



EDITORIAL

The species–area relationship: an exploration of that ‘most general, yet protean pattern’¹



The generality of the increase in the number of species with the physical space sampled has long been known and commented on by natural scientists (e.g. Watson, 1859; Arrhenius, 1921; Rosenzweig, 1995). Although the basic phenomena were reasonably well described and understood by the time of the seminal contributions of Preston (1962) and MacArthur & Wilson (1967), analyses of the variation in form of the various types of species–area relationship (SAR) have continued to receive attention (reviewed in, e.g. Connor & McCoy, 1979; Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007). This is because the SAR is a fundamentally important pattern within ecology and understanding the processes that shape the particular form taken by each type of SAR is crucial for both ecological biogeography and conservation biogeography (see reviews in Lomolino *et al.*, 2010; Ladle & Whittaker, 2011).

Having recently completed, with our colleague François Guilhaumon, a wide-ranging analysis of the form of a major class of SAR (Triantis *et al.*, 2012), we were motivated to compile a so-called virtual issue of the *Journal of Biogeography* to illustrate the development of ideas concerning SARs over the period since the journal was launched in 1974. The virtual issue features papers previously published in the journal, and will be made available as a downloadable cross-linked set for as long as interest in the particular set of papers warrants it. The selection includes a number of influential contributions to understanding SARs and their application and we hope may be of value to researchers and educators interested in running seminars on species–area relationships.

¹A title in part borrowed from Lomolino (2000), who by the deployment of the word protean highlighted the variability in form taken by the relationship.

Whilst the increase in species richness with area is general, it is not universal to all data sets and circumstances. What form the relationship takes in particular circumstances is of key concern both for what it reveals of the factors controlling diversity pattern and for the predictive value of SARs in relation to the biodiversity consequences of anthropogenic change (habitat alteration and destruction, climate change, etc).

We highlight three aspects of the selection before briefly commenting on the papers themselves. First, partly for lack of a consistently applied terminology for different types of SAR, there has been insufficient attention to the significance of different data structures for the form taken by SARs (Scheiner, 2003, 2009, 2011). In reading each of the papers assembled in this virtual issue an important start point is thus for the reader to determine what type of SAR is involved. Second, there are a number of essentially methodological problems involved in the analysis of SARs, for which increasingly sophisticated solutions have been proposed as computational power and statistical packages have improved. These problems are evident in the debates concerning the form of island SARs, whether or not they feature the so-called ‘small-island effect’ and whether or not they reach asymptote (e.g. Lomolino, 2000; Williamson *et al.*, 2001; Gentile & Argano, 2005). Third, and most interesting to the general reader, the papers selected demonstrate an abiding concern with the interpretation of SARs and with determining the individual factors and mechanisms that contribute to the variation in species richness across different spatial and temporal scales, environmental conditions and taxa (e.g. Johnson & Simberloff, 1974; Shmida & Wilson, 1985; Lomolino, 2000; Jonsson *et al.*, 2011).

There are several different forms of SAR, but we hold that the most important distinction is whether cumulative totals are calculated across a set of areas or whether

the actual number of species found in each area is used in the analysis. This distinction in turn is reflected in the difference between two major classes of SAR, termed here species accumulation curves (SACs) and island species area–relationships (ISARs) (following Whittaker & Fernández-Palacios, 2007; Triantis *et al.*, 2012). In order to construct SACs, the cumulative species total across a series of (usually nested) areas is plotted as the dependent variable, versus area. ISARs, on the other hand, are analyses in which a set of distinct islands is used: the number of species found in each island constitutes the dependent variable (*y*-axis) and the area of each island constitutes the independent variable (*x*-axis). ISARs are also often calculated for other types of semi-isolated patches, or habitat islands, while SACs can be calculated for areas of mainland or island as determined by the aims and purposes of the user. Alternative – and more fully developed – terminologies are available (cf. Scheiner, 2003, 2011; Gray *et al.*, 2004; Dengler, 2009). We recommend that the reader consults Scheiner (2011) for further guidance.

FROM THE JSTOR ARCHIVE

Of the 24 papers selected for the virtual issue, six older papers are available via JSTOR, while 18 are online in the Wiley Online Library site. Of the six JSTOR papers, Johnson & Simberloff (1974), which was published in the first volume of the journal, provides a notable example of an ISAR analysis of plants from the British Isles, framed with reference to MacArthur & Wilson’s (1967) theory of island biogeography. They develop an approach based on multiple regression in order to dissect the explanatory power of several variables alongside island area. By way of contrast, Shmida & Wilson (1985) provide a seminal contribution to species–area theory illustrated by an analysis of SACs for plant data from Israel, demonstrating how the environmental context

from which samples are drawn may influence the form of SACs. The paper is notable for its introduction of the notions of mass effects and ecological equivalency as co-determinants of local diversity and was one of the first papers to address the varying causal mechanisms of species diversity as system scale increases.

Zimmerman & Bierregaard's (1986) paper provides a very straightforward species–area analysis, for the number of frog species in seven reserves in the Brazilian Amazon. Their paper is noteworthy, however, for also providing a comparative assessment of area requirements based on autoecology, specifically of the breeding habitat requirements of the frogs, as a critique of over-reliance on the use of SARs as conservation biogeographical tools (see recent review by Triantis & Bhagwat, 2011). Continuing the theme of habitat dependency and heterogeneity, Deshayé & Morisset (1988) provide an example of how breaking down islands into different major habitat types can lead to improved ISAR model fits. Consideration of habitat diversity and heterogeneity has often been found to be productive in developing more effective models of species richness across insular systems (Buckley, 1982; Triantis *et al.*, 2003). In some contexts, of course, the effect of area is overwhelmed by that of other factors, to such a degree that area may not be the most powerful variable or may provide no significant model: an example of this being provided by Dunn & Loehle's (1988) paper on the flora of habitat islands in Wisconsin. Our final paper selected from the JSTOR archive is by Watters (1992). It struck us as interesting for several reasons. First, because it provides an aquatic example, by using freshwater drainages of the Ohio River as its units of analysis; second, because it analyses ISARs at two interrelated trophic levels, for both fish and a particular group of their parasites; and third, because it is concerned with the shape of the SAR.

Of the remainder of the papers, we may group them into: (1) papers concerned primarily with describing and evaluating different models for SARs, (2) papers concerned with SAR shape and its theoretical meaning, of which several are particularly focused on the detection of the so-called small-island effect, (3) two papers that demonstrate ways in which fits may be improved by incorporating variables such as habitat diversity and energy availability into a modified 'area' effect, and finally (4) some examples of recent

work applying SAR models to other biogeographical problems.

DEVELOPING THE MODEL SET: METHODOLOGICAL CONSIDERATIONS

Flather (1996) tests for the best functions, from within a set of nine candidate models, employing data drawn from the North American breeding bird survey. His paper was concerned exclusively with SAC data and he drew on a wider literature to identify some models not originally connected with the species–area relationship literature. Subsequently, Tjørve (2003, 2009) and Williams *et al.* (2009) each reviewed these and other models for use with SAC and/or ISAR data, providing a comparative framework in which the properties of a set of around 20 candidate models were explored. Tjørve (2003, p. 827) goes so far as to state: 'There are two main types of species–area curves: sample curves that are inherently convex and isolate curves, which are sigmoid. Both types may have an upper asymptote'. Note that this classification of SARs is mainly based on the biological features of the units used for the analysis (Preston, 1962) and not on the sampling scheme or the manipulation of species numbers for each unit (Scheiner, 2003; Triantis *et al.*, 2012). The assertion that isolate curves are sigmoid in form remains contentious (below). The paper by Williams *et al.* (2009) is particularly useful both in classifying the candidate SAR models into a smaller number of 'families', based on their mathematical properties, and in providing a road map for the application and comparison of the alternative models (see Triantis *et al.*, 2012). Dengler (2009) has also contributed usefully to this theme by reviewing and comparing several functions for use in SAC and ISAR analyses, with attention to the resulting shapes of the relationships, addressing in an analysis of several data sets some of the same questions subsequently examined in a more comprehensive survey by Triantis *et al.* (2012). It should be noted that these authors use differing overall schemes for classification of curve types (compare also with Dengler & Oldeland, 2010; and see Scheiner, 2009, 2011).

Finally, in this group, we selected a paper by Gentile & Argano (2005), who undertook a comprehensive analysis of ISAR data for 124 islands from the Mediterranean and Macaronesia. In their analysis they explored a set of linear, semi-logarithmic, logarithmic and sigmoid models and in addition under-

took an analysis of the 'small-island effect' (SIE) using a breakpoint regression method. The SIE is itself another area of controversy, with debate raging as to whether SIEs, which have been claimed in several studies, are a biological reality or an artefact of the method used to detect them (e.g. Lomolino & Weiser, 2001; Triantis *et al.*, 2006, 2012; Burns *et al.*, 2009; Tjørve & Tjørve, 2011; Triantis & Sfenthourakis, 2011). The paper by Gentile & Argano (2005) is also of interest for their effort to evaluate scale-dependency in ISAR form.

THE FORM AND SHAPE OF THE CURVE: THEORETICAL CONSIDERATIONS AND EMPIRICAL EVALUATION

In general, the traditional approach to fitting SARs, especially with respect to ISAR data, has been to fit the simplest possible model, preferably one that linearizes the relationship, thereby rendering it tractable for further analysis (e.g. Rosenzweig, 1995). In an influential Millennium Guest Editorial, Lomolino (2000) developed a theoretical case for a more complex form of ISAR, featuring a form of SIE, whereby small islands fail to demonstrate a positive ISAR until a critical area threshold is reached, and whereby the upper end of the relationship tends towards an asymptotic form. He also added a potential secondary phase of increase in species richness corresponding to islands large enough to allow *in situ* speciation. He explored these ideas more fully and empirically in a subsequent paper, which paid particular attention to the SIE (Lomolino & Weiser, 2001). Lomolino's case for a sigmoid model was subsequently criticized by Williamson *et al.* (2001), who were at pains to emphasize that, in their view, 'the species–area relationship does not have an asymptote' (see also Lomolino, 2002; Williamson *et al.*, 2002). The questions raised in this exchange formed a key motivation for our own analysis of the form of ISARs (Triantis *et al.*, 2012).

This section of the virtual issue is made up with three further papers. The first, by Matter *et al.* (2002) is interesting in that it derived a new species–area function based on metapopulation theory, which the authors then compared to the extreme value function and power function models in analyses of five island data sets. The second is a short article by Tjørve & Tjørve (2011) which critically evaluates the SIE. Completing this section is our own analysis of the fit of 20 competing models applied to 601

ISAR data sets (Triantis *et al.*, 2012). The most comprehensive such analysis to date, making use of recent developments in ecological statistics, it is concerned with identifying the most general ISAR models and model shape, and also tests for scale dependency in model fitting. Overall, we show that simple models are mostly to be preferred and that insofar as there is a typical ISAR, it is convex upwards without an asymptote. Published ISAR data include a great variety of emergent patterns and other candidate models can certainly be fitted and may be preferable for particular data sets. However, visual examination of the several hundred adequate models involved in our analysis also revealed that the more complex models, such as sigmoid forms, generally provided no ecologically intelligible advance over simpler models, such as the overall 'best' model, which was found to be the power function (Arrhenius, 1921).

IMPROVING UPON ISARS

Notwithstanding our interest in the form taken by SARs and especially by ISARs, it will be clear upon exploring this literature that there is often a lot of variation in diversity that is not explained solely by area, even when as many as three parameters are used in model fitting (see also Buckley, 1982; Deshayé & Morisset, 1988; Kohn & Walsh, 1994; Adler *et al.*, 2005). We therefore include just two papers that illustrate how more powerful explanatory models are often provided by including other variables either directly combined with area, or in addition to area, in model fitting exercises: the first deals with habitat diversity (Triantis *et al.*, 2003), and the second, by Jonsson *et al.* (2011), follows up earlier work on species–energy theory (e.g. Wright, 1983).

SPECIES–AREA RELATIONSHIPS APPLIED

The final group of papers was selected to illustrate some of the ways in which SARs have been applied in other areas of biogeography. First, Krauss *et al.* (2003) illustrates the value of ISAR analyses within conservation biogeographic theory, highlighting the differences in response to habitat fragmentation between specialist and generalist species of butterflies. Kier *et al.* (2005), in an important paper developing a global map of plant diversity, employ an SAC approach to provide link-

age between different scales of available data, demonstrating in the process that z -values (the 'slope' parameter) differ from region to region: an important observation in relation to projections of species extinctions arising from habitat loss (see also Giam *et al.*, 2011; Triantis & Bhagwat, 2011). Karger *et al.* (2011), in a similar approach, use the power model to correct regional species richness estimates for the effect of area as part of an analysis of elevational gradients in richness using ferns as a model system. Finally, we have included a paper by Algar & Losos (2011) using SARs in a rather different context, to compare the diversity of anoles in insular and mainland systems, where part of the goal was to compare rates of speciation having first accounted for area effects.

PROSPECTS

The species–area relationship has been described as one of ecology's few laws, but in practice the SAR is not a single form of construct, but rather an important class of related macroecological patterns. The relationship is not uniform, but emergent tendencies are evident when enough data of suitable quality are combined for analysis (e.g. Rosenzweig, 1995; Santos *et al.*, 2010; Triantis *et al.*, 2012). The papers in the virtual issue provide a sample of the development of ideas surrounding species–area relationships, and some of the major issues involved in their detection, description and interpretation. We suggest that resolving the outstanding questions concerning the overall form of the SAR across temporal and spatial scales will act as major stepping stones for a deeper understanding of both species–area relationships and broad-scale variation in species richness generally.

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