

Plant mathematics and Fibonacci's flowers

Asymmetric cell division is an intriguing but unlikely explanation for the patterns of leaves.

Sir— The generation of leaf pattern (phyllotaxis) has long been a topic of interest and debate among plant biologists and mathematicians, as observed by Amar Klar in his Concepts essay¹. As Klar points out, the various models proposed for the production and maintenance of such biological patterns lack full supporting experimental data. These models, nonetheless, are based on (and reflect) biologically relevant observations and, contrary to Klar's assertion, lead to testable predictions. In contrast, Klar's new model based on asymmetric stem-cell division does not take into account some relevant biological observations that do not support his hypothesis.

During the maintenance of phyllotactic patterning, nascent multicellular organs (leaf primordia) determine the position of incipient primordia. For example, experimental data show that primordia can be initiated in the 'wrong' position by modifying either the hormonal² or biophysical^{3,4} context of the tissue, and that these induced primordia provide a feedback

loop to determine the position of the next leaf. Most evidence supports short-distance chemical signalling as the mechanism involved in designating the site of primordium initiation, with biophysical alteration in cell-wall extensibility as a key executor of the morphogenic programme initiated. The biochemical nature of the 'morphogen' is unknown, but progress is being made in its identification.

With respect to the initiation of phyllotactic pattern, the first primordia are generated from a multicellular ball, the plant embryo. Mathematical modelling convincingly demonstrates how an asymmetric pattern of a theoretical morphogen can be generated from an initially uniform field and how such asymmetry could lead to phyllotactic patterns⁵. Again, the biochemical identity of the proposed morphogen is unproven, but candidate molecules have been suggested⁶. In contrast, histological and clonal analysis of higher plant apical meristems has so far failed to reveal any consistent pattern of stem-cell division or

stem-cell lineage in relation to leaf formation⁷. A phyllotactic model using asymmetric cell division would predict the existence of such a prepattern.

Moreover, disruption of cellular patterning in the meristem does not lead to disruption of phyllotactic pattern⁸. It may be possible to imagine asymmetric division guiding leaf position in bryophytes (in which a single apical cell does undergo repeated asymmetric division to generate daughter cells that become incorporated into leaf-like organs), but in angiosperms (flowering plants), Klar's phyllotactic hypothesis represents a model too far.

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Macroecology is distinct from biogeography

Sir— According to H. J. Fisher in Correspondence¹, the scientific concerns of the recently emerged discipline of macroecology are a subset of those of biogeography, and hence the former is simply a sub-discipline of the latter. As evidence, Fisher observes that some macroecologists have written books on biogeography. We believe that his view is mistaken.

Biogeography is the science that attempts to document and understand spatial patterns of biodiversity². Macroecology is a way of studying relationships between organisms and their environment that involves characterizing and explaining statistical patterns of abundance, distribution and diversity—exploring the domain where ecology, biogeography, palaeontology and macroevolution come together³. Some overlap of interests between macroecology and biogeography has always been acknowledged (as has too, for example, between ecology and evolution), but in definitions that make clear their separate aims and identities.

Fisher's point that the same scientists have written on biogeography and macroecology in fact highlights precisely

the fact that they recognize the distinction.

Differences between macroecology and biogeography in scope and aim are apparent from the subjects covered in the macroecology symposium that prompted Fisher's comments. These included the ecological and evolutionary implications of the scaling of vascular networks; intraspecific optimization as a cause of interspecific allometry; the relationship between life history, population dynamics and extinction risk; neutral models of the assembly of local ecological communities from regional metacommunities; whether speciation rates are influenced by body size; and whether diversification is driven by key innovations (see ref. 4).

All these issues in macroecology may help us to understand the distribution and diversity of life on Earth, and so they may inform a range of disciplines that includes biogeography. But they are not biogeography.

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The search for general principles in ecology

Sir— According to H. J. Fisher in Correspondence (*Nature* **417**, 787; 2002), macroecology is largely contained within biogeography, which documents and interprets patterns in biodiversity at large temporal and spatial scales. I disagree.

Macroecology aims to identify general principles or natural laws underlying the structure and function of ecological systems, which are apparent in the patterns of distribution and abundance of entities composing these systems, no matter what the scale of the analysis. Macroecology analyses some of the same patterns (for example, latitudinal patterns in species diversity), but its emphasis is not restricted to patterns apparent at large spatial scales, nor to contingent explanations.

Thus, macroecology can be understood as an approach to the study of ecological systems centred on the search for general and invariant principles underlying their diversity and variability. It is neither biogeography nor a large-scale version of community ecology, but a new overall perspective on ecological complexity.

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