Your move

Patterns in Nature: The Analysis of Species Co-occurrences, by James G. Sanderson and Stuart L. Pimm, 2015, The University of Chicago Press, 205 pp. ISBN: 9780226292724, Price $45 (Hardback); http://press.uchicago.edu

I'm tired of reading about checkerboards. This, perhaps, is not the most auspicious way to begin reviewing a book entirely on the theme of those apparent patterns in species distributions where certain species never co-occur. The original debate goes back to Diamond (1975), who noticed checkerboards in the occurrence of bird species on islands off New Guinea. He attributed these to 'assembly rules', which in the original definition were largely restricted to competitive interactions among species occupying similar niches. His thesis was soon under siege from Connor & Simberloff (1979), who used a simplistic null model to claim that the patterns were no different from random expectations.

What followed was a long-standing, arguably vitriolic and ultimately tiresome spat. As Sanderson & Pimm note, "This debate was not ecology's finest hour." Neither side landed a knockout blow; the fight didn't so much end as fade into irrelevance as most of the audience stopped paying attention. Hence my general feeling of ambivalence whenever the topic of checkerboards comes up. They are a useful heuristic tool in teaching undergraduates to think about distributions and species interactions, and therefore feature in most textbooks, but are no longer a focus of much research or theory. If one cannot with any confidence demonstrate that checkerboards are informative of process then maybe there's no point bothering to look for them, or arguing about them.

Enter Sanderson & Pimm, who are not about to let the dust settle. Their text is an accessible summary of the crux of the debate, and an attempt to persuade a general readership that the proper design of null models provides the key to resolving all such disagreements. They "regard the analysis of species cooccurrences to be a solved problem", a phrase that towards the end of the final chapter becomes no more compelling through its frequent repetition. Many, including myself, would dispute this assessment. What they achieve in their book, rather than a resolution, is to resurrect the debate in the light of recent theoretical developments, particularly the means to more fully explore the null model space (Miklós & Podani 2004). Regardless of whether you ultimately agree with their conclusions, this makes it an important and worthwhile read.

One of the key points they make is subtle, but nonetheless central to community ecology, which is what we mean when we speak of 'random' variation. This shorthand term seldom implies that no meaningful process determines the patterns observed. Rather it conveys that the complex set of overlapping, interacting and inextricable processes at play makes some systems effectively unpredictable. Throw a die onto a flat surface and the angle, velocity, torque and height all determine the side that will finish face up. The fact that we understand the forces acting upon a rolling die does not make it possible to correctly guess (or fix) the result. Ecological systems are the same; the outcome can appear no different from chance, even while deterministic processes are entirely responsible.

This point is crucial to the original debate. Connor & Simberloff (1979) never said that communities were randomly assembled (though this misunderstanding is widespread), but instead that patterns could not be distinguished from those which a stochastic process might have generated. It is generally agreed that the original null models as applied by Connor & Simberloff had many flaws, albeit necessitated by a combination of inadequate computing power and limited development of matrix theory at the time. Bringing new tools and insights into play allows more meaningful tests of Diamond's original hypotheses.

Many (if not most) checkerboards are uninteresting from the perspective of community assembly. The analytical framework established by Connor & Simberloff counted as checkerboards those patterns created by single-island endemics, which by definition do not co-occur with any species that are not found on the same island. Likewise species found only on the largest island might owe their presence to geographical features or sampling effects rather than any interaction with other species, and no competition need be invoked. Sanderson & Pimm contend that examining pairwise checkerboards can resolve this issue by identifying examples of those species which are widespread within the islands under study but nevertheless fail to co-occur for meaningful reasons. Many checkerboards are unlikely to occur even in the null model space; what matters is whether particular patterns of distribution between named species are unusual given their frequency among null simulations. They refer to this as the 'natural metric', a term that makes me uncomfortable as it implies that any other approach is somehow 'unnatural'.

To give a flavour of their logic, a familiar argument is made that closely related species, particularly congeners, are unlikely to coexist due to similarity in resource usage. The authors also note however that some congeneric species co-occur more often than expected by chance, for example the freshwater ducks of Vanuatu. This single example immediately undermines the argument that we can predict potential checkerboards *a priori*. One should not write off unexpectedly frequent coexistence of two *Anas* species as dependency on a common habitat whilst at the same time attributing checkerboards among other sister species to competition; unfortunately this is a trap that Sanderson & Pimm fall into. For this reason I am underwhelmed by their *post-hoc* filtering of outliers among species pairs in their patterns of co-occurrence compared to the null model set (which they refer to as a 'sieving procedure'). Taking only these pairs then searching for features that might make them the subject of strong competition – bill dimensions in the Galapagos finches for example – makes for a compelling narrative but not for a strong test of fundamental theory. It's a classic demonstration of the Prosecutor's Dilemma.

Furthermore, I retain some scepticism that constrained null models provide an irrefutable resolution to the debate. There will always be the danger of 'researcher degrees of freedom': decisions made in the design stage that cause the desired outcome to be more or less likely to occur. If one selects species and islands to test based on *a priori* assumptions about which are most likely to exhibit checkerboards, then it should come as no surprise that checkerboards emerge. The reader is forced to place great trust in the transparency of the authors' intentions as it would only take minor post-hoc tinkering to ensure that a variety of outcomes could be obtained. Finally, in attempting to extend the methods to other ecological contexts such as gradient analyses and interaction webs, Sanderson & Pimm succeed only in assaulting several straw men without delivering transformative insights. I finished the final chapters content that the existing consensus on these topics remains robust.

The prose is written in a narrative, conversational style. Whether this suits your personal taste may be a matter of preference. Some of the more intemperate passages are likely to fan the flames rather than cool tempers, and may provoke, rather than persuade, key audiences. While a bias towards the Diamond-led faction is openly acknowledged, there is also much friendly fire. Regardless of whether you finish convinced by their arguments, Sanderson and Pimm have achieved one major objective, which is to have made checkerboards and their analysis relevant to a new generation of biogeographers, and worthy of discussion once again. For that alone I recommend it.

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