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COMMENTARY

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Scaling mount SAR: Commentary on Matthews et al. (2021) *The Species–Area Relationship: Theory and Application*

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The issue of spatial scaling has grown in recent decades from a minor geeky obsession to a mainstream methodological preoccupation in virtually all fields of science. Increasingly, scientists of all stripes have been challenged to scale up their understanding of physical, chemical and even social processes from test tube or patch to global scales, driven both by the opportunity of increasingly sophisticated global data sources and by the need to address urgent and interconnected global challenges. In this respect, as in so many others, ecologists have been well ahead of the crowd: we as a field have been in the business of scaling up biodiversity for more than a century. The main tool for doing that upscaling has been the species–area relationship (SAR).

The SAR has been percolating in the collective consciousness of biogeographers since the late 18th century, but the idea was formalised and brought to wider attention by the competing works of Arrhenius (1921) and Gleason (1922). In its essence, the idea is simple: more area generally contains more species. However, the sub-additive scaling of biodiversity (twice as much area generally contains *less* than twice as many species) makes the challenge of upscaling biodiversity decidedly non-trivial, an issue that has inspired theoretical and empirical research in equal measure. It has been a full century now since the SAR first became widely appreciated among ecologists, and a quarter-century since the last major book on the topic (Mike Rosenzweig's *Species Diversity in Space and Time*, 1995); it is high time someone revisited the topic in light of recent work. Fortunately, Tom Matthews, Kostas Triantis and Rob Whittaker have done just that with their new book: *The Species–Area Relationship: Theory and Application* (2021).

In many ways, Matthews et al. (2021) come in stark contrast to Rosenzweig's (1995) volume. While Rosenzweig's book is an extensive exploration of a single author's views, the new volume includes the work of 44 contributors from 35 institutions, spanning 19 chapters and almost as many sub-disciplines. The book includes the insights and perspectives of a large fraction of the key players working on this topic; its contributors list reads like a Who's Who of spatial ecology and macroecology researchers: Blackburn and Borda-de-Água, Harte and Hubbell, Šizling and Storch, Thuiller and Tjørve, Ugland and Ulrich, to name just a few tantalisingly alliterative pairs. If Rosenzweig's book feels spacious and expansive (even chatty in places), the new volume feels dense and tightly stuffed with diverse treats, and even a bit claustrophobic in places. In part that is a result of downsized pages and fonts: Rosenzweig's pages are 20% larger than those of the newer book, but the words per page are about the same. Where Rosenzweig had the opportunity to slowly build an extended discourse, each of the chapters in Matthews et al. stands alone as a separate narrowly focused account. The book is full of scattered gems: it includes the best account I have seen of the history of the SAR concept (Chapter 2), valiant attempts to generalise SARs to the scaling of ecological function (Chapter 5) and trophic networks (Chapter 12), and applications of SARs to identify biodiversity hotspots (Chapter 13) and predict extinctions (Chapters 14 and 17) and many more.

However, the richness and diversity of perspectives comes at a price: despite the valiant efforts of the editors, the book as a whole does not (and indeed can't) build up to a single coherent argument. The breadth of authorship brings with it a diversity of approaches and expertise, but also inconsistencies in style and tone, and occasional overlaps and gaps. On a topic that is rife with terminological inconsistency, the editors do a good job of enforcing a common framework for all, which is largely adhered to by most authors. They simplify Scheiner's (2003) influential typology of SARs to its most fundamental dichotomy: contrasting ISARs ('Island' or 'Isolate' SARs for analyses comparing the species richness of sets of discrete sites of different sizes) and saSACs ('sampling area Species Accumulation Curves', for comparisons across subsamples of different sizes nested within larger contiguous areas). However, this methodological distinction makes clear some of the internal tensions within the field, one that leaves its muddy footprints on the book as well.

The book's first section (Part I) includes an initial discussion of these issues, and a detailed history of the SAR concept. This is followed by a series of chapters (Part II) discussing different aspects of SAR diversity: applications to different kinds of archipelagos, the use of different mathematical functions to describe SARs, the application of SAR ideas to functional and phylogenetic diversity, and the scaling properties of alien invasions over time and space. These four rather disparate topics are not closely linked, but each is interesting; I was particularly impressed with Matthews and colleagues' clever use of Structural Equation Modelling to tease apart the drivers of SAR shapes in a global island database (Chapter 3). Part III, on theoretical advances, is at least as rich and diverse. Its six chapters range from descriptions of the logical and geometrical constraints behind widely used SAR methods, the scaling of trophic webs, and links between SAR shapes and community theory. These include particularly lucid explorations of spatial biodiversity scaling in Maximum Entropy and Neutral theories (Chapters 10 and 11) and an intriguing exploration of applying Extreme Value theory to SARs (Chapter 9); this section by itself is worth the ticket price. This is then followed by a plethora of SAR applications (Part IV), in particular exploring uses in conservation prioritisation and management, and finally a single chapter (Part V) summarising future research priorities.

However, there are some interesting or troubling lacunae among all that richness, especially concerning the ISAR/saSAC methodological divide. While Part II is a reasonable mix of ISAR and saSAC approaches, the 'theoretical advances' explored in Part III are focused almost exclusively on saSACs. It is odd and worrying that the considerable theoretical literature on island systems (going back to MacArthur and Wilson at least) hardly enters into the discussion; have there really been no recent advances in this area of theory? Part IV includes a mixture of contributions from both camps once again, and indeed it bridges the conceptual gap to an extent, as the 'relict' SARs of islands formed in new hydroelectric projects (Chapter 17) begin as subsamples but become isolates as the waters begin to rise. Yet, the single chapter of the book's final section (Part V) on future perspectives and research priorities unaccountably restricts its purview to ISARs alone. This feels like a missed opportunity: many of the points raised there (five of the seven subheadings covered, by my reckoning) could apply equally well to either SAR variant, and those issues that apply only to isolates (e.g. the 'small island effect') could easily be matched with a few saSAC-specific challenges (e.g. parsing the interacting effects of spatial scale and sampling intensity). In a book (and a discipline) so badly riven with contrasting perspectives, it would have been better to end by setting a unified and integrating agenda for the future.

Throughout the book, examples are given of ideas and models that are developed independently by multiple authors, often decades apart, and frequently in different languages or disciplines. The first SAR dataset was arguably published in 1859, more than 60 years before the first SAR was plotted (in Arrhenius, 1920), and the idea that random placement of individuals would produce a curved SAR was pioneered by Rommell (1920) and Arrhenius (1920), a further 60-plus years before it was rediscovered by Coleman (1981). I suppose I ought to find that worrying—indicating wasted effort, a failure of the literature to appreciate ideas ahead of their time, a tendency to ignore non-anglophone scientists and a consequent tendency for ecologists to keep reinventing conceptual wheels. Nonetheless, I found myself oddly cheered by our collective ability to rediscover overlooked truths. Decades ago, I attended a talk by Steve Ellner about the difference between 'noisy' and 'chaotic' dynamics. To explain the distinction, Ellner asked us to imagine the consequences if a prominent ecologist in the audience were to be struck by lightning at that moment. We who witnessed this immolation would of course be terribly upset by the experience, but in a noisy, stochastic world, the ripples of the event would gradually fade, and the discipline would eventually revert to the course it would otherwise have taken. Conversely, if scientific progress is chaotic, Ellner argued, the consequences of the tragedy would grow with time, as the students and colleagues that the deceased would otherwise have taught, collaborated with or inspired would now miss those critical interactions and insights, as would their students and colleagues in turn, so that with each passing year the field would spin off along increasingly different pathways. In noisy dynamics perturbations dampen down over time, whereas in chaotic systems they are amplified. Our ability as a community to rediscover the insights and models that we'd collectively produced but overlooked in the past gives me confidence that our progress as a discipline is 'noisy' rather than 'chaotic'.

Good ideas may take a while to be germinate, but ultimately they *do* take root, so that we as a field are haltingly but inexorably ratcheting forward. This valuable but uneven volume is good evidence of that: it too is a bit noisy in places, but that may be because it has a lot to say. We've collectively made good progress in the past few decades, and Matthews et al. (2021) provide a tide line to show us how far we've come. We have waited a quarter century for this book, published in what is in many respects the SAR's centenary year. It was worth the wait.

CONFLICT OF INTEREST

The author confirms that he has no conflict of interest regarding this publication or its contents.

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