

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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