

## The forest architecture hypothesis for diversity maintenance

Can tree species coexist by differing in size? T. Kohyama<sup>1</sup> recently put forward a convincing case that they can. While there is no shortage of plausible hypotheses for coexistence of competing species, few have received satisfactory tests. The 'forest architecture' hypothesis of Kohyama, however, is refreshing in that it has received a strong test soon after formulation. The nature of the hypothesis and the approach to testing it using models and field data merit close examination.

Kohyama formulates the forest architecture hypothesis in terms of a mathematical model designed to explain coexistence of three numerically dominant, non-pioneer tree species in the warm temperate rainforest of Yakushima Island, southern Japan. Examination of this model reveals four key elements: (a) one-sided competition for light, with larger individuals affecting smaller individuals (but not vice versa), independent of species identities; (b) segregation of species by height so that the species tend to occupy different layers of the forest when mature (on Yakushima Island the layers are canopy, subcanopy and understorey); (c) a trade-off across species between mature height and survival, reproduction or regenerative ability; and (d) spatio-temporal variation in size structure due to the opening and closing of gaps.

### Competition, segregation and trade-offs

To understand how these elements lead to coexistence, note from (a) that mature canopy trees will experience intraspecific competition for light because of height differences within the species, even though they will not experience interspecific competition because of (b). Such intraspecific competition is likely to place an upper limit on the density of canopy trees. The canopy will not capture all the light, but the light that does pass through may not be sufficient to support a population of trees of shorter stature. A canopy species with a high mortality rate, or low reproductive or regeneration rate, is likely to be limited at a level that lets substantial light through to lower layers, as such a species needs high light per unit leaf area to make up for its unfavourable demographic parameters. The trade-off (c) means that species of shorter stature can make do with lower light per unit leaf area, and therefore have

the possibility of maintaining a population below the canopy. A subcanopy species will be limited both by interspecific competition from the layer above, and by intraspecific competition. It may also be limited at a level that allows sufficient light to penetrate below to sustain lower layers, given that trade-offs give species in lower layers compensating advantages for their reduced access to light.

The hypothesis as discussed so far would seem to explain coexistence based on the ability of species with poorer access to resources to make do with 'left overs'. In this respect, the hypothesis is related to Grubb's lifeform niche hypothesis<sup>2</sup>, and Vance's light interference model<sup>3</sup>. However, in forests, and in Kohyama's model, all trees start out small, regardless of species, and so canopy seedlings will experience competition from understorey and subcanopy trees. If such below-canopy layers are sufficiently dense, the canopy may not be able to regenerate. In particular, if a species in a lower layer has too high an advantage in regeneration rate, it may become dense enough to prevent regeneration of a species in a higher layer. The trade-off (c) giving lower layers an advantage in regeneration could thus prevent regeneration of the canopy if this advantage is too great. Thus, for coexistence, the functions specifying the trade-off (c) must lie within certain limits (Fig. 1).

### The role of gaps

Kohyama's model confirms that coexistence of three layers is possible with elements (a), (b) and (c). Coexistence of any number of layers seems possible given the right sort of trade-off (c). What then is the role of gaps, that is, (d)? Added to the model, gaps increase the range of parameter values consistent with coexistence and reduce the time to equilibrium. How might gaps have these effects?

The opening of gaps makes it easier for all species to regenerate through reduction in competition for light. However, not only seedlings benefit from gap openings. Lower layers of the forest may form in a gap before the canopy reaches its maximum closure so that these lower layers may grow for a time at higher light levels. Consequently, following a gap, there may be a succession not necessarily as a change in species composition but as a change in the percentages of the incident light captured by the various

species, with the lower layers capturing more light earlier in the succession and the canopy finally dominating. Like succession in the disturbance hypothesis<sup>4,5</sup>, such a process should aid species coexistence, although it is not emphasized in the literature on forest gaps<sup>6,7</sup>.

Two features of Kohyama's model favour such a succession in light interception. First, saplings of the canopy species have lower growth rates. Second, small individuals may survive gap formation, and these will come disproportionately from species of shorter stature, increasing the likelihood that lower layers of the forest can form in time to experience periods of significantly reduced competition from higher layers.

### Testing the model

To test the hypothesis that elements (a-d) explain coexistence of three species on Yakushima Island, Kohyama estimates the parameters of the model from permanent-plot data, and sees whether or not such parameter estimates are consistent with coexistence. The inputs to the model from the field data are growth rates of individuals by species (taking account of an individual's size, and the sizes of other individuals in a stand), recruitment rates and mortality rates. The model is a multi-species version of age- and size-structured growth following the classic work of Sinko and Streifer<sup>8</sup>, which is then embedded in a model of opening and ageing of gaps in the spirit of Levin and Paine<sup>9</sup>. It is capable of representing rather complex dynamical processes, yet it is simple enough

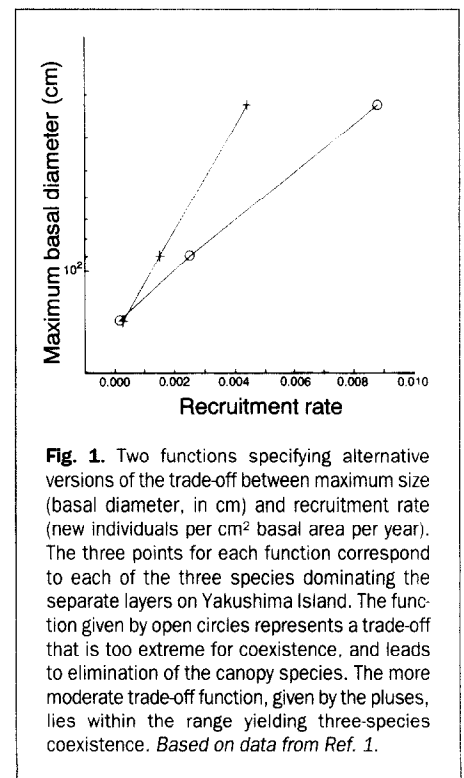


Fig. 1. Two functions specifying alternative versions of the trade-off between maximum size (basal diameter, in cm) and recruitment rate (new individuals per cm<sup>2</sup> basal area per year). The three points for each function correspond to each of the three species dominating the separate layers on Yakushima Island. The function given by open circles represents a trade-off that is too extreme for coexistence, and leads to elimination of the canopy species. The more moderate trade-off function, given by the pluses, lies within the range yielding three-species coexistence. Based on data from Ref. 1.

that most parameters can be estimated, and that the fundamental mechanisms involved can be understood. It thus represents a powerful alternative to the complex forest simulators that often have not yielded to easy interpretation<sup>10</sup>.

If the forest architecture hypothesis is correct, and if the model is indeed sufficient to capture the major features of forest dynamics, then two important predictions can be made. First, with good estimates of the parameters, simulations of the model should give a stable coexistence. Second, important quantitative features of the forest, such as age and size structure and their dynamics within gaps, should be reproduced by the model. Having these two predictions borne out amounts to a simultaneous test of the hypothesis and the particular model representation of it. If the second prediction were not borne out, there would be reason to be worried that the model is inadequate to capture the variation in forest structure on which the mechanism of coexistence depends. That does not seem to be the case here, and so we can regard the first prediction as a strong test of the forest architecture hypothesis.

Based on point estimates of the parameters of the model, the hypothesis appears to account for coexistence of only the subcanopy and the understorey species. The reason for this failure is that the trade-off function specified by circles in Fig. 1 gives too high a recruitment advantage to the subcanopy and understorey species and, as a consequence, the canopy species is excluded. However, the second trade-off function, which lessens this advantage, does lead to stable coexistence of all three species.

Kohyama says that the second trade-off function lies within the range of the accuracy of the data, although he does not give a 95% confidence region to support this claim. If he had, we would be able to say that the data are consistent with the forest architecture hypothesis of coexistence of all three species. However, we have seen that the data are also consistent with insufficiency of the hypothesis for coexistence of all three species. Only improvements in estimates of the parameters with more data can settle the issue.

### Coexistence mechanisms

We find much merit in Kohyama's approach to hypothesis-testing using models. While far from being new to ecology, it has not often been applied to hypotheses on coexistence mechanisms. Many such hypotheses share the requirement that species should differ sufficiently in ecologically significant ways in order to coexist<sup>11</sup>; the forest architecture hypothesis is no exception. However, the magnitude of the differences that must exist between species for coexistence to be possible is always at issue. For example, Latham<sup>12</sup> found differences in regeneration attributes of forest trees that may well contribute to diversity maintenance, but we do not know whether these differences alone are sufficient for coexistence. These differences must be considered in relation to associated trade-offs that prevent any individual species from monopolizing resources over too broad a range of conditions<sup>13</sup>. Here we have seen that the trade-off between recruitment rate and stature has the effect of limiting light absorption by upper layers of the canopy, and that it also provides the

species in lower layers with the possibility of persisting on the left-over light. Importantly, this trade-off function must lie in the correct range so that it provides enough, but not too much, recruitment advantage to species in lower layers.

With these constraints on the trade-off, we can turn around the problem of sufficient differences between species for coexistence: given the species differences in stature, does the trade-off function lie in the correct range for coexistence? This can only be determined by Kohyama's method of modelling the dynamics of the system.

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## Estimating extinction rates: Joseph Banks' legacy

More than one speaker at a recent discussion meeting at the Royal Society, London, UK, pondered what Sir Joseph Banks (1743–1820) would have made of the topic under consideration. The meeting, held 27–28 October 1993, co-organized by the Royal Society and the Linnean Society, brought together participants from a variety of disciplines to address the issue of estimating extinction rates. Consideration of connections between this theme and Banks was stimulated because the meeting was held to mark the 250th anniversary of his birth. With a life which encompassed pursuits as diverse as botanist, traveller, Privy Counsellor,

President of the Royal Society and a central role in encouraging the European colonization of Australia, there were ample bases upon which connections could be forged. Most, however, concerned what Banks would have made of the recent species losses suffered by many of the places he visited on his voyage with James Cook on the Endeavour.

Any meeting about extinction is likely to have an air of gloom about it, and at times this one was no different. *Homo sapiens* has not been kind to Banks' legacy of faunas and floras whose composition and magnitude were then only beginning to be understood. This said, in a series

of excellent presentations, the speakers repeatedly developed some important themes which point a way to improvements in the estimation of extinction rates, past, present and future, and to a better understanding of the reasons for, and the dynamics of, extinction.

### Extinctions and poor data

The primary obstacle to any investigation of rates of extinction is the general paucity and poor quality of appropriate data. With regard to the study of past rates, most thought and effort in the development of analytical techniques which take account of biased and incomplete information has probably been made in the context of fossil assemblages. An array of methods has been applied to address the complications presented by: (1) taxonomic problems, (2) the need to estimate species losses more indirectly than losses of higher taxa, (3) more