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The Formidable Challenge of Answering Simple Questions in Community Ecology

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Patterns in Nature: The Analysis of Species Co-occurrences by James G. Sanderson and Stuart L. Pimm. The University of Chicago Press, 2015. US$45.00, £31.50 (184 pages) ISBN 978-0-226-29272-4

There is an enduring tension in ecology between the search for generality and our propensity to see patterns everywhere. Assessing the extent to which ‘obvious’ patterns differ from what might be expected by chance alone has been at the centre of one of the most heated of ecological debates. First, the pattern: Diamond's [1] observation that certain pairs of similar bird species coexist only rarely on the same island, something that he ascribed to competitive exclusion in his set of rules for the assembly of communities. Then, Connor and Simberloff's counter-assertion [2] that these patterns could be explained simply by randomly placing species onto islands. No need for competition, no need for rules. This difference in views grew famously ugly, but the central ecological question (what can we infer about mechanisms of coexistence from patterns of species co-occurrence?) and the associated technical challenges (what sort of patterns would we expect in the absence of any such mechanism? How can we best compare reality to this null expectation?) continue to stimulate considerable thought. In their clear and entertaining new book, Sanderson and Pimm review the intellectual content of this debate, restate their own solutions to the two technical challenges, and consider the developing mutualism between natural historical understanding and computational methods.

Sanderson and Pimm are firm in their belief that patterns of coexistence remain fundamental to community ecology; but, more generally, this book is a paean to the well-stated null, relevant to all branches of ecology in which experimental manipulation and extensive replication are impractical if not impossible. Most of us working in such fields will agree with them that ‘…building sensible null models turns out to be fiendishly difficult’. Simply put, the extent to which a null should be constrained to resemble reality is not obvious; and even when that decision has been made, one is still left with the task of constructing and sampling from the universe of possible nulls. The authors illustrate these problems in the specific case of island incidence matrices, where the presence or

absence of a species on a particular island is represented by a 1 or a 0. It is some achievement to have made this section so readable and fascinating. The conclusion is that Miklós and Podani's [3] trial-swap algorithm has rendered the generation of random incidence matrices a solved problem.

Having satisfied themselves that they can effectively generate ‘random’ communities, Sanderson and Pimm then turn to the issue of how to compare reality (the observed incidence matrix) to the null? Here, the metric is key, and the authors come down firmly on the side of using pairwise rather than community ensemble metrics, which they consider to needlessly obscure unusual pairwise patterns: ‘Why is it that the full richness of nature… must always be boiled, distilled, spun and precipitated into a single number?’ This seems sensible, even if their description of how to identify ‘unusual’ pairs of species, and their subsequent worked examples, lack some of the clarity of earlier sections. Equally, the final chapters extending the preferred approach to analysis of species coexistence along environmental gradients, and to interactions within ecological networks, feel rather superficial compared with the earlier substance; yet even here, the book provides a useful source of testable hypotheses.

The book is not without faults. Although the text has obviously been carefully crafted for clarity, the same cannot be said of the figures and tables; and the prose, so lucid when describing methods or concepts, labours over numerical results: for example, ‘This number of co-occurrences or more occurred in all but 989,090 of the one million null matrices’ would surely be better phrased as ‘in just 1% of the null matrices’. It is also important to state what the book is not. Although the brisk review of many of the key texts in community ecology, particularly from the 1970s through to the early 2000s, provides a valuable service to newer generations of ecologists, it is not a review of recent community ecology: only three of the cited works have been published since 2010, and some major recent insights into community assembly stemming from the explosion of data on phylogenetic relationships [4] and biological traits [5] are not considered. The book is also not a how-to manual, but it would have been useful to cite software that can implement relevant methods (for instance, the trial swap algorithm has been available in the vegan package in R [6] since 2008; J. Oksanen pers. comm).

However, rather than criticise the book for what it is not, I recommend it for what it is: a valuable and stimulating review of decades of work. The focus on intellectual content is refreshing, because there seems little to be gained from rekindling what the authors term an ‘academic war’, and, overall, I feel that the major contributions arising from both entrenched positions are well recognised here (the occasional pointed aside notwithstanding). There is a clear moral too, that increased openness can help us to avoid future ‘wars’. For instance, in 1979, Connor and Simberloff were frustrated that

Diamond's data (finally published in 2009 [7]) were not available to them. As Sanderson and Pimm put it, ‘The unavailability of the data clearly contributed to the increasing hostility.’ Was it worth these decades of hostility? Are we now in a much stronger position to robustly predict how ecological communities will respond to an uncertain future? I am not sure. But, I am convinced by the authors’ statement that doing so will require increased cooperation between those able to identify, analyse, and explain repeated patterns in nature.

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