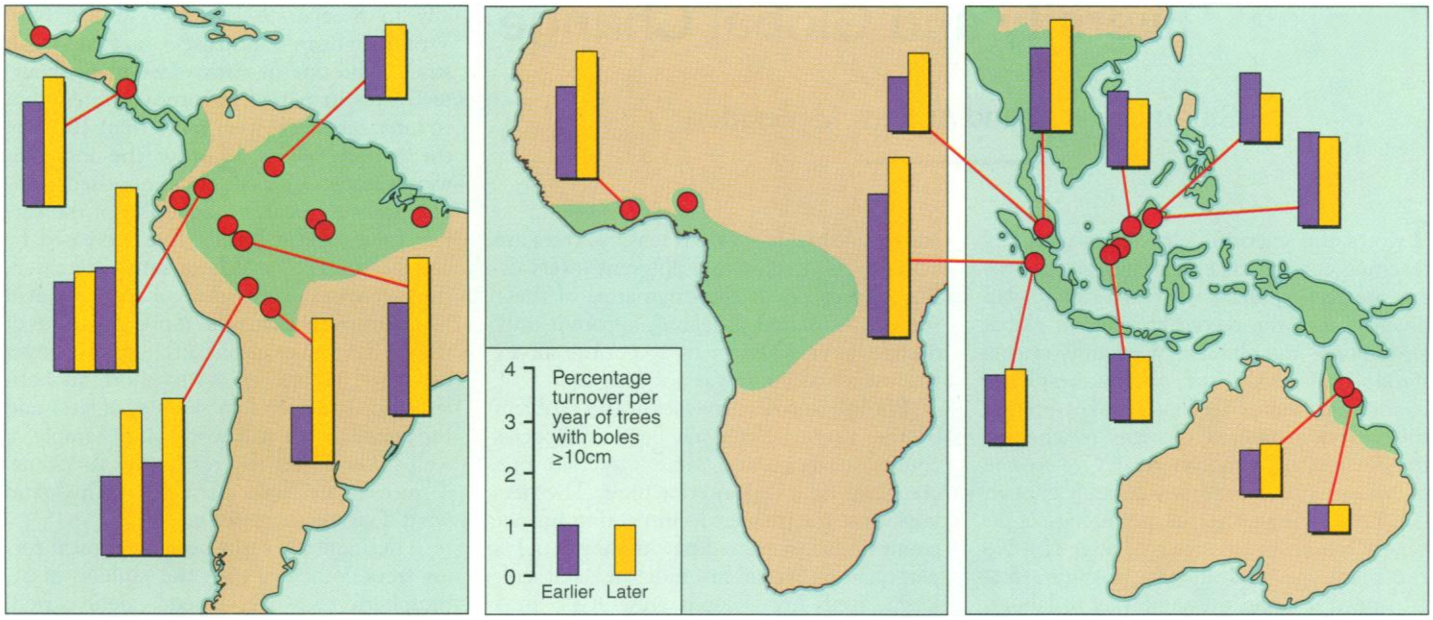
To eliminate such local explanations (and so increase the plausibility of global ones), Phillips and Gentry examine 19 sites sampled repeatedly across two different periods. (This requires three successive inventories.) These sites are well distributed geographically in 8 separate locations in the New World, eight in Southeast Asia, two in Australia, and one in Africa (see map). Fourteen sites increased in turnover rates; that is, later turnovers were more than 100% of the earlier values. Most of the increases were substantial. Four sites increased turnover rates to greater than 150% of the earlier value, and a further five increased by more than 125%. Where rates decreased, the decreases were small. Four sites had later turnovers that were more than 97% of the earlier value; in one site, later turnover decreased to only 71%. In short, in both the large-scale random samples of sites and the smaller (but still worldwide) sample of well-studied sites the results are the same. Turnover rates have increased. Why? And what do these increases mean?

The increasing turnover of tropical forest trees coincides with the buildup of atmospheric CO_2 over an equivalent period. Phillips and Gentry are sensibly cautious about attributing cause to this correlation, for there are numerous possible confounding factors. Disturbances to the sites themselves, through the repeated trampling of the scientists working there, could be an explanation. Or the sites, when they were selected, could have been those spared locally from the normal regime of natural disturbances. Eventually these sites would be disturbed. Both of these explanations predict that increased turnover would have occurred in older established sites first, decades before the marked recent changes.

Amazonian rainforest. Increases in tree turnover here may have profound consequences for the number of species in the ecosystem.

But this is not the observed pattern. Alternatively, there could be local microclimatic changes effected by adjacent deforestation, but some of the sites are remote from this threat. Simply, it is the consistency and simultaneity of the changes on several continents that lead Phillips and Gentry to their conclusion that enhanced productivity induced by increased CO_2 is the most plau-

S. L. Pimm is in the Department of Zoology and the Graduate Program in Ecology, University of Tennessee, Knoxville, TN 37996, USA, and A. M. Sugden is the editor of *Trends in Ecology & Evolution*, Elsevier Trends Journals, 68 Hills Road, Cambridge CB2 1LA United Kingdom.



Tree turnover. Sites in which the turnover of tropical forest trees has been measured. Earlier (purple) and later (gold) turnover values are shown as percentage turnover per year of trees with boles at least 10 cm. From Table 2 in (*4*).

sible candidate for the cause of the increased turnover.

Although this is an attractively simple explanation, other global hypotheses deserve attention. Either individually or synergistically, changes in temperatures, nutrient availability, and photosynthetically active radiation, possibly mediated by changing cloud cover, could produce similar results. At most sites, local long-term data for these factors are lacking.

Recent trends need not be a consequence of contemporaneous environmental changes. Increased tree mortality over a short interval may reflect, for example, a phase of enhanced recruitment a century before. On these sites, it may take 10 to 100 years for most tree boles to reach 10 cm (*6*). Certainly, atmospheric carbon has been increasing over the last 10 to 100 years. Yet so have other global variables that might affect recruitment or mortality. Global climatic oscillations that enhance storm activity and so cause increased blowdown of canopy trees could increase mortality. Phillips and Gentry exclude sites subject to regular hurricanes and cyclones, sites where turnover rates ought to be highly variable. But new LANDSAT data from Amazonia reveal previous blowdowns across large areas of continental tropical forest beyond the hurricane belt (*7*), suggesting that we have much to learn about the large-scale, long-term effects of storms.

What are the consequences of increased turnover? Tropical forests are important stores of both carbon and biological diversity: Both will be affected. Phillips and Gentry suggest that there will be an increasing predominance of light-demanding plants and climbers and the eventual extinction of some slow-growing shade-tolerant trees. The light-demanding trees have less dense wood than the shade lovers. Thus, mature tropical forests will sequester less carbon per unit area and may ultimately act as sources, not sinks, for atmospheric carbon.

Increased turnover of individual trees need not change the number of trees per site, nor need it necessarily change the number of species. Yet a decrease in diversity over large areas is the most likely outcome. The effect of increased turnover is not likely to be a simple speeding-up of overall community and ecosystem processes, but a progressive impoverishment of tropical diversity. The loss of diversity is in those ecosystems that are among the richest—so there is more to lose.

Certainly, we present only an indirect argument linking global change and biodiversity. Ideally data are required on the turnover of species, not just individuals, in these tropical forests. Then we could test directly whether the increased turnover of individuals leads to increased turnover in species and that, in turn, to a decrease in diversity. [Increased species turnover does accompany a diversity decrease on islands (*8*).] That ideal means we must be able to identify the species—not a trivial task in tropical areas where the species are many and the taxonomists are few.

Few individuals could walk through the tropics and identify the trees like Al Gentry (or birdsongs like his colleague Ted Parker). Their deaths and those of their coworkers in a plane crash in Ecuador last year robbed ecology of unique talents. It is a testimony to Gentry's broad vision that, from the painstaking efforts of tropical ecologists and foresters over decades, we now have a better understanding of the changes in these species-rich systems. Long-term, large-scale studies of many species are the most difficult to undertake and the most difficult to fund. Phillips and Gentry show that they may be the most worthwhile.

References and Notes

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9. We thank H. A. Mooney and S. Hubbell for comments.