

1 • *The Species–Area Relationship: Both General and Protean?*

THOMAS J. MATTHEWS, KOSTAS A. TRIANTIS AND ROBERT J. WHITTAKER

The history of the species–area field is long and rife with debate. Workers have argued about the form of the relationship, its interpretation, and the reasons for its existence. This argument is not trivial and without consequence.

(McGuinness, 1984, p. 424)

An introduction to a book on the species–area relationship (SAR) would be incomplete without the oft-repeated statement that the SAR, which describes the increase in richness observed with increasing sample area (Figure 1.1A), is the closest thing to a general law in ecology (Schoener, 1976; Rosenzweig, 1995; Lawton, 1999; Lomolino, 2000; Tjørve & Tjørve, 2017). However, while its characterization as a ‘law’ can be debated, there is no disputing the fact that the SAR is an almost universally observed phenomenon. It has been described for practically all taxa, across multiple spatial and temporal scales and in a range of systems and landscape types (MacArthur & Wilson, 1967; Connor & McCoy, 1979; Rosenzweig, 1995; Lomolino, 2000; Drakare et al., 2006; Triantis et al., 2012; Bolgovic et al., 2015; Matthews et al., 2016a; Dengler et al., 2020). The few cases where the expected relationship is not observed are where other variables exert a much stronger influence on richness than area and either negatively co-vary with area (e.g. likelihood of wildfire; Wardle et al., 1997) or vary independently of area. As a pattern, it has intrigued ecologists and biogeographers for over 200 years (Chapter 2). Indeed, the SAR has formed the focus of much of our own research (e.g. Triantis et al., 2008, 2012; Whittaker et al., 2014, 2017; Matthews et al., 2016a, b). It represents a fundamental component of numerous ecological and biogeographical theories, including the equilibrium theory of island biogeography (MacArthur & Wilson, 1967) and the unified

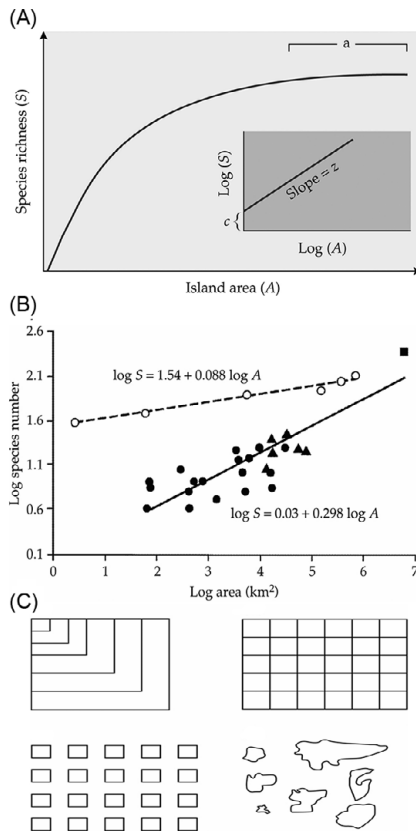


Figure 1.1 Three key representations of the Species–Area Relationship. (A) An idealized power model SAR, which describes a curved relationship in arithmetic space and a straight-line relationship in its log–log form. (B) E. O. Wilson’s (1961) figure of SARs for ponerine and cerapachyine ants in Melanesia. Solid dots represent islands (ISARs); open circles, cumulative areas of New Guinea up to and including the whole island (SACs); triangles, archipelagos (not used in the regression); and the square, the whole of South-East Asia. (C) Some alternative configurations of area that might be involved in different studies: the bottom right represents a group of isolates that could be the basis for an ISAR, whereas the other three sampling scenarios would be used to construct a SAC. (A) From Lomolino et al. (2017; figure 13.8); (B) and (C) from Whittaker and Fernández-Palacios (2007; figure 4.2 and box 4.2, respectively; part (B) was originally adapted from Wilson, 1961)

neutral theory of biodiversity and biogeography (Hubbell, 2001; Chapter 11). In addition, SAR models have been widely used in applied ecology and conservation science and represent one of the most important tools in the conservation biogeographer’s toolkit (Rosenzweig, 2004;

Whittaker et al., 2005; Chapters 13–17). For example, the SAR is a cornerstone of the applied ‘reconciliation ecology’ research agenda (Rosenzweig, 2003, 2004).

1.1 The Many Types of Species–Area Relationship

At this stage it is necessary to define what exactly is meant by the term ‘species–area relationship’. While the SAR may appear to be a relatively uncomplicated concept, its application within the ecological literature is often somewhat ambiguous. Most of this ambiguity concerns the fact that there is not a single type of SAR, but instead there is a suite of relationship types with more or less distinct data structures. While the search for an agreed classification and terminology has generated much debate (e.g. Scheiner, 2003; Gray et al., 2004; Dengler, 2009), there are only two variables involved in each case: area and species number, and so the problem can be quickly described. First, the areal units analysed may be geographically separated or contiguous, permitting their analysis either as separate entities or as a nested sequence. Second, each species can be counted once as area is accumulated (whether from a nested sequence of contiguous areas or not) or separately in each (sub-)area. Third, for the accumulation curve structure, the value of richness entered for a given size of area can represent a single data point or the average richness value of multiple samples of that size (Dengler et al., 2020).

The upshot is that several forms of species accumulation curve (SAC) can be identified as types of species–area relationship (Type I–III curves in Scheiner’s 2003 typology) but just one type of data structure of ‘isolate’ area versus species number per isolate (Gray et al., 2004), which some term island species–area relationships (ISARs; Type IV SARs in Scheiner, 2003) (e.g. Triantis et al., 2012; Matthews et al., 2016a, b). Further, SACs are often constructed using non-area-based measures of sampling effort (e.g. trap hours) and so sample area-based SACs can be distinguished as a subset of SACs.

At its most basic, SACs are constrained by their mode of construction to display a monotonic increase in species richness. A SAC must either remain constant or increase with each increment in area (Figure 1.2), such that the total richness of the study system is described by the final data point. By contrast, sometimes a larger island can have fewer species than a smaller one and, in certain rare circumstances, there can even be a negative overall ISAR or the relationship may be negative over a limited span of the area range of a study system (Figure 1.2).

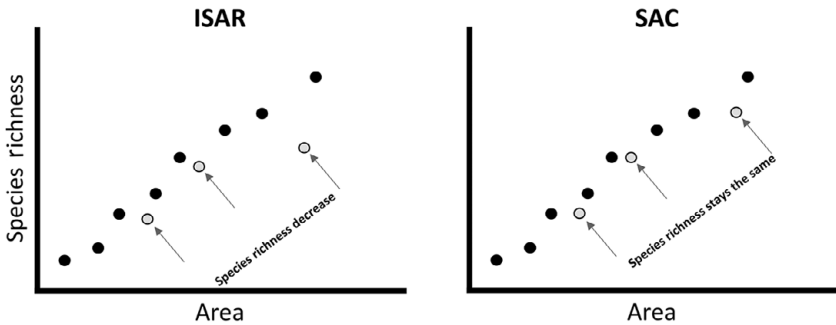


Figure 1.2 Two hypothetical species–area relationships. To the left, an island (isolate) species–area relationship (ISAR) in which there is scatter around the mean trend, to the extent that some islands are less rich than one or more smaller island; to the right, a species accumulation curve (SAC). The SAC is constructed by adding the new species encountered per each extension of area, such that the SAC is constrained never to decrease. As each island may contain different subsets of species, the ISAR only crudely constrains the possible overall system richness, whereas the final data point for the SAC describes the overall system richness.

The lack of a generally agreed terminology distinguishing SAR types has presented a real hindrance to the development of a shared understanding. Studies comparing SARs often combine ISARs and SACs without acknowledging that the two types have different properties (but see e.g. Drakare et al., 2006; Matthews et al., 2016b). For example, the seminal SAR figure of Wilson (1961) for ponerine and cerapachyine ants in Melanesia compares an ISAR (island data) with a SAC (‘mainland’ New Guinea), a feature that is often neglected in work citing or reproducing it (see Figure 1.1B). Indeed, some have argued that, to fairly compare SARs from different systems, the whole sampling design must be identical, including range of area, type of SAR (SAC or ISAR) and if SACs are the focus of study, the accumulation order, sampling intensity, plot shape, use of continuous or discontinuous plots and, if the latter, the locations of the discontinuous plots within the study extent (see Chapter 7; see Figure 1.1C for some examples of SAR construction approaches).

In this volume, we have encouraged authors to make explicit reference to the type(s) of SAR (e.g. ISAR, SAC or both) that their chapter is focused on. However, and as with most things in science and life in general, different people have different opinions on the correct terminology to use and we have not imposed a standard usage. For instance, in certain chapters SACs are referred to as nested SARs, and the term saSAR

is used in some chapters to refer to sample–area based SACs. We acknowledge that our own use of the term ‘island SAR’ (or Isolate SAR) may not be the best solution as ISARs might be constructed using data not from isolates but for other irregularly sized geographical units of varying degrees of geographical isolation (e.g. countries or biogeographic provinces).

1.2 A Flexible Biogeographical Law

Our work has generally focused on the ISAR, whether that be for true islands (e.g. Triantis et al., 2012) or habitat islands (Matthews et al., 2016a). What has struck us during this work (and in reading the work of many others) is that the idea that the ISAR is universal is only really true in the sense that larger areas tend to have more species than smaller areas. Beyond that, many characteristics of ISARs have been found to differ (often quite considerably) between datasets. Lomolino (2000; see also Whittaker & Triantis, 2012) recognized this when he described the ISAR as ‘protean’. The adjective ‘protean’, meaning ‘versatile’, ‘flexible’ and ‘able to change easily’, is derived from the Ancient Greek God ‘Proteus’. According to Greek mythology, Proteus was an early prophetic sea-god who had the ability to foresee the future, but would frequently change his shape to avoid those who asked him to share his prophetic knowledge. The name Proteus suggests the ‘first’, and the ISAR is considered to be one of the first discussed general patterns related to the diversity of life. One other obvious way that the ISAR can be considered a protean pattern is the fact that the mathematical form of the relationship often varies between datasets (Triantis et al., 2012; Matthews et al., 2016a; Leveau et al., 2019). In practice, we can often fit multiple models successfully to the same dataset. We then have the challenge of trying to work out which is the best model, that is, the closest approximation to the true form of the relationship. This may be attempted as a statistical exercise, that is, as a black box type of approach. Alternatively, we may regard the process of model fitting rather differently, as an exercise in hypothesis testing, that is, we may have theoretical grounds for predicting a particular form or a particular set of alternative forms that are linked to distinct mechanisms or processes. The step of model fitting is then used to determine the plausibility of the initial hypothesis or of selecting from a set of multiple–working hypotheses those which remain standing and then, of these, which has the greatest verisimilitude. Hence, SARs have what we might think of as phenomenological flexibility, as we are describing a suite of slightly different aspects of how diversity and area are related and then, for these different phenomena, there are advocates for particular mathematical

models to represent the SAR. Indeed, over thirty different functions have been proposed (Chapter 7).

While the variation in ISAR form between datasets has (so far) precluded the identification of a universal model that provides the best fit to all datasets, the discovery of generalities regarding how and why ISARs vary has improved our understanding of the processes shaping diversity patterns more generally (see the Foreword). We know for example that the factors that influence species richness vary across spatial scale (Shmida & Wilson, 1985; Rosenzweig, 1995; Whittaker et al., 2001; Turner & Tjørve, 2005) and thus the ISAR should be scale-dependent (see Figure 1.3A). These different factors should also affect the nature of the relationship of species richness with area. Recent meta-analyses have shown that ISAR slope (z) increases from habitat, to continental shelf, to

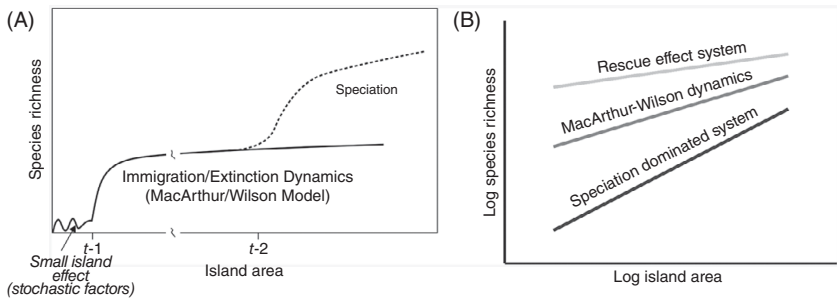


Figure 1.3 Two contrasting models of ISAR form. (A) The theoretical relationship of species richness with area in arithmetic space according to Lomolino (2000). Starting at the left side, there is little change in species number until a critical threshold is reached, but beyond threshold t_1 , species number increases rapidly, as a function of the immigration/extinction dynamics of the equilibrium model of island biogeography. With islands larger than t_2 , species number shows a further increase, as it is afforded by in situ speciation. The ‘small-island effect’ is shown by many island datasets (see also Chapter 19), but the generality (and even existence) of the second threshold and the upward curve towards the right side of the plot is contested. (B) As archipelago isolation increases, the ISAR slope (z) generally increases. Rescue effect systems are the least isolated and hence species populations on smaller islands are continually rescued from extinction by supplementary immigration, resulting in high intercepts and low slopes. Islands of intermediate isolation experience higher rates of species turnover and therefore feature steeper slopes and lower intercepts. Speciation dominated systems refer to remote archipelagos in which larger islands gain species through in situ diversification, generating the steepest slopes and lowest intercepts. This panel is only approximated by analyses of empirical datasets (e.g. Matthews et al. 2016a). (A) From Lomolino (2000; figure 6) under license from John Wiley and Sons; (B) from Whittaker et al. (2017; figure 4A) and reprinted with permission from AAAS

oceanic islands (Triantis et al., 2012; Matthews et al., 2016a). The shallowest slopes and higher intercepts characterize systems with minimal isolation, in which island–extirpation events are typically rapidly reversed by recolonization (‘rescue effects’) and which therefore feature comparatively high richness even on the smaller islands. By contrast, remote oceanic islands receive such low rates of immigration that colonizing lineages can diversify in isolation. In these systems, in theory, the smallest islands have low species richness because their small, unreliable resource bases cannot sustain marginal populations of small size or permit the origin and persistence of newly formed endemics. In practice, as we argue in Chapter 3, the more remote oceanic archipelagos can be so isolated that the configuration of the archipelago itself exerts a strong influence on ISAR form, in part overriding the effect on slope and intercept exerted by distance from the mainland (and see Matthews et al., 2019).

Thus, different processes are expected to result in different slopes; the difference is expected to be most pronounced when speciation-dominated systems are compared to systems where MacArthur–Wilson dynamics prevail and speciation has a secondary or no role (Figures 1.3 and 1.4). The cichlid

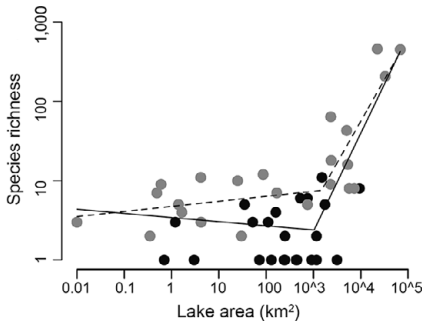


Figure 1.4 The effect of adaptive radiation on the ISAR (lighter points = lakes with speciation; darker points = lakes without speciation). The fit of two-slope ISAR models are shown (solid line = whole dataset; dashed line = lakes with speciation only). For the whole dataset model fit, the pre-breakpoint slope does not significantly differ from zero, the breakpoint occurs at 1,030 km² and the post-breakpoint slope (1.29) is significant and positive. For the model fit to the lakes with speciation, the pre-breakpoint slope does not significantly differ from zero, the breakpoint occurs at 1,470 km² and the post-breakpoint slope (0.99) is significant and positive. In both cases the two-slope model provides a better fit to the data than a one-slope regression model according to AIC_c. The data are of cichlid fishes in forty-six African lakes. From Wagner et al. (2014; figure 3b) under license from John Wiley and Sons

species of the Great African Lakes provide an illustration of these differences, but also of a clear threshold effect where there appears to be no relationship between species and area until a minimum lake area has been reached. Above this threshold, those lakes in which in situ diversification has occurred demonstrate a clear positive relationship. The *Anolis* lizards of the Caribbean provide another pertinent example of a threshold in the speciation–area and species–area relationships (Losos & Parent, 2010; figures 15.3 and 15.5).

Elements of the above arguments were codified in Rosenzweig's (1995) seminal scale-structured model of species–area relationships, which, however, included both ISARs and SACs (see Scheiner, 2003; Whittaker & Fernández-Palacios, 2007). His interprovincial curve represents an ISAR fitted between distinct biogeographical provinces, which he argued should exhibit a slope always >0.6 and generally close to unity (see Rosenzweig, 1995, 1998, 2001) (Figure 1.5A). SACs within continents, his intraprovincial curves, should be flatter and with higher intercepts than regular ISARs found within the province, which should display a range of values depending on their degree of isolation. Figure 1.5B was inspired by Rosenzweig's model but differs in showing exclusively ISARs. Given the propensity for remote oceanic archipelagos to generate endemics in situ, the expectation is for the between-archipelago or archipelagic species–area relationship (ASAR) to provide a steep relationship, where the relevant within-archipelago ISAR only crudely predicts the archipelagic value and, again, there is variation in the overall richness of different archipelagos (Figure 1.5A and B) in perhaps widely different locations. This reasoning is supported by analyses showing that i) for oceanic archipelagos, inter-archipelago species–area relationships (ASARs) are systematically steeper than the constituent ISARs (e.g. Triantis et al., 2015) and ii) ISARs estimated for endemic species are typically steeper with lower intercepts than those for non-endemic native species for the same archipelago (Figure 1.5C; Triantis et al., 2008). The final panel (Figure 1.5D) presents another generalization, which is that, for forest habitat island systems, ISARs calculated for generalist bird species are flatter and with higher intercepts than those for forest specialist bird species (Matthews et al., 2014). That i) specialist species, more reliant upon and restricted to the focal habitat, have the steeper slopes and ii) island endemic species have steeper slopes than non-endemic species (which may have populations on other islands or landmasses exchanging propagules with the islands in question) appears to be part of the same pattern, relating to the extent to which, as Rosenzweig put it, the islands in question are acting as sources or as sinks.

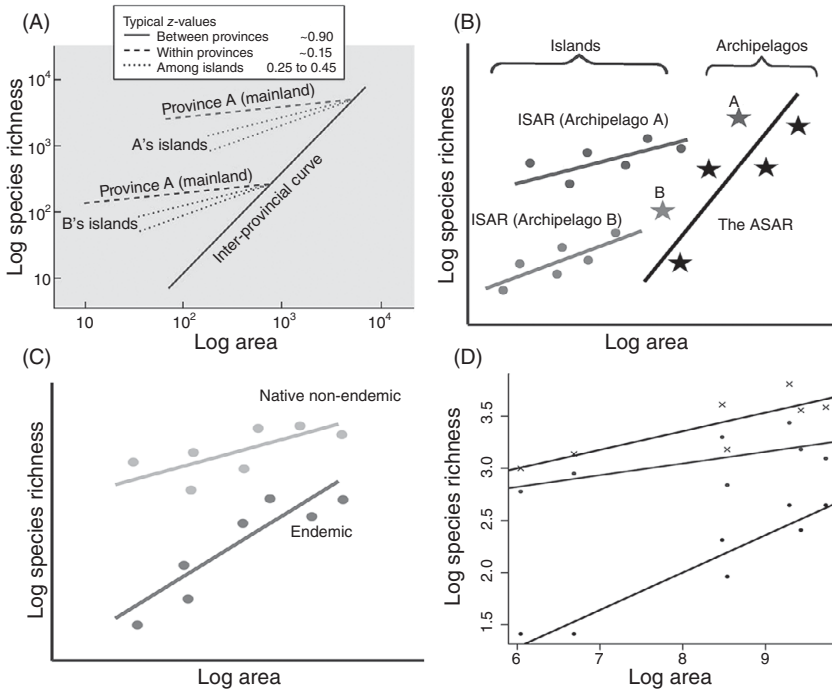


Figure 1.5 Generalized species–area relationships as a function of scale and isolation. (A) Rosenzweig’s scale-structured model of species–area relationships, comprising a mix of SAC and ISAR types. (B) The archipelago species–area relationship (ASAR) and two of its constituent archipelago ISARs. Points A and B on the ASAR represent the archipelago diversity for archipelagos A and B, respectively. (C) ISARs constructed using endemic species and native non-endemic species. (D) Three ISARs for the same bird habitat island (seven islands) dataset: the bottom curve is for habitat specialist bird species, the middle curve is for habitat generalists and the top curve (and the crosses) for all bird species combined. The lines are the fit of the power (log–log) ISAR model. See text for further details. (A) From Rosenzweig (1995; figure 9.11; modified by Lomolino et al., 2017) and reprinted with permission from Cambridge University Press; (B) and (C) from Whittaker et al. (2017; figure 4c and figure 4b, respectively) and reprinted with permission from AAAS; and (D) from Matthews et al. (2014; figure 1e) under license from John Wiley and Sons

1.3 From Species–Area Relationships to Diversity–Area Relationships

Recently, and echoing the shift in macroecology and biogeography more generally, ISAR research has expanded to include other facets of diversity, such as functional (FD) and phylogenetic (PD) diversity

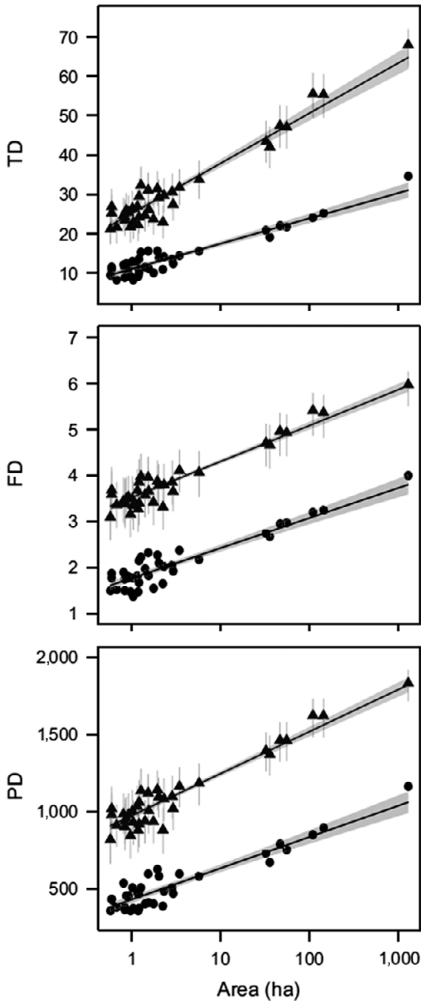


Figure 1.6 The relationship between island area and taxonomic diversity (top), functional diversity (middle) and phylogenetic diversity (bottom) for seventy-seven breeding bird species recorded on thirty-six islands in the Thousand Island Lake, China (surveyed between 2007 and 2016). The circles are observed diversity and the triangles diversity estimated using multi-species occupancy models. The lines are linear regression model fits (with the 95 per cent confidence intervals around each point in the case of the occupancy models) to the two sets of data after accounting for island isolation. Functional diversity was measured using a dendrogram-based metric and phylogenetic diversity using Faith's index. The grey bars represent 95 per cent Bayesian credible intervals of posterior mean estimates of TD, FD and PD. From Si et al. (2018; figures 1a, c and e) under license from John Wiley and Sons

(Whittaker et al., 2014; Mazel et al., 2015; Chapter 5). Figure 1.6 provides an example of an ISAR and the corresponding functional diversity–area and phylogenetic diversity–area relationships for a dataset of breeding birds in a lake island archipelago in China (Si et al., 2018). As has been argued for community ecology in general (e.g. Webb et al., 2002; Kraft et al., 2008), there is a hope that a focus on functional and phylogenetic diversity in SAR/diversity–area relationship studies may help us better understand the processes that underpin SARs/diversity–area relationships and ultimately the mechanisms that underpin community assembly. In addition, it enables us to better predict the impact of habitat loss on these other facets of biodiversity, which may have some value for developing models of ecosystem function (see Chapter 5). However, as many FD and PD metrics generally co-vary strongly with taxonomic diversity (TD), discerning the additional information provided by these metrics requires assessment of whether and how the trends diverge from null expectations (e.g. Whittaker et al., 2014). Going forward, the evaluation of other diversity–area relationships alongside SARs represents a challenging but promising avenue for future research in the field.

1.4 The Present Volume

This book is loosely structured into five sections. The first section comprises the present chapter and a chapter on the history of the SAR (Chapter 2). The SAR has a long history; one that includes several early studies published by Scandinavian authors, which have been overlooked in the mainstream ecological literature until recently (Tjørve et al., 2018). Chapter 2 provides an overview of these early studies, the development of mathematical SAR theory and the subsequent application of the SAR in a wide range of fields, such as island biogeography and conservation biogeography.

More recently, the last ten to fifteen years have seen i) the publication of several meta-analyses that have aimed to draw out general SAR patterns (e.g. Triantis et al., 2012; Matthews et al., 2019) and ii) the expansion of SAR theory to other types of diversity (e.g. Mazel et al., 2015) as well as non-traditional species assemblages (e.g. alien species; Baiser & Li, 2018). The second section of the book covers these ideas, including, in regard to the former, an expansion of a recently published global model of ISARs that aims to explain variation in parameters of the power ISAR model between datasets (Chapter 3) and a more general

discussion of the determinants of SAR shape, including the idea that SAR drivers can be organized as a hierarchy of different processes and factors (Chapter 4). In regard to the latter, reviews of functional diversity and phylogenetic diversity–area relationships (Chapter 5) and alien species–area relationships (Chapter 6) provide comprehensive accounts of these topics.

Due in part to increases in computer power, increased mathematical training in ecology and biology courses and the now wide range of available software packages for ecological data analysis, the last twenty years has seen a resurgence in theoretical SAR research: both in terms of pure SAR research questions and in the development of (macro) ecological theories in which the SAR is a fundamental component. The third section of the book, focused on theoretical advances in SAR research, includes chapters dedicated to both of these types of theoretical developments, including topics such as the search for mathematical SAR functions (Chapter 7), the scaling and geometric properties of SARs (Chapter 8), extreme value theory and the SAC (Chapter 9), trophic SARs (Chapter 12) and the role of SARs in two recently proposed unified macroecological and biogeographical theories: the maximum entropy theory of ecology (Chapter 10) and the unified neutral theory (Chapter 11).

The fields of conservation biology and conservation biogeography are concerned with impacts of environmental change on biodiversity and on generating useful applied information that can be used in conservation and sustainable biodiversity management. As a general rule, conservation biology is focused more on local scale questions, whilst conservation biogeography is the subset of that broader field that revolves around issues operating at coarser spatial (and often temporal) scales. However, the SAR is a fundamental tool in both disciplines and has been used, amongst other things, to estimate the number of species likely to become extinct as a result of habitat loss and climate change (e.g. Ladle, 2009; Triantis et al., 2010) and to identify potential biodiversity hotspots and protected areas in both the terrestrial and marine realms (e.g. Neigel, 2003; Guilhaumon et al., 2008). The fourth section of the book focuses on the applied uses of the SAR, including reviews of the aforementioned applications (hotspot identification – Chapter 13; extinction predictions – Chapter 14), as well as novel contributions such as the use of network theory in island biogeography research and the importance of intra-archipelago configuration (which is of both pure and applied interest) (Chapter 15),

the importance of geometry in habitat loss research and extinction predictions (Chapter 16) and the introduction of the concept of relict species–area relationships to estimate the conservation value of reservoir islands in flooded forest landscapes (Chapter 17). The section concludes with a chapter on the application of SARs in the marine realm, with a particular focus on the issues involved in interpreting marine SARs at large spatial scales (Chapter 18).

The final section of the book, consisting of a single chapter (Chapter 19), is based around a metaphor M. L. Rosenzweig used in the preface of his 1995 book, comparing the study of species diversity patterns with a dinosaur that has come alive and is challenging us. This final chapter also brings together some of the general findings of the previous chapters and identifies outstanding research questions and areas where further work is needed; we hope providing a catalyst for future ISAR-based research.

Ultimately, our aim in this volume has been to bring together a diverse array of leading researchers on SAR issues in order to: i) generate a comprehensive treatment that is relevant to a wide range of fields, ii) provide a useful general resource for students and researchers interested in the SAR and iii) provide a substantial novel contribution to the literature. We hope that it may serve to increase interest in the SAR as a pattern (or set of patterns) and to stimulate further developments in the field.

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References

- Baiser, B. & Li, D. (2018) Comparing species–area relationships of native and exotic species. *Biological Invasions*, **20**, 3647–3658.
- Bolgovics, Á., Ács, É., Várbíró, G., Görgényi, J. & Borics, G. (2015) Species–area relationship (SAR) for benthic diatoms: A study on aquatic islands. *Hydrobiologia*, **764**, 91–102.
- Connor, E. F. & McCoy, E. D. (1979) Statistics and biology of the species–area relationship. *The American Naturalist*, **113**, 791–833.
- Dengler, J. (2009) Which function describes the species–area relationship best? A review and empirical evaluation. *Journal of Biogeography*, **36**, 728–744.
- Dengler, J., Matthews, T. J., Steinbauer, M. J., Wolfrum, S., Boch, S., Chiarucci, A., Conradi, T., Dembicz, I., Marcenò, C., García-Mijangos, I., Nowak, A., Storch, D., Ulrich, W., Campos, J. A., Cancellieri, L., Carboni, M., Ciaschetti, G., De Frenne, P., Dolezal, J., Dolnik, C., Essl, F., Fantinato, E., Filibeck, G., Grytnes, J.-A., Guarino, R., Güler, B., Janišová, M., Klichowska, E., Kozub, L., Kuzemko, A., Manthey, M., Mimet, A., Naqinezhad, A., Pedersen, C., Peet, R. K., Pellissier, V., Pielech, R., Potenza, G., Rosati, L., Terzi, M., Valkó, O., Vynokurov, D., White, H., Winkler, M. & Biurrun, I. (2020) Species–area relationships in continuous vegetation: Evidence from Palaeartic grasslands. *Journal of Biogeography*, **47**, 72–86.
- Drakare, S., Lennon, J. J. & Hillebrand, H. (2006) The imprint of the geographical, evolutionary and ecological context on species–area relationships. *Ecology Letters*, **9**, 215–227.
- Gray, J. S., Ugland, K. I. & Lamshead, J. (2004) Species accumulation and species–area curves – A comment on Scheiner (2003). *Global Ecology & Biogeography*, **13**, 473–476.
- Guilhaumon, F., Gimenez, O., Gaston, K. J. & Mouillot, D. (2008) Taxonomic and regional uncertainty in species–area relationships and the identification of richness hotspots. *Proceedings of the National Academy of Sciences USA*, **105**, 15458–15463.
- Hubbell, S. P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton, NJ: Princeton University Press.
- Kraft, N. J. B., Valencia, R. & Ackerly, D. D. (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, **322**, 580–582.
- Ladle, R. (2009) Forecasting extinctions: Uncertainties and limitations. *Diversity*, **1**, 133–150.
- Lawton, J. H. (1999) Are there general laws in ecology? *Oikos*, **84**, 177–192.
- Leveau, L. M., Ruggiero, A., Matthews, T. J. & Bellocq, M. I. (2019) A global consistent positive effect of urban green area size on bird richness. *Avian Research*, **10**, 30.
- Lomolino, M. V. (2000) Ecology's most general, yet protean pattern: The species–area relationship. *Journal of Biogeography*, **27**, 17–26.
- Lomolino, M. V., Riddle, B. R. & Whittaker, R. J. (2017) *Biogeography. Biological diversity across space and time*, 5th ed. Sunderland, MA: Sinauer Associates.
- Losos, J. B. & Parent, C. E. (2010) The speciation–area relationship. *The theory of island biogeography revisited* (ed. by J. B. Losos and R. E. Ricklefs), pp. 415–438. Princeton, NJ: Princeton University Press.

- MacArthur, R. H. & Wilson, E. O. (1967) *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Matthews, T. J., Cottee-Jones, H. E. & Whittaker, R. J. (2014) Habitat fragmentation and the species–area relationship: A focus on total species richness obscures the impact of habitat loss on habitat specialists. *Diversity and Distributions*, **20**, 1136–1146.
- Matthews, T. J., Guilhaumon, F., Triantis, K. A., Borregaard, M. K. & Whittaker, R. J. (2016a) On the form of species–area relationships in habitat islands and true islands. *Global Ecology & Biogeography*, **25**, 847–858.
- Matthews, T. J., Rigal, F., Triantis, K. A. & Whittaker, R. J. (2019) A global model of island species–area relationships. *Proceedings of the National Academy of Sciences USA*, **116**, 12337–12342.
- Matthews, T. J., Triantis, K. A., Rigal, F., Borregaard, M. K., Guilhaumon, F. & Whittaker, R. J. (2016b) Island species–area relationships and species accumulation curves are not equivalent: An analysis of habitat island datasets. *Global Ecology & Biogeography*, **25**, 607–618.
- Mazel, F., Renaud, J., Guilhaumon, F., Mouillot, D., Gravel, D. & Thuiller, W. (2015) Mammalian phylogenetic diversity–area relationships at a continental scale. *Ecology*, **96**, 2814–2822.
- McGuinness, K. A. (1984) Equations and explanations in the study of species–curves. *Biological Reviews*, **59**, 423–440.
- Neigel, J. E. (2003) Species–area relationships and marine conservation. *Ecological Applications*, **13**, 138–145.
- Rosenzweig, M. L. (1995) *Species diversity in space and time*. Cambridge: Cambridge University Press.
- Rosenzweig, M. L. (1998) Preston’s ergodic conjecture: The accumulation of species in space and time. *Biodiversity dynamics: Turnover of populations, taxa, and communities* (ed. by M. L. McKinney and J. A. Drake), pp. 311–348. New York: Columbia University Press.
- Rosenzweig, M. L. (2001) Loss of speciation rate will impoverish future diversity. *Proceedings of the National Academy of Sciences USA*, **98**, 5404–5410.
- Rosenzweig, M. L. (2003) Reconciliation ecology and the future of species diversity. *Oryx*, **37**, 194–205.
- Rosenzweig, M. L. (2004) Applying species–area relationships to the conservation of diversity. *Frontiers of biogeography: New directions in the geography of nature* (ed. by M. V. Lomolino and L. R. Heaney), pp. 325–343. Sunderland, MA: Sinauer Associates.
- Scheiner, S. M. (2003) Six types of species–area curves. *Global Ecology & Biogeography*, **12**, 441–447.
- Schoener, T. W. (1976) The species–area relations within archipelagoes: Models and evidence from island land birds. *Proceedings of the XVI International Ornithological Conference* (ed. by H. J. Firth and J. H. Calaby), pp. 629–642. Canberra: Australian Academy of Science.
- Shmida, A. & Wilson, M. V. (1985) Biological determinants of species diversity. *Journal of Biogeography*, **12**, 1–20.
- Si, X., Cadotte, M. W., Zhao, Y., Zhou, H., Zeng, D., Li, J., Jin, T., Ren, P., Wang, Y., Ding, P. & Tingley, M. W. (2018) The importance of accounting

- for imperfect detection when estimating functional and phylogenetic community structure. *Ecology*, **99**, 2103–2112.
- Tjørve, E. & Tjørve, K. M. C. (2017) Species–area relationship. *eLS (Encyclopedia of Life Sciences Online)*, pp. 1–9. Chichester: John Wiley & Sons.
- Tjørve, E., Tjørve, K. M. C., Šizlingová, E. & Šizling, A. L. (2018) Great theories of species diversity in space and why they were forgotten: The beginnings of a spatial ecology and the Nordic early 20th-century botanists. *Journal of Biogeography*, **45**, 530–540.
- Triantis, K. A., Borges, P. A. V., Ladle, R. J., Hortal, J., Cardoso, P., Gaspar, C., Dinis, F., Mendonça, E., Silveira, L. M. A., Gabriel, R., Melo, C., Santos, A. M. C., Amorim, I. R., Ribeiro, S. P., Serrano, A. R. M., Quartau, J. A. & Whittaker, R. J. (2010) Extinction debt on oceanic islands. *Ecography*, **33**, 285–294.
- Triantis, K. A., Economo, E. P., Guilhaumon, F. & Ricklefs, R. E. (2015) Diversity regulation at macro-scales: Species richness on oceanic archipelagos. *Global Ecology & Biogeography*, **24**, 594–605.
- Triantis, K. A., Guilhaumon, F. & Whittaker, R. J. (2012) The island species–area relationship: Biology and statistics. *Journal of Biogeography*, **39**, 215–231.
- Triantis, K. A., Mylonas, M. & Whittaker, R. J. (2008) Evolutionary species–area curves as revealed by single-island endemics: Insights for the interprovincial species–area relationship. *Ecography*, **31**, 401–407.
- Turner, W. R. & Tjørve, E. (2005) Scale-dependence in species–area relationships. *Ecography*, **28**, 721–730.
- Wagner, C. E., Harmon, L. J. & Seehausen, O. (2014) Cichlid species–area relationships are shaped by adaptive radiations that scale with area. *Ecology Letters*, **17**, 583–592.
- Wardle, D. A., Zackrisson, O., Hörnberg, G. & Gallet, C. (1997) The influence of island area on ecosystem properties. *Science*, **277**, 1296–1299.
- Webb, C. O., Ackerly, D. D., McPeck, M. A. & Donoghue, M. J. (2002) Phylogenies and community ecology. *Annual Review of Ecology, Evolution, and Systematics*, **33**, 475–505.
- Whittaker, R. J. & Fernández-Palacios, J. M. (2007) *Island biogeography: Ecology, evolution, and conservation*, 2nd ed. Oxford: Oxford University Press.
- Whittaker, R. J. & Triantis, K. A. (2012) The species–area relationship: An exploration of that ‘most general, yet protean pattern’. *Journal of Biogeography*, **39**, 623–626.
- Whittaker, R. J., Araújo, M. B., Jepson, P., Ladle, R. J., Watson, J. E. M. & Willis, K. J. (2005) Conservation biogeography: Assessment and prospect. *Diversity and Distributions*, **11**, 3–23.
- Whittaker, R. J., Fernández-Palacios, J. M., Matthews, T. J., Borregaard, M. K. & Triantis, K. A. (2017) Island biogeography: Taking the long view of nature’s laboratories. *Science*, **357**, eaam8326.
- Whittaker, R. J., Rigal, F., Borges, P. A. V., Cardoso, P., Terzopoulou, S., Casanoves, F., Pla, L., Guilhaumon, F., Ladle, R. J. & Triantis, K. (2014) Functional biogeography of oceanic islands and the scaling of functional diversity in the Azores. *Proceedings of the National Academy of Sciences USA*, **111**, 13709–13714.

- Whittaker, R. J., Willis, K. J. & Field, R. (2001) Scale and species richness: Towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.
- Wilson, E. O. (1961) The nature of the taxon cycle in the Melanesian ant fauna. *The American Naturalist*, **95**, 169–193.