

congeners compete for the same set of establishment sites, the availability of which is little affected by other taxa. Empirical evidence from other tropical forests suggests, however, that this is unlikely. Although it is reasonable to assume that closely related taxa have similar requirements, most tropical trees seem to have broad, overlapping niches<sup>2-4</sup> and so are likely to compete for establishment sites with a wide variety of taxa, and not just with close relatives. There is little reason, therefore, to argue that a 'see-saw' model of interaction between congeneric pairs, discounting diffuse competition, is an informative approach to the dynamics of a forest containing more than 200 tree species.

Kelly and Bowler present evidence of out-of-phase recruitment fluctuations in rare and common congeners. Recruitment fluctuations were inferred from proxy age distributions, dividing trunk diameters by species-specific mean recent growth rates to estimate individual trees' ages. A problem with this procedure stems from the assumption that diameter distributions are a reliable indicator of age distributions. The fragility of this assumption is well known to dendro-ecologists working in temperate forests<sup>5-8</sup>, where growth-ring counts allow ages to be estimated accurately. The often-poor correspondence between diameter distribution and age structure<sup>5-9</sup> probably arises because stand dynamics have subjected different age classes to different growth histories, as well as spreading a given age class across a wide range of diameters.

The implications for Kelly and Bowler's method are exemplified by data from a temperate forest<sup>9</sup> showing that 'recruitment fluctuations' inferred from diameter distributions and age-diameter relationships do not necessarily coincide with those suggested by the actual age data (Fig. 1). Therefore, although tree-diameter distributions can reasonably be used to draw broad inferences about age structure (such as distinguishing

between all-aged and even-aged populations), attempting to date recruitment fluctuations by such a method is probably overly ambitious<sup>5-7</sup>.

In view of the difficulties of reliably dating recruitment fluctuations, and the questionable basis of the model, the case for mediation of coexistence of congeners by environmental fluctuation is unconvincing. Although there is every reason to believe that environmental instability contributes to coexistence in general<sup>10</sup>, establishing even the potential for its special relevance to the regeneration of congeneric trees in tropical forests would require clear evidence that seedlings of coexisting congeners overlap far more in space and time than they do with those of more distantly related associates.

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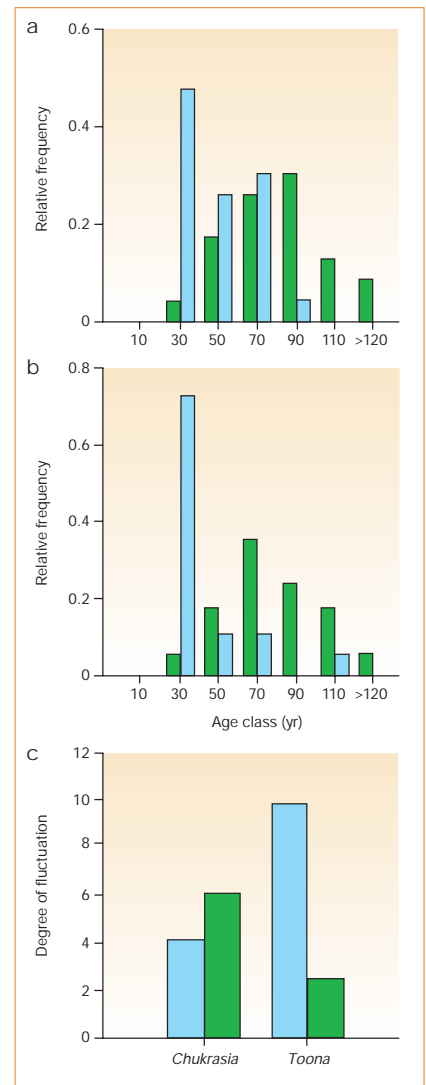
Plant ecology

## Coexistence of tropical tree species

For decades, ecologists have struggled to explain how so many tropical tree species can coexist. Kelly and Bowler<sup>1</sup> propose that differences in recruitment fluctuation and competitive abilities among closely related tree species could promote coexistence, and data from a tropical deciduous forest in western Mexico seem to confirm their predictions. We argue, however, that the tests of their model's predictions make fundamentally flawed assumptions about both size-age relationships in trees and the factors that influence population size structures. As such, their results are potentially misleading and lack the necessary rigour to 'reject all other theories of coexistence'.

Kelly and Bowler's model of species coexistence predicts that rare species should exhibit greater deviation in recruitment than common species. To test this, they compared differences between expected and observed age-class distributions for ecologically similar congeners. In essence, they predicted that abundant species should show fewer deviations in historical recruitment trends, and thus have 'smoother' age-class distributions.

Determining the age of tropical trees is



**Figure 1** Comparisons of real (blue bars) and size-derived (green bars) age distributions for two tropical tree species that form annual growth rings. **a**, *Chukrasia tabularis*; **b**, *Toona ciliata*. **c**, Degree-of-fluctuation (*d*) values for real and size-derived age distributions. Data were obtained from canopy trees in a 50-hectare, permanent forest-dynamics plot at the Huai Kha Khaeng wildlife sanctuary, western Thailand. Real age distributions were obtained from tree-ring analysis. Estimated tree ages were calculated from cored trees by dividing stem diameter by a taxon-specific mean annual growth rate. Note that the estimated age distributions differ in both shape and scale from the real age distributions and that the values of *d* for the estimated distributions provide no indication of *d* for the real age distributions.

challenging because most such species do not form annual growth rings<sup>2</sup>. Kelly and Bowler circumvent this problem by using average diameter-growth rates to convert tree size to age (that is, age = size/growth rate). This, however, makes the improbable assumption that average lifetime growth rates are the same for every tree in a species' population. Evidence from both temperate and tropical forests contradicts this assumption<sup>3,4</sup>. Tree growth is indeterminate, and in natural forests the availability



**Figure 1** Recruitment fluctuations as indicated by population age structure (green bars) and by use of stem diameter as a proxy for age (orange bars) in a population of *Weinmannia racemosa* ( $n=216$ ) in an old-growth temperate forest in New Zealand<sup>9</sup>. Fluctuations are represented as proportional deviations (observed - expected/expected) from a negative exponential curve<sup>1</sup>. Despite the highly significant overall relationship between age and diameter ( $r=0.81$ ,  $P<0.0001$ ), there is no correlation between 'real' and proxy fluctuations ( $r=0.03$ ,  $P=0.94$ ).

of resources required for growth varies in time and space. Trees of the same age may thus be small or large, depending on their individual growth history, making a species' size distribution an unreliable surrogate for its age distribution.

In Fig. 1 we present size and age data from two tropical tree species to illustrate the shortcomings of inferring historical recruitment fluctuations from age distributions derived from size distributions. Our aim is to demonstrate the potential errors involved in converting size- to age-class distributions and their influence on the degree-of-fluctuation statistic, *d*. Because *d* is, by design, sensitive to minor deviations from an expected distribution, it is not surprising that the values of *d* obtained from the size-derived age distribution in Fig. 1 bear no relationship to those from the real age distribution. Consequently, inference of abundance-related patterns in the magnitude of *d* obtained from size-derived age distributions is meaningless.

A more fundamental problem with Kelly and Bowler's analysis is the assumption that deviations from expected age-class distributions are solely due to temporal fluctuations in recruitment. Size-class distributions are complex functions of three factors: recruitment, growth and mortality. To interpret deviations in size- or age-class distribution simply as recruitment fluctuations is to assume that average growth and mortality rates are constant over time. Stochastic events such as wind storms, fires or climatic anomalies may alter growth and mortality rates for years or decades. Disentangling the effects of growth, mortality and recruitment on a continuous distribution of tree sizes is impossible without further information on past growing conditions — data that are rarely available for tropical forests.

Significant advances have been made in the study of tropical-forest dynamics at the scale of years, through large-scale forest-dynamics plots<sup>5</sup>, and millennia, through palaeoecological studies<sup>6</sup>. Neither has provided a satisfactory answer to the question of tree-species coexistence. Kelly and Bowler refocus the question on the largely unexplored middle ground — the scale of decades to centuries. However, lacking real tree ages, their theory remains untested.

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**Kelly and Bowler reply** — Both comments concern our use<sup>1</sup> of the relationship between tree age and tree diameter. However, none of the points raised invalidates our original conclusion regarding storage dynamics. Lusk asks for independent evidence that competition is not diffuse, and argues that recruitment fluctuations cannot be dated reliably from fluctuations in size distribution. He highlights a key result that preceded our model<sup>1</sup>: the observation that the size profile of the rarer of two closely related and similar species is in every case more irregular than that of the commoner species<sup>2</sup>. This observation cannot be explained by assuming diffuse competition. Rather than contradicting our model, we suggest instead that the empirical evidence regarding niche breadth may be incomplete.

Our identification of focused competition could be related to our comparison of congeners, an idea that is supported by evidence that, when phylogenetic relatedness is taken into account, functional variation in several physiological traits is predicted by characteristics other than presumed 'functional' (niche) types<sup>3,4</sup>. Woody communities are composed, on average, of roughly 30% congeners<sup>5</sup>, and we may well have identified a general process of forest dynamics.

Second, absolute dating of fluctuations is not crucial to our model, or for discarding others. Our conversion from size to age profiles defines equivalent time spans over which to compare fluctuations within individual pairs. No other model of coexistence predicts that the rarer species will be the superior competitor; the uniformity of that pattern in our data discounts alternative models.

As a counter-example to our method, Lusk derives fluctuations from separate profiles of age measured directly and age derived from diameter. The relationship between the two is to be expected in a population with little or no recruitment fluctuation, as is the case for the *Weinmannia racemosa* data<sup>6</sup> used by Lusk. We have found that, where two-dimensional plots are available<sup>7,8</sup>, mean diameter increases roughly linearly with age, and the variance of diameter for a given age also increases with age. With such a relationship and without recruitment fluctuations, the two measures of fluctuation would initially correspond, but over time this correspondence would degrade through statistical fluctuation alone, as in Lusk's figure. From his raw data, we calculate that the degree of fluctuation for these is about 0.5, a value that is comparable with that for the smoothest profile in our target species, the common *Bursera instabilis*<sup>1</sup>, and is consistent with statistical

variation alone. The deviation values for our rarer species vary from about 3 to 5.

Baker and Wilson make the point that growth responses differ in different environmental conditions, thereby producing different relationships between age and diameter. But our method assumes that species with a large degree of ecological and evolutionary similarity will respond similarly to the same environmental conditions. We compared morphologically similar congeneric species, which in one instance were sister species, having first checked that the paired congeners had the same habitat use and shade tolerance<sup>2,9</sup>. The compared species occurred together, with congener populations being interdigitated so that nearest neighbours could be either conspecifics or congeners. Baker and Wilson's "wind storms, fires or climatic anomalies" would be hard put to have different effects within our paired congeners.

By contrast, Baker and Wilson compare species in different genera, each of which is in a different tribe within a large family (Meliaceae; > 550 spp., > 50 genera<sup>10</sup>), signifying considerable genetic distance. The authors do not establish ecological comparability at the level that we did for our paired comparisons. From Baker and Wilson's Fig. 1, we estimate sample sizes of roughly 20 individuals for each species. For samples of this size, statistical variation in the measure of deviation could be as large as the values that they present.

We encourage identification of the limits of our assumptions regarding the diameter–age relationship; their definition will help to identify limits to documenting the Kelly–Bowler dynamic in nature. Unfortunately, a single example, even if it were relevant, cannot define such limits. Definition of the point where measurable similarity no longer usefully predicts unmeasurable similarity will require either better knowledge of the diameter–age relationship, or better analytical and simulation techniques. It would be a pity if Baker and Wilson's example were to dissuade ecologists from reasonable use of a historical record that is not otherwise readily available for many long-lived species.

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