

## Forest turnover, diversity, and CO<sub>2</sub>

The data are thin and subject to bias. The ideas are not earthshaking; in fact, they square pretty well with some theories. Nevertheless, it attracted a lot of attention and generated a lot of argument when Phillips and colleagues published two papers on worldwide patterns in forest turnover in the tropics. In one paper<sup>1</sup>, they showed a trend for increasing rates of turnover through time, in the other<sup>2</sup>, they showed that high turnover was a predictor of high tree diversity. Recently, Sheil<sup>3</sup> and Phillips *et al.*<sup>4</sup> rekindled their earlier debate<sup>5,6</sup> with opinion articles in *Oikos*.

The theories behind the two observations are straightforward. The trend for increasing turnover is most likely due to gradually increasing CO<sub>2</sub> concentration<sup>1</sup>. Elevated CO<sub>2</sub> increases plant growth, so it is reasonable to hypothesize that overall forest growth is increasing, and if trees grow faster, recruitment and mortality rates (the metrics of turnover) would increase. The diversity correlation also fits well-known theories: high diversity tends to correlate with high productivity<sup>7</sup> or with intermediate productivity<sup>8,9</sup>; according to either, moderate increases in forest productivity could increase diversity.

Nevertheless, judging from some of the reactions I have heard over the past two years, Phillips's ideas are more heretical than Jeremy Rifkin's. Many forest ecologists have explanations for why the results are wrong: in fact, one of the co-authors of Phillips's presentation at a meeting of the Association for Tropical Biology withdrew authorship immediately beforehand due to concerns about the analyses. The criticisms have been of three general types: statistical, arguing that the data do not show the claimed trend when analyzed correctly; artefactual, claiming that the patterns are due to biases inherent in small forest plot data; and theoretical, maintaining that the suggested mechanisms do not work. Sheil<sup>3,5</sup> and Hall *et al.*<sup>10</sup> voiced some of these concerns in print. On the other hand, Pimm and Sugden<sup>11</sup> published a more favorable summary of Phillips and Gentry<sup>1</sup>.

Why did the Phillips papers generate so many negative responses? Clearly, part of it is competitive jealousy: Phillips *et al.* took a simple dataset and turned it into two papers in the most important US science journals. But another part was legitimate scientific skepticism: the data are crude, based on various plot sizes, at widely varying census intervals, from subjectively chosen sites, so it is perfectly reasonable to examine them closely. I repeated straight-

forward regressions using the data shown in the two papers<sup>1,2</sup> and found the two stated correlations. However, it is easy to raise questions. Figure 1 in Ref. 1, in particular, is a guaranteed red flag: it greatly overstates sample size by tallying each datum many times, once for each year between censuses. If the graph of turnover versus time is drawn with only one point per datum<sup>10</sup>, the increasing trend is not as striking, and there is a hint that it is manufactured from a low rate in Asia – where studies were earlier – and a high rate in Latin America. Hall *et al.*<sup>10</sup> show that the variance in mortality rates measured in small plots is high and that global trends will be very difficult to prove without much larger samples.

Nevertheless, the patterns are there when all data are combined, and they warrant theorizing. The question is, though, whether Phillips *et al.*'s theories make sense, or whether there are more mundane or artefactual explanations. Sheil has suggested several potential biases in small-plot data which could lead to erroneous correlations<sup>3,5</sup>. One is the 'majestic effect'<sup>4</sup>: ecologists put plots in exceptionally tall and unbroken canopy. These sites might initially have low turnover, but would gradually revert to a more disturbance-prone canopy and suffer increasing mortality. (Likewise, if someone repeatedly placed plots around large light gaps, mortality rates might decrease through time).

Another potential bias in long-term census data is caused by variation in census interval – the longer the interval, the lower the mortality (or recruitment) rate will appear<sup>5</sup>. This is simply because high-mortality species weed themselves out in early years, so that longer intervals are based more on longer-lived species. If recent census intervals were shorter than early ones, then a recent increase in mortality would be easily explained. Furthermore, Sheil<sup>3</sup> suggests that the diversity correlation with turnover might be an artefact of successional changes in diversity. In a graphical model, he indicates that more recently disturbed forests have much higher diversity than older forests, and also higher turnover. Thus, in a series of forest plots from various stages in this recovery gradient, the most diverse would have the highest turnover.

Phillips *et al.* countered these criticisms. They point out that Sheil's graphical model of diversity-succession is wrong, as older forests are not generally less diverse than younger<sup>4</sup>. Also, they show that there is no tendency for plots in their

dataset to lose basal area<sup>4</sup>, suggesting that the majestic effect is unimportant. I tried testing the majestic effect with data from our 50 ha plot on Barro Colorado Island, Panama: the five hectares with the most tall canopy (>20 m) in 1983 did have low mortality during 1982–1985 (76% of the plot's average), and this rose slightly by 1990–1995 (86% of average), just as Sheil predicts. Moreover, these five hectares did have excess basal area in 1982 (12.0% of the plot's), and this declined by 1995 (to 11.8%), as predicted by Phillips.

Finally, regarding the census-interval effect, Phillips *et al.* countered by showing that recent censuses do not have shorter intervals<sup>6</sup>. Moreover, the pronounced decline in turnover rate in longer intervals that Sheil illustrates at Budongo – a highly disturbed site in Uganda – would probably not be found in old-growth forests, where mortality-prone pioneer species are rare<sup>12</sup>. At Barro Colorado, annual mortality of trees >10 cm dbh (diameter at breast height) over 13 years was 2.26%, while in the 3–5 year intervals within the longer interval, it was 2.21% (mean of 3 intervals).

A final class of arguments about Phillips *et al.*'s conclusions is theoretical or mechanistic, and the diversity correlation fares pretty well in these discussions. Increasing the frequency of disturbance in forest should lead to higher densities of invasive species, and in old-growth, where such species are rare, it seems reasonable to predict that this would lead to higher diversity in small plots. It is questionable, though, whether higher turnover is due to higher forest productivity, as Phillips *et al.* assert. They did not find a correlation between turnover and total rainfall (although both correlate with diversity), as might be expected from some diversity theories: a positive association between moisture and diversity – observed in many terrestrial communities – has been attributed to a correlation between moisture and productivity<sup>7</sup>. Perhaps high-turnover sites are not more productive, but simply more disturbed (more wind, weaker soils?), and these disturbances promote diversity. Likewise, moist sites may be more productive but not more dynamic.

Although increased turnover seems likely to correlate with slightly higher local diversity, it seems very unlikely to be a driver of broad diversity patterns. Most tree species in a forest are in a small (shade-tolerant) demographic space<sup>12</sup>, and the added diversity in highly diverse forests comes in this group. It seems much more likely that the converse holds – that major diversity differences drive slight changes in forest turnover. Low-diversity forests have more uniform canopies where neighboring trees better protect each other from windthrow.

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Mechanisms to explain a global increase in forest productivity are even more debatable. Sheil<sup>5</sup> raises the possibility that increasing turnover was caused by recent strong El Niños. The El Niño of 1983 caused drought and mortality in Borneo<sup>13</sup> and at Barro Colorado<sup>14</sup>. Were these effects broad enough to generate the worldwide pattern Phillips and Gentry see? Phillips *et al.*<sup>6</sup> argue that they were not. For example, most of the Ecuadorian and Peruvian plots that showed sharp increases in turnover during the late 1980s were not known to suffer from El Niño events. Pimm and Sugden<sup>11</sup> added that other climatic shifts – such as storm frequency – could also affect forest turnover, but it is hard to imagine a climatic variable that would cause simultaneous increase in turnover all around the globe.

This is why Phillips and Gentry<sup>1</sup> settled on the CO<sub>2</sub> hypothesis, but it is also difficult to defend. Although lab-grown plants do show improved growth in the short-term when fed more CO<sub>2</sub>, long-term effects in the field are by no means clear-cut: some experiments have produced negative results. Productivity of individuals or communities could easily be limited by other factors. It thus seems very unlikely that forests around the tropics would all show a simultaneous spurt of productivity due to elevated CO<sub>2</sub> – there are too many different forests with different factors limiting growth. I prefer to think that the apparent increase in turnover is a statistical anomaly.

Phillips *et al.* might be right, and they might be wrong. To decide, we obviously need further tests. Predictions are clear: turnover should keep increasing with CO<sub>2</sub> concentrations, and direct measures of primary productivity should correlate with diversity measures. Our series of a dozen large forest plots<sup>15</sup>, where problems with small samples and varying methods are avoided, will provide some clear answers. Beyond these simple correlations, though, we need sophisticated and pluralistic approaches that consider simultaneously the importance of density dependence, resource use, competitive differences and random forces in determining diversity of species and guilds in tropical forests. Simple models considering factors in isolation cannot explain much.

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## Policing: it pays the strong to protect the weak

Recent work by Steve Frank<sup>1–3</sup> of the University of California develops an interesting new approach to an unresolved puzzle in evolutionary biology: how groups of lower-level units have evolved to form higher-level cohesive functional units. Such cooperation appears across the whole spectrum of life, from the earliest replicators forming cooperative units of sufficient complexity to allow accurate copying of genetic material, through the orderly mendelian segregation of chromosomes within cells, right up to animal societies. The problem in explaining cooperation and group formation is in explaining why selfish individuals (which obtain benefits from the group without paying any costs) do not prosper, causing the group to disintegrate. This problem is strongly related to the 'tragedy of the commons' described in economic theory<sup>4</sup>. Here, competition for a shared resource induces individuals to be

ever more rapacious, ultimately overexploiting the resource to the detriment of all. How can this selfish behaviour, which one would expect to be favoured by selection in the short term, be held in check?

One suite of commonly used arguments for explaining how cooperation can survive comes from game theory. Cooperation can be shown to flourish in games such as the prisoners' dilemma, where two individuals encounter each other in a series of similar situations where each can choose to act selfishly or cooperatively, and the pay-offs to each depend on the strategies played by both. This requires that the two individuals meet more than once, that they can recognize each other from previous encounters and can remember how the other behaved in previous encounters. These requirements clearly restrict the applicability of such game-theory solutions.

Another potential mechanism behind cooperation is kin selection. Common genetic material between individuals should lead to reduced selection for selfish behaviour. Frank<sup>1</sup> uses a simple model of cooperation to illustrate that relatedness can repress competition. Let  $w_{ij}$  be the fitness for an individual  $j$  in group  $i$ . Let  $z_{ij}$  be the competitive intensity of that individual ( $0 < z_{ij} < 1$ ). Further, let  $z_i$  be the mean competitive intensity of all the individuals in group  $i$ . Frank assumes that these can be related through the expression

$$w_{ij} = \left( \frac{z_{ij}}{z_i} \right) (1 - z_i) \quad (1)$$

In this model, individuals gain a share ( $z_{ij}/z_i$ ) of the group's productivity, but this productivity itself decreases as the average competitive intensity of group members increases. Frank (using the approach worked out by Taylor and Frank<sup>2</sup>) shows that the evolutionary stable competitive ability is given by

$$z_{ij} = z_i = 1 - r \quad (2)$$

where  $r$  is the kin selection coefficient of relatedness (increasing  $r$  signifies increasing