

observations of Toh *et al.* The interrelationships of Ty proteins will be reported elsewhere².

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Forest succession

MOST forest ecologists will agree with the conclusion of Finegan¹ that in real forests, succession commonly has characteristics of both the contrasting models he has described: a 'holistic' facilitation model where successive species replace each other and a 'reductionist' model where all species arrive at the outset.

Finegan is wrong, however, to say that no direct studies have been made of forest succession. Many studies do indeed rely on contemporaneous observations of forest patches of purportedly known age and history, but in the Eastern tropical rainforests there have been four studies of forest patches through time which clearly illustrate various departures from the two paradigms. These studies, originally reported in the specialist forestry literature, were used in the analysis of dynamic processes in a general account of the Eastern rainforests².

At Kepong, Malaysia, forest on an abandoned field has been monitored since 1947³. Here, the flora changed little between 1949 and 1960 because of a fern blanket, which was eventually shaded out, so from 1960 to 1976 there was a marked change, though climax species were still scarce. At Sungai Kroh, Malaysia, a similar succession was monitored for 17 years from 1946 to 1963⁴. Here, some tree species, including the dominant species, were present throughout while others progressively arrived. No fern blanket developed. At Sungai Menyala, Malaysia, a secondary forest established in 1917 has been monitored since 1947^{2,5}; here spasmotic floristic change is still occurring. After natural catastrophic destruction by repeated cyclones, succession at Kolombangara in the Solomon Islands has been under observation since 1964, and analysed for the first 6.6 years^{2,6}. The latter two studies also include areas of 'climax' forest which are showing 'cyclic replacement'⁷ (rather than 'directional change in time' as Finegan¹ defines succession) much more rapid than suggested by con-

ventional wisdom about the stability of primary equatorial forests. Finegan excluded cyclic replacement from his discussion. It does not involve directional change in time and is the process whereby climax ecosystems are maintained in the absence of catastrophic destruction. (The latter is followed by 'secondary' succession (as it is usually termed) back to climax.) Cyclic replacement is occurring at Sungai Menyala.

At Kolombangara island, the north-coast forests are believed to be repeatedly destroyed by cyclones; they show succession as discussed by Finegan. The west-coast forests, by contrast, are outside the influence of cyclones and show cyclic replacement. Sungai Menyala and Kolombangara demonstrate the value of long-term studies, and in fact these studies have continued longer than any others in climax tropical forest. The Kolombangara study includes the monitoring of recruitment, growth and mortality of seedlings of the 12 main large tree species and how these are influenced by different amounts of leafy canopy overlying them. For these species the total population is being monitored and the resultant understanding of their autecology has aided the analysis of the contrasting dynamics of successional (north-coast) forests and cyclically replacing (west-coast) forests. So far, nine sets of observations over 6.6 years have been analysed, and a further analysis is planned to start in 1986, covering another three sets of observations to 21 years. Both the Kolombangara and Sungai Menyala forests are under threat of conversion to more lucrative land-use, the much-discussed fate of many tropical rainforests, despite the contribution they have made to ecological understanding of forests^{2,8–11}, which itself underpins silviculture. The longer the studies continue, the more they reveal.

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FINEGAN REPLIES—I thank Whitmore for pointing out this gap in my review¹. The studies he cites are interesting and illuminating and deserve a wider audience
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(although I was unable to find Whitmore's ref. 5 and am unable to comment on it).

One point concerning long-term studies is worth making here. Two of those cited by Whitmore^{2,3} provide structural and floristic description only, and therefore cast very little light on the mechanisms of the successions which are clearly occurring. Measures of species abundance against time can be used to support almost any mechanistic model of succession, from the initial floristic composition ideal to a number of composite processes, as shown in my Fig. 4¹. No amount of description, whether inferred or obtained directly, will overcome this problem; hence the last paragraph of the review. Whitmore's studies at Kolombangara exemplify the sort of approach which is needed⁴.

I did not discuss cyclic replacement because there is a clear ecological basis for separating this process from the successions I review, involving differences in initial environmental conditions and sources of colonizing individuals. As Whitmore himself has pointed out, pioneer trees participate only infrequently in cyclic replacement patterns^{4,5}. I should have restricted my formal definition of succession by referring to processes occurring in cleared areas large enough to permit the establishment of a vegetation dominated physiognomically by pioneer trees.

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