Cambridge University Press
978-1-108-47707-9 — The Species–Area Relationship
Edited by Thomas J. Matthews , Kostas A. Triantis , Robert J. Whittaker
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The Species–Area Relationship

The species–area relationship (SAR) describes a range of related phenomena that are fundamental to the study of biogeography, macroecology and community ecology. While the subject of ongoing debate for a century, surprisingly no previous book has focused specifically on the SAR. This volume addresses this shortfall by providing a synthesis of the development of SAR typologies and theory, as well as empirical research and application to biodiversity conservation problems. It also includes a compilation of recent advances in SAR research, comprising novel SAR-related theories and findings from the leading authors in the field. The chapters feature specific knowledge relating to terrestrial, marine and freshwater realms, ensuring a comprehensive volume relevant to a wide range of fields, with a mix of review and novel material and with clear recommendations for further research and application.

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The Species–Area Relationship

Theory and Application

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Foreword

MARK V. LOMOLINO

'Size matters'. At face value, this appears to be an overly simplistic and vacuous statement. In reality, however, it is a surprisingly insightful declaration of the influence of size on nearly all natural phenomena, including all those involving life throughout its 3.6-billion-year history on this planet.

My first introduction to the pervasive relevance of size was in a characteristically captivating lecture by the esteemed physiological ecologist Brian McNab. 'Size matters,' he told us. 'The most important factor influencing all physiological processes – thermoregulation, metabolism, digestion, locomotion, etc., is body size.' Professor McNab would go on to say (while we struggled to keep up with the frenetic pace of his renderings of graphs on the chalkboard and his singular stream of insights), 'If a picture is worth a thousand words, then a graph must be worth millions!' The connection back to his original statement on size was that, for the preponderance of graphs we hurriedly scratched down in our notes, the x-axis was body size.

Turn the pages some ten years later to lectures in what would seem to be a starkly unrelated course – Biogeography, and James Hemphill Brown would time and again return to the fundamental importance of size. Perhaps more than any other scientist of his time, Professor Brown understands that some very fundamental principles of physics govern the marvellous myriad of natural phenomena, from chemical activity and fluid flow among cells to the properties and processes regulating the activity, longevity and diversity of individuals, species populations, biological communities and, indeed, the entire biosphere.

Given this background and, in particular, the pervasive relevance of size as a property influencing fundamental properties of the natural world, the long and distinguished history of research on the species–area relationship can be recognized as a scaled-up restatement of McNab's axiom – in this case, *the most important factor influencing the characteristic properties and processes of all species, ecological communities and* *ecosystems is their size, or 'area'*. Area dictates the total amount of energy from solar radiation reaching the primary producers and subsequently transferred to all consumers and decomposers. Area thus also limits the total number (or mass) of individuals that can be supported at any particular time and, through a complex set of processes and rules governing division of energy, space and other key resources, it ultimately determines the diversity of species.

Accordingly, the species–area relationship has attracted the attention of scientists throughout the histories of the fields of ecology, evolution and biogeography, and likely long before the earliest articulation of these disciplines. Indeed, in their struggles for survival, the earliest hunters and gatherers must have understood that their likelihood of encountering more and a greater variety of food plants and game animals increased with the size of their search area. The first scientifically rigorous descriptions and postulations of underlying causes for the species–area relationship, however, would await many generations of advancements, as it required an upscaling of our collective knowledge of the natural world from local to regional and eventually a global scale.

With the eventual burgeoning accumulation of empirical descriptions of how diversity of an ever-expanding menagerie of species and taxa varied across the globe came an increased sophistication in the tools to analyse and theories to explain this very fundamental pattern of nature. Within the past two decades, our empirical knowledge, theoretical constructs and analytical powers have advanced to what appears to be a watershed moment in our quest to understand the nature of biological diversity and its dependence on area. The co-editors of this volume have seized on this opportunity and produced what may well serve as a landmark contribution in modern science.

The collected contributions by distinguished biogeographers and ecologists have been organized into five sections. In Part I, a summary of the history of research on the species–area relationship (SAR) is provided, including a description of the dichotomy of island SARs versus species accumulation curves. The heuristic value of these patterns in terms of their relevance to developments in a variety of fields, including island biogeography and conservation biology, is then summarized.

Part II includes a number of interesting chapters on diversity–area relationships, including their alternative forms, underlying factors and processes, and comparisons between emergent patterns for natives versus alien species, and for alternative measures of biological diversity, including functional and phylogenetic diversity.

Part III focuses on theory and analytical approaches for describing and extrapolating from empirical patterns. Included in this section are chapters explicitly identifying assumptions behind alternative renderings of species–area curves, their relevance to related patterns in community structure such as beta diversity (community dissimilarity), the geometrical underpinnings of nested SARs and the implications of maximum entropy theory, extreme value theory, neutral theory and food web theory.

Part IV addresses the applied relevance of species–area research, including a variety of innovative approaches for identifying such important properties and phenomena as biodiversity hotspots, susceptibility of particular types of species to anthropogenic extinctions, temporal dynamics in species–area curves, the importance of shape and other geometric moments beside area, the use of 'relict' SARs to assess conservation value and applications to marine systems.

Part V comprises a single chapter that provides an especially important and provocative synthesis of the salient lessons from this collective body of contributions. The chapter author goes on to provide an outline of how to develop a more integrative understanding of this all-pervasive pattern in the geography of nature – outlining a unifying theory of SARs and how this may be developed to provide a genuinely holistic understanding of how and why diversity varies across space and time.

It is indeed an honour to have been invited to contribute to this hallmark contribution to biogeography, if only in a small way by adding a few thoughts from research my colleagues and I have conducted on the SAR and related patterns in the geography of nature. First, and at a most general level and likely relevant to all issues discussed in these collected works, we assert that in order to develop a more holistic understanding of this or any other pervasive pattern in biogeography, our conceptual constructs and empirical inferences should be based on the fundamental, unifying principles of the discipline (see Lomolino, 2016; Lomolino et al., 2017, p. 144). In short, these principles assert that all patterns in the geography of life result from: (1) non-random patterns in variation of environmental conditions across the geographic template; (2) the influence of this variation on the fundamental biogeographic processes of immigration, extinction and evolution; (3) the influence of these fundamental processes on each other (e.g. the arrival of new species altering the likelihood of extinction or evolution of resident species) and (4) system feedback in the form of ecological interactions among species, which influence the fundamental capacities of other species to immigrate, survive and evolve.

The second point follows from the first and in particular its emphasis on the fundamental processes, which exhibit scale dependence. That is, with respect to island species–area relationships specifically, immigration, extinction and evolution are strongly influenced by the fundamental dimensions of islands – that is, their isolation and size (area). One salient but easily overlooked product of this spatial scale dependence is that even such a long-studied and apparently simple pattern as the SAR may exhibit a protean persona – appearing to take on different forms depending on the spatial scale (extent) and the underlying processes that tend to dominate at that scale. As I postulated in previous papers, this protean nature includes the tendency for the SAR to be relatively flat on small islands (where colonizations and extinctions tend to be stochastic), assume the expected or 'canonical' curve for islands of intermediate size (where immigration and extinction may approximate an equilibrial condition consistent with MacArthur and Wilson's theory) and then the slope of the relationship may increase again on the largest islands (where in situ evolution supplements the species pool) (see Lomolino, 2000, 2001).

The third point from our research on these patterns touches on an admittedly darker but equally pervasive concern over how we approach research on the geography of the natural world. As an increasing number of other scientists have observed, there doesn't exist one ecosystem anywhere across our planet that hasn't been touched, if not fundamentally transformed, by humanity. Recently, this has been clearly demonstrated by a series of elegant and innovative studies conducted by S. Faurby and J. C. Svenning (2015), who were able to recreate the natural (pre-humanity) geographic gradients in native communities at regional to global scales – patterns that often differ substantially from contemporary patterns perceived to represent the 'natural' state.

In our own research in reconstructive biogeography, Alexandra van der Geer, Georgios Lyras and I discovered that human activities have qualitatively altered the SAR for mammals on oceanic islands (van der Geer et al., 2017; see also Helmus et al., 2014). To understand why this occurred, we need only to consider the impacts of human activities in light of the fundamental unifying processes. Anthropogenic transformations of the geographic signatures of nature are to be expected given that our effects on extinctions, immigrations and evolution of native wildlife and plants are species-selective. That is, human activities differentially impact species as a function of a variety of traits – the most important of which is their body size. For example, anthropogenic extinctions of terrestrial vertebrates across the globe during the late Pleistocene and early Holocene decimated the native megafauna – the largest species, which required the largest areas to maintain their populations. Species introductions appear to have further compounded this bias against larger, area intensive species (i.e. those requiring large spaces to persist as viable populations) – the most common species listed on our tallies of those introduced to islands are typically dominated by relatively small species (mice, rats and shrews). The overall impact across the world's archipelagos was a wholesale distortion of the natural, underlying patterns in species diversity – an affect that may have cascaded through species assemblages on islands as the overabundance of exotic mammals impacted native wildlife and plants across the world's archipelagos.

This leaves us with a haunting question for each of the contributors to this volume and indeed for anyone interested in understanding and conserving biological diversity of native biotas: *To what degree are the patterns we have been studying throughout the history of biogeography, evolution and ecology artifacts of the power of our species to transform the primordial signals of nature across the planet?* We have only recently amassed the databases and developed the analytical tools required to answer this question, but, given the ominous global changes on the horizon, it seems imperative we address this challenge before all too many more species join the lost legions of the ghosts of biotas past.

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Preface

The species–area relationship is one of the longest known general patterns in ecology and biogeography: a simple enough emergent macroecological property on first glance, it remains in some ways poorly understood, beguilingly varied in form and enigmatic. Wider and contemporary interest in the species–area relationship (SAR) is evidenced by the results of a Google Scholar search undertaken in September 2019 using 'species–area relationship' as the topic field and all available years, which yielded 12,800 articles (almost 2,000 of which were published in the previous two years), distributed across a diverse array of fields, including ecology, zoology, forestry, microbiology, anthropology, biophysics and virology. All the more surprising then that, to our knowledge, no book has previously been published that focuses specifically on the SAR. When the idea of a SAR focused book was first proposed to us by Michael Usher, we contemplated writing a co-authored text. However, we subsequently decided that the field would be better served by an edited volume that provided both a synthesis of SAR material and a compilation of some of the most interesting recent advances in SAR research; topics that, due to their recent emergence in the literature, have yet to be brought together in any book or review.

The book which has resulted is thus broad in scope, with each chapter providing an in-depth evaluation of a particular area of SAR research, in cases largely empirical and in cases via review. It also provides an overview of recent advances in community ecology, macroecology and biogeography more generally: we hope it will therefore be of interest even to those who begin with no specific interest in the SAR.

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