

## The varied form of species–area relationships



It has often been commented that the species–area relationship (SAR), whereby the number of species increases with area sampled, is one of ecology's few general laws. Moreover, the SAR has long been an important focus within island biogeography and a key tool within conservation biogeography (Gerstner *et al.*, 2014). In particular, it has frequently been used to project likely species losses as a function of habitat loss and fragmentation. This means that understanding the form of SARs and what controls their parameters is important from several perspectives (see Whitaker & Triantis, 2012, and accompanying papers).

The first problem we face is that there are several, quite differently constructed forms of SAR. While progress has been made in categorizing them, with Scheiner (2003) identifying six main forms, a common understanding has yet to be reached on the properties and distinctions involved (Scheiner, 2009). Furthermore, Scheiner's (2003) nomenclature of types I, IIA, IIB, IIIA, IIIB and IV lacks the associative (if imprecise) character of terms such as the collector's curve or the island species–area relationship. The collector's curve refers to plots of increasing cumulative species number with collecting effort, which is simple enough but nonetheless fails to recognize the several distinctive ways in which they may be constructed. The island species–area relationship (ISAR) is a term used by some (e.g. Triantis *et al.*, 2012) to refer to Scheiner's type IV curve. In type IV curves the number of species occurring within each of a set of insular habitats or islands is plotted and regression models fitted as a function of the area of each isolate.

The SAR literature is often confusing simply because authors make little effort to distinguish which form or forms of SAR they are discussing. This is important because while, for example, the power model is often found to be a good (even the 'best') model for many data sets (Triantis *et al.*, 2012), the parameters of the model are likely to vary systematically

depending on a range of properties, scale of system, taxon, regional richness, and what form of data structure (Scheiner's types I to IV) is involved. The implications for conservation may be profound. An illustration of the sensitivity of outcomes to system properties and methods of analysis was provided recently following publication of analyses of endemic–area relationships based on contiguous habitat within continents (He & Hubbell, 2011). These analyses produced very different implications for projected species extinction rates and conservation responses in comparison to earlier work that focused simply on species accumulation curves for all native species and hence generated considerable controversy and debate (e.g. Pereira *et al.*, 2012). Similarly, recent work on endemic–area relationships for oceanic islands using the power (log–log) model ( $\log S = \log c + z \log A$ ), specifically on the parameters of ISARs for single-island endemics, has shown that they typically have higher  $z$  values ('slopes') and  $c$  values ('intercepts') than have ISARs for non-endemic native taxa (Triantis *et al.*, 2008). This reflects emergent ecological differences between the two groupings of species. 'Non-endemic native species' includes many transient, ephemeral or 'sink' species, which may occur in a particular patch or isolate, but which are unable to sustain populations in the isolate in the absence of propagule/gene flow from elsewhere. In contrast, the SARs for local endemic species generally reflect longer-term evolutionary dynamics (Triantis *et al.*, 2008).

Illustrating two very different scales of SAR analysis, two recently published papers in the *Journal of Biogeography* each provide valuable insights into the form of SARs. The first study, by Karger *et al.* (2014), tackles an important theoretical question concerning whether an 'echo pattern' (Rosenzweig & Ziv, 1999) occurs, i.e. whether the clear ISAR found for most island systems scales down to local variations in richness at plot level. In an analysis of montane fern diversity in islands in

Southeast Asia, they explore whether detection of the echo pattern depends on the focal scale (plot size/disposition) at which the local richness is estimated. Their results show the expected roles for area and isolation in regulating species diversity when analysed at the island scale but these factors decline in importance when examining finer-scale diversity data (richness estimated for plots and for transects composed of varying numbers of plots). The relationship between local and regional richness has been much studied and, while potentially theoretically informative, has produced confusing outcomes, in part, at least, because of scale-dependency in terms of how local and regional scales are set (e.g. see Koleff & Gaston, 2002). By linking a local–regional richness analysis with an ISAR analysis, Karger *et al.* (2014) advance our understanding of both patterns. They interpret their data as indicating that the available species pool declines in importance as a regulator of diversity at the local scale. Their analyses imply that local communities are frequently saturated, displaying local variation in richness explicable as a function of local environmental variation rather than the richness of the island system as a whole.

The second study, by Gerstner *et al.* (2014), provides a much larger-scale analysis, for plant species richness based on 1032 geographical areas worldwide. While nested data structures are often used in analyses of continental SARs, they generated data of a type IV data structure (as defined above). Their focus is on quantifying the variation in the parameters of the power model ( $S = cA^z$ ) for areas of continental land mass ranging from 13 to 575,400 km<sup>2</sup>. In conservation applications in particular, a fixed  $z$  value is often used (typically of 0.18–0.25) in extrapolations of future species losses resulting from habitat loss (e.g. Brooks *et al.*, 1997). However, previous work has cast some doubt on the validity of assuming a single global  $z$  value. To test this Gerstner *et al.* (2014) group their data by floristic kingdoms (reflecting

evolutionary history), biomes (reflecting contemporary environmental controls) and land-cover classes (reflecting human alteration of landscapes). Their results show poor support for a single global SAR and that grouping the data by biomes provided more satisfactory models than grouping by land cover or by floristic kingdoms. Thus, unsurprisingly, the global model tends to overestimate richness in tundra and underestimate richness for the richest forest biomes. In terms of the  $z$  parameter, while the global model value came out at 0.179, almost precisely on the 0.18 value classically recognized in the literature, values for individual biomes ranged from 0.078 for boreal forest/taiga to 0.454 for tropical and subtropical coniferous forests. These differences are not trivial. For example, taking the area and species information from the commonly used Barro Colorado Island dataset (a 50-ha tropical forest plot in Panama containing 229 tree species) as an example, and using the backwards version of the power model, we estimate that a 50% reduction in the amount of habitat could be used to indicate 27 extinctions using the traditional  $z$  value of 0.18, and 62 extinctions using the new biome-specific  $z$  of 0.454. Gerstner *et al.* (2014) also show that cultivated land has a surprisingly high value of 0.269 in contrast to a value of 0.177 for pasture, indicating something of the complexities involved in applying island theory to anthropogenically modified landscapes. Variations in  $c$  parameters were equally interesting, and in combination these differences highlight the importance of using appropriately calibrated SAR models rather than following classic canonical or global models for applications within conservation biogeography.

Together, these two studies illustrate the strengths and weaknesses of reliance on analysis of SARs within ecology, biogeogra-

phy and conservation biogeography. First, there are clear emergent trends and patterns in SARs and our understanding of these patterns is advancing. However, second, there is also evidence of scale dependency and of systematic variations between different geographical contexts (biomes, degrees of isolation, etc.). Thus, the use of traditionally popular  $z$  values (e.g. 0.18 and 0.25), which are not validated for specific scales and ecological contexts, to estimate extinctions resulting from habitat loss is likely to result in erroneous predictions. This issue is particularly pertinent given the current rates of natural habitat loss referred to by Gerstner *et al.* (2014). In our view the translation of such insights into improved conservation guidance remains an important and urgent element of the research agenda for conservation biogeographers in the early 21st century.

ROBERT J. WHITTAKER\*  
AND THOMAS J. MATTHEWS

*Conservation Biogeography and  
Macroecology Programme,  
School of Geography and the Environment,  
University of Oxford, South Parks Road,  
Oxford, OX1 3QY, UK  
\*E-mail: robert.whittaker@ouce.ox.ac.uk*

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