

The Species–Area Relationship

Theory and Application

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6 • *Species–Area Relationships in Alien Species: Pattern and Process*

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6.1 Introduction

Earth is home to a remarkable diversity of life. We share our planet with trillions of individual animals and plants and unimaginable numbers of microbes. These organisms belong to millions of species, most of which remain undescribed (Mora et al., 2011), distributed over land and through the aquatic realms in a staggering array of forms. It is the job of biologists to understand the rules that underpin this complexity, yet it has not proved an easy task. Gradually, however, we have started to identify regularities in the diversity and distribution of life. We understand the broad process by which diversification occurs (Darwin, 1859), even if we are still haggling over the details (Sherratt & Wilkinson, 2009). We have also managed to identify regularities in how the resulting diversity is distributed across the planet (Brown, 1995; Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007). Species richness is generally greater at low compared with high latitudes, for example, and in larger relative to smaller geographic areas. This latter pattern is the species–area relationship (SAR), of course, and is our focus here.

The fact that species richness tends to increase with area has been known for more than a century (Chapter 2) and there is an enormous scientific literature documenting the form(s) of the relationship and proposing and testing hypotheses for the underlying mechanism(s) (e.g. Chapters 3 and 4). For most of the history of life, patterns in the distribution of species have been the result of natural processes of speciation, extinction and migration and the wide range of evolutionary, ecological, environmental, life history and behavioural factors that determine variation in those processes. In the last few centuries, however,

these natural processes have increasingly been perturbed and supplanted by anthropogenic influences on the diversity and distribution of life. Rates of speciation, extinction and migration have all been affected by human activities, including habitat destruction and fragmentation, over-harvesting, agriculture and trade. Rates of extinction and migration in particular having increased worldwide in the last 500 years or so, by an estimated two-to-three orders of magnitude above standard background levels (Lawton & May, 1995; Gaston et al., 2003). Patterns of variation in these rates have also been affected, with rates especially elevated on islands (Moser et al., 2018).

The impacts of humanity on rates of migration have led to a new line of research into SARs. Humans have primarily affected migration by deliberately or accidentally translocating species beyond the natural biogeographic limits of their distributions, to areas where they do not naturally occur. These ‘alien’ species may establish viable populations in their new recipient areas. Currently, emergent populations of alien species are being recorded worldwide at an average rate of around one a day, with no sign that the rate of accumulation is slowing down (Seebens et al., 2017). Alien species that spread widely from the original location of establishment and which have negative impacts on the environment or socio-economic activities in their new range are termed invasive (CBD, 2002). The negative impacts of some alien species, coupled with the rate at which new aliens are accumulating, have created a strong impetus to understand the process by which some species invade and has led to the burgeoning research field of invasion biology (Richardson, 2011). One interesting question here is the extent to which alien species follow the same rules as native species when it comes to patterns of diversity. In this chapter, we review the increasing body of research exploring alien species richness in the context of geographic area.

First, we assess the extent to which the richness of alien and native species respond in similar ways to geographic area. This job has been facilitated by the recent publication of a review and analysis of studies that have assessed alien and native SARs for the same taxon in the same set of areas, based on twenty-three studies reporting thirty-six native-exotic pairs for both plant (twenty-two) and animal (fourteen) assemblages (Baiser & Li, 2018). Second, we assess how the addition of alien species to areas affects the overall patterns of SARs. Third, we assess what the relationship between area and richness for alien species tells us about the mechanisms controlling the species–area relationship.

6.2 Alien SARs

While studies in the ecological literature are near-unanimous in finding that the number of species is a positive function of area, there is a range of forms that the positive function can take (Chapters 4 and 7). Studies that report SARs for alien species, however, as far as we are aware, are unanimous in reporting species richness as a power function of area (although that is not to say another SAR function may provide a better fit in certain cases), such that:

$$S = cA^z, \quad (6.1)$$

or to linearize the relationship for convenience:

$$\log S = \log c + z \log A, \quad (6.2)$$

where S is species richness, A is area, z is the exponent (slope) of the relationship and c is the intercept.

While it is possible to plot the relationship using nested areas (type I, *sensu* Scheiner, 2003), such that smaller areas are subsets of larger ones, only two studies of alien SARs that we are aware of have adopted this approach (Hulme, 2008; Tarasi & Peet, 2017). This is too small a sample to draw conclusions about the effect of nesting areas on the form of alien versus native SARs (although typically type I SARs as a group have shallower slopes than other forms; Rosenzweig, 1995). All other studies plot variation in species richness across discrete areas of different sizes, with a slight preponderance of studies analysing areas that are true islands (i.e. areas of land separated by water) versus different sized areas of a contiguous landmass (e.g. different ecoregions within a continent; Baiser & Li, 2018). Traditionally, island SARs are thought to have steeper slopes than relationships from different sized areas of mainland (Rosenzweig, 1995).

Power function SARs can vary in terms of slope, intercept or both, but most attention is typically focused on the slope. Baiser and Li (2018) found that the slopes for alien SARs did not differ, on average, from the slopes for native species plotted from the same taxon in the same area (across studies, mean $z = 0.233$ versus 0.248 , respectively). Thus, alien species richness increases with area at the same rate as does native species richness: in both cases, a ten-fold increase in area leads roughly to a 1.7-fold increase in the number of species present. Further analyses incorporating information on taxon and location revealed SAR slopes to be steeper for studies of plants than for animals and across islands versus different-sized patches of mainlands (mainly island SARs but two nested

SAR datasets were included), but still not to differ between alien and native relationships in these taxa and locations (Baiser & Li, 2018). Thus, plant richness accumulates faster with area than does animal richness and faster with area on islands than on mainlands, but in each case still at the same rate for alien and native species.

Comparison of SAR intercepts, on the other hand, reveals consistent differences between alien and native species: in all cases, intercepts were on average higher for native species than for aliens (Baiser & Li, 2018). Intercepts were also higher for plants than for animals. Thus, a given area in general has more species of plants than of animals and more native species than alien species. However, it is worth noting that all but three of the fourteen studies for animals relate to vertebrates; we would expect areas of a given size to have fewer species of plants than of some invertebrate taxa, given the relative richness of different groups (Mora et al., 2011).

The resulting average SARs reported for native and alien animals and plants by Baiser and Li (2018) are presented in Figure 6.1, in the range 10 to 10,000 km². Slopes for island SARs would be slightly steeper than these depictions and slopes for mainland SARs slightly less steep. Overall, the relationships suggest a general trend for there to be more alien species

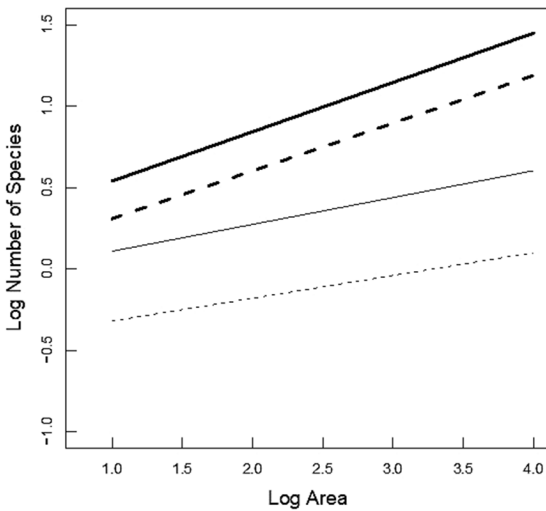


Figure 6.1 Depiction of the average species–area relationships identified by Baiser and Li (2018) in their review of the literature, calculated from the average c - and z -values for native and alien plants and animals, between areas of 10 and 10,000 km². Thick lines = plants, thin lines = animals, solid lines = natives, dashed lines = aliens.

of plant in a given area than native species of animals in the studied groups (though see the caveat about the lack of invertebrate studies) and for the difference to be larger in larger areas. A total of 13,168 plant species are known to have been naturalized somewhere in the world, corresponding to 3.9% of the extant global vascular flora (van Kleunen et al., 2015; Pyšek et al., 2017), versus just over 400 bird species (Dyer et al., 2017a) and around 150 mammal species (Capellini et al., 2015; Blackburn et al., 2017). In fact, there are more species of naturalized plant than there are native species of bird (around 11,000; HBW & BirdLife International, 2017) or mammal (c. 5,400; Wilson & Reeder, 2005). Given that the species richness of all these groups increases with area, we would expect alien plants to outnumber the native species of birds and mammals and many other taxa.

Additional studies document SARs for alien species, but without corresponding comparative data for native species. For example, global data on the combined richness of more than 15,000 alien species from eight taxonomic groups (vascular plants, ants, spiders, fishes, amphibians, reptiles, birds and mammals) across 446 regions of the world also showed a general positive effect of area ($z = 0.35$), with a steeper slope for island (0.53) versus mainland (0.25) regions (Dawson et al., 2017). The lack of equivalent slopes for native species in this and other studies makes them of lesser interest for a comparative assessment of SARs in aliens versus natives and so we do not consider them further here.

6.3 Aliens in SARs

The general similarity in the slopes of alien and native SARs for a given taxon and the larger intercepts of the latter imply that SAR analyses that do not account for the origins of the species included will produce results that differ little from analyses that exclude aliens. The average slope and intercept values for alien and native plant and animal SARs shown in Figure 6.1 translate into five times as many native as alien plant species in a given area, on average, and 3.5–4.0 times as many native as alien animal species. Thus, SARs that do not distinguish native and alien species will, in general, tend to have slightly higher intercept values, and minimally different slope values. That said, there is a reasonable amount of variation in the slopes and intercepts of alien and native SARs across studies, so that in some cases the presence of alien species can make a substantial difference to the observed relationship.

For example, Whittaker et al. (2014) plotted SARs for spiders and beetles of different provenance across nine islands in the Azores. The overall SAR for all spider species ($c = 2.915$, $z = 0.25$) was heavily driven by the presence of alien species ($c = 2.38$, $z = 0.268$), which constituted two thirds of the species in the analysis and similar proportions of the richness of individual islands. The SAR for indigenous spiders has both a lower intercept (2.034) and slope (0.220). Thus, the presence of alien spiders substantially alters the intercept of the SAR for Azorean spiders and to some degree also the slope. Aliens similarly dominate the beetle fauna of these islands, constituting more than 60 per cent of species. They subsequently elevate the Azorean beetle SAR substantially and again affect the slope to some degree (Whittaker et al., 2014).

Sax and Gaines (2005) found that SARs for native and alien plants on oceanic islands showed common slopes (0.31) and intercepts (1.46), such that these islands house equivalent richness of both groups. The addition of alien species effectively doubles the plant richness of these islands. Sax and Gaines (2005) plot SARs for plants in five sets of areas before and after human intervention (i.e. before versus after human-mediated extinction and naturalization). They found that in all cases, the slopes of the relationships remained effectively constant, but the intercepts increased. However, the magnitude of the increases relates to the richness and isolation of the areas. Isolated, species-poor oceanic islands increase the most (100 per cent increase), followed by California Channel Islands (44 per cent), with well-connected, species-rich Californian mainland counties increasing in plant richness the least (17 per cent). In this example, aliens are thus causing the richness of species-poor and species-rich areas to converge.

6.4 Mechanisms Underlying Alien SARs

The burgeoning number of alien species establishing populations worldwide provides strong motivation on its own to study patterns of variation in their richness. Alien species are a classic example of a natural experiment (Diamond, 1986), in which human actions intentionally or accidentally bring about changes in natural systems that can be considered analogous to experimental manipulations. As such, they represent an opportunity to explore the mechanisms that underpin variation in diversity: i) through the extent to which they show similar or divergent patterns to native species and ii) given similarities and differences in the way different hypothesized mechanisms may act on alien compared to

native species (Sax et al., 2005; Cadotte et al., 2006). What then do the regularities in alien versus native SARs tell us about the determinants of richness in both groups?

6.4.1 Sampling Effects

Arguably, the simplest answer to this question is ‘nothing’. This position arises from the observation that the number of alien species in an area is typically a strong and positive function of the number of alien species that have been introduced to that area (termed colonization pressure; Lockwood et al., 2009). For example, Blackburn et al. (2008) showed that the SAR for alien birds established on a sample of thirty-five islands worldwide had a more or less identical slope (but lower intercept) to the SAR for alien birds introduced to those islands (0.18 versus 0.20). This suggests that alien bird richness was effectively a constant proportion of the number of species humans had translocated to an island, with variation in colonization pressure therefore being the primary driver of the alien SAR slope. Dyer et al. (2017b) showed that colonization pressure was by far the strongest predictor of alien bird species richness worldwide, albeit with other anthropogenic (time since first introduction, distance to a historic port) and environmental (native species richness) factors explaining additional variation in richness. A positive relationship between alien species richness and colonization pressure is expected because, at least in closed systems such as many oceanic islands or archipelagos, the latter sets a ceiling on the former (Lockwood et al., 2009): thus, the relationship is between Y and $X + Y$, where Y is alien species richness (the number of introduced populations that establish in an area) and X is the number of introduced populations that fail. The null expectation for relationships of this form, which are termed ‘spurious’ (Prairie & Bird, 1989; Brett, 2004), is positive rather than zero. While alien species can in theory disperse between geographic regions, in practice few aliens spread widely enough that the richness gains from spread outweigh losses due to the failure of introduced populations to establish (most populations fail; Williamson, 1996). Therefore, any SAR we observe for established alien species may actually be a SAR for introduced alien species, with no additional processes required to generate the established alien SAR beyond random extinction.

Unfortunately, it is currently difficult to establish the generality of the relationship between alien species richness and colonization pressure, because, aside from birds, data on colonization pressure are few and far

between. The fact that the relationship is spurious suggests that alien SARs will necessarily be due at least in part to colonization pressure, regardless of taxon. How large that part is depends on how many introduced populations subsequently fail to establish, because, in spurious relationships of this type, the correlation is small when Y is much smaller than X . For example, Brett (2004) used simulations to show that $X + Y$ explains around 50 per cent of the variation in Y ($r \approx 0.7$) when X and Y are equal, falling to around 5 per cent ($r \approx 0.22$) when $Y/X = 0.2$, with only modest effects of sample size (the absolute magnitudes of X and Y). Thus, alien SARs will be less likely to be a function of colonization pressure when most introductions fail ($Y \ll X$). In the island bird data analysed by Blackburn et al. (2008), the numbers of successes and failures were about equal and so we would expect the alien SAR to be strongly determined by colonization pressure. It might not be unreasonable to assume that establishment success rates are relatively high for large and adaptable homeothermic taxa like birds, which therefore may not be representative of the extent to which colonization pressure influences alien SARs in other taxa. Yet again, the lack of information on colonization pressure hampers a robust assessment of the situation, although such data as do exist show that establishment success rates can be highly variable within taxa (Jeschke & Strayer, 2005).

If alien taxa show SARs largely because colonization pressure is a positive function of area, this begs the question of why the number of species introduced should increase with area. The most likely answer is that human population size (Pyšek, 1998; Blackburn et al., 2008) and the associated volume of traded goods imported (Moser et al., 2018) both increase with area. These relationships mean that the number of alien species introduced accidentally through trade would be expected to increase with area and so too would opportunities for deliberate introductions. Indeed, multivariate analysis for alien bird introductions to islands showed that area did not explain variation in colonization pressure if human population size was also included in the model (Blackburn et al., 2008). What is interesting, however, is that, for island data, both human population size and trade increase with area with exponents close to 1 (Blackburn et al., 2008; Moser et al., 2018), while the exponent for colonization pressure is close to the typical z -value for island SARs ($z = 0.2$; Blackburn et al., 2008). In fact, we might reasonably expect such a relationship from sampling effects alone.

In a classic paper, Preston (1962) derived an expected z -value for island SARs of around 0.27, assuming a specific ('canonical') lognormal

form for the species abundance distribution, a given minimum number of individuals necessary for a species to persist and that the number of individuals on an island is proportional to its area. Larger areas house more individuals and, as a result, more species on the basis of the underlying species abundance distribution. The canonical lognormal form of this distribution means that, while the number of individuals scales proportionally to area, the number of species scales with z close to 0.25 (different species abundance distributions give different predicted z -values; May, 1975). Given that the introduction of alien individuals, especially those introduced by chance, may be thought of as a random sampling process from an underlying pool of species with a given species abundance distribution, it is interesting that this process produces a slope for the introduced alien SAR that is close to the theoretical expectation. This implies that islands are sampling introduced individuals in proportion to their area. The alien SAR could then arise because a proportion of those introduced species goes extinct that is unrelated to area. However, two unanswered questions are: i) does random sampling from an underlying species abundance distribution give a slope for the introduced alien SAR that is close to that observed given that, at this stage, we have no constraint imposed for a minimum number of individuals and ii) would we expect extinction rate to be unrelated to area if the number of individuals sampled by a location is proportional to its area?

6.4.2 Simulating the Establishment Process

To answer these questions and assess whether a sampling model can produce patterns consistent with those we observe in alien SARs, we conducted a bespoke simulation experiment (Figure 6.2) in the R software environment (Version 3.5.1) for statistical and graphical computing (R Core Team, 2018). A species abundance distribution was constructed in the package *mobsim* (May et al., 2018) from a log-normal distribution with K species and $I = 1 \times 10^7$ individuals; where for the examples shown $K = 100$ (Figure 6.3A–C), 1,000 (Figure 6.3D–F) or 10,000 (Figure 6.3G–I).

For 100 iterations we randomly introduced individuals from our species abundance distribution to ten islands in varying total numbers (100, 200, 500, 1,000, 2,000, 5,000, 10,000, 12,500, 15,000, 20,000 individuals introduced in total across all species), where we assume that the larger numbers of individuals are introduced to larger islands. For each simulation, we extracted the total number of species that were

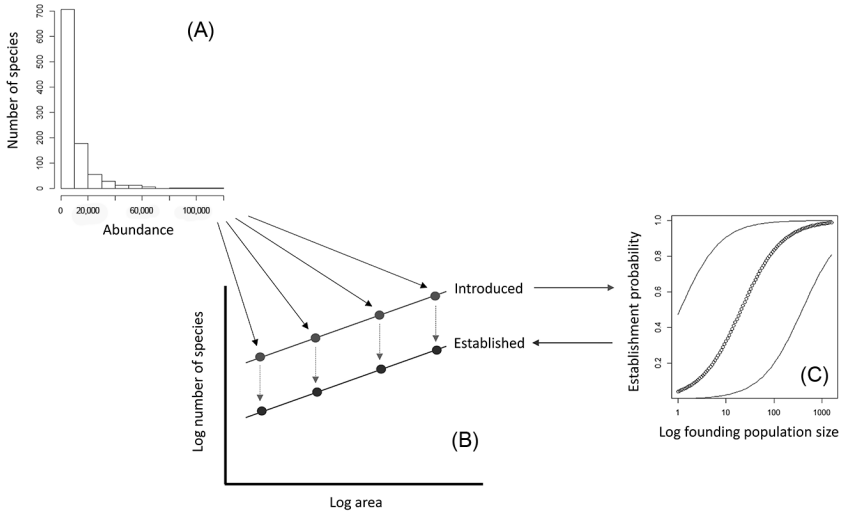


Figure 6.2 An illustration of the simulation model. For each of a set of islands (four in this example), a number of individuals is sampled at random from an underlying lognormal species abundance distribution (A), with the number of individuals proportional to island area. The number of species in those random samples gives the introduced species–area relationship for the islands (upper points and line in B). The probability that each species establishes a viable population is a stochastic function of its founding population size (C), such that some introduced species fail to establish (predominantly species with low founding population sizes). Those failures transform the introduced alien species–area relationship into the established alien species–area relationship (lower points and line in B). (A) depicts the actual species abundance distribution with 10,000,000 individuals and $K = 1,000$ and (C) depicts the actual functions for establishment as a function of propagule pressure, with the central line (comprised of open circles) corresponding to Equation (6.3) (Cassey et al., 2018) and the lines either side to Equation (6.3), but adding 3 or subtracting 3 from the intercept.

introduced to a given island across those introduced individuals, to calculate an introduced alien SAR (upper points; Figures 6.2 and 6.3), assuming that island area was proportional to the number of introduced individuals.

Each introduced species has a founding population size (the total number of individuals of that species introduced in that iteration of the simulation, i.e. propagule pressure *sensu* Cassey et al., 2018). We then evaluated the probability that a species introduced with a propagule pressure of q individuals would be likely to establish successfully on an island by comparing the mean probability of establishment for a given

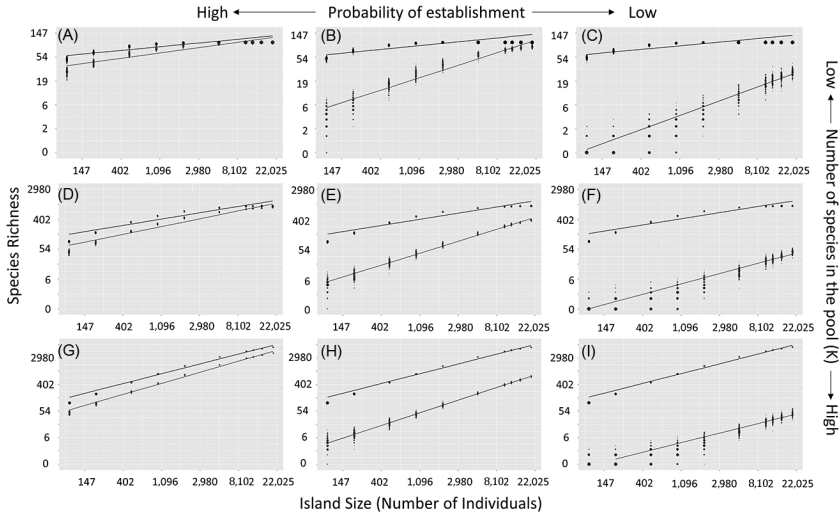


Figure 6.3 The outcome of simulations to model introduced (upper lines and points in each plot) and established (lower lines and points in each plot) alien species–area relationships (SARs). Introduced alien SARs were produced by random samples from an underlying species abundance distribution (Figure 6.2A) with 1×10^7 individuals and $K = 100$ (A, B, C; Low), 1,000 (D, E, F) or 10,000 (G, H, I; High) species. Established alien SARs were produced by the failure of some introduced species to establish, where establishment probability can be high (A, D, G), medium (B, E, H) or low (C, F, I). The equations for the regression lines are given in Table 6.1.

propagule pressure q (taken from the logistic function provided in figure 3 in Cassey et al. (2018) and reproduced here as Figure 6.2C) as follows:

$$\text{logit}(\text{Establishment Success}) = -3.10 + 2.35 * \log_{10}(q), \quad (6.3)$$

with a random uniform integer between zero and one. If the probability of establishment (for a given propagule pressure) was greater than the random integer then the introduced species was considered to be successfully established on the island. Otherwise the species failed to establish. For each simulation we extracted the total number of species that were successfully established on a given island to calculate the established alien SAR (lower points; Figures 6.2 and 6.3). We examined variation in the form of the logistic relationship between establishment success and propagule pressure (Figure 6.3B, E and H) by adding 3 to (Figure 6.3A, D and G) or subtracting 3 from, the intercept (Figure 6.3C, F and I) in Equation (6.3).

Real data for island bird introductions (Blackburn et al., 2008) show more or less parallel slopes for introduced and established alien SARs. Our simulations show that the precise form of the SARs for introduced and established species depends upon both the number of species in the pool, K , and how establishment success relates to propagule pressure (Table 6.1; Figure 6.3). Fewer introduced species establish when establishment probability for a given propagule pressure is lower (e.g. cf. Figure 6.3A–C), as expected. However, how this affects the slope of the established alien SAR also depends on K (cf. Figure 6.3C, F and I).

The difference between the slope values of introduced and established alien SARs increases as establishment probability decreases, and decreases as K increases (Table 6.1). The first of these two effects is because decreasing establishment success has its largest impacts on alien species richness on small islands (cf. Figure 6.3A and C), where propagule pressures will be lower, dragging down the slope of the established alien SAR relative to that for introduced species. This leads to greater differences in the intercepts for introduced and established alien SARs. Increasing K increases the number of species that get introduced, but decreases the average propagule pressure for each of these species, thus decreasing the likelihood that they will establish. The effect of higher K in lowering establishment success is greatest at larger island sizes, because the much higher introduced alien richness on these islands is largely accompanied by smaller propagule pressures. This leads to relatively higher failure rates on large islands as K increases (cf. Figure 6.3C and I). In combination, these two effects lead to similar slope values for introduced and established alien SARs when establishment probability is high and K is low (Figure 6.3A) – most species on most islands succeed – and when establishment probability is low and K is high (Figure 6.3I) – most species on most islands fail. In other words, parallel SARs for introduced and established species are more likely when establishment success is equalized across islands.

Simulated slope values (Table 6.1) are generally steep relative to those observed for introduced (Blackburn et al., 2008) and established (Baiser & Li, 2018) alien SARs. The introduced SAR slope depends on K alone and, hence, the ratio of individuals to species in the simulations. When the underlying species pool consisted of $I = 1 \times 10^7$ individuals and $K = 100$ species, this slope approximated that observed for island birds (c. 0.20), but steepened as the number of species increased. This suggests that a low ratio of K/I might approximate the species pool from which birds introduced to islands were drawn. What that ratio might be

Table 6.1 The intercept and slope values for the regression lines shown in Figure 6.3. The probability of establishment (P_{est}) does not affect the form of the SAR for introduced aliens, which is therefore the same (given stochastic variation) for all P_{est} for a given K . Medium P_{est} derives from Equation (6.3), with high and low P_{est} based on this equation but adding or subtracting 3 from the intercept (see Section 6.4.2). All slopes and intercepts are significantly different from zero at $P < 0.001$.

K	Invasion stage	High P_{est}		Medium P_{est}		Low P_{est}	
		Intercept	Slope	Intercept	Slope	Intercept	Slope
100	Introduction	3.33 ± 0.08	0.16 ± 0.01	3.33 ± 0.08	0.16 ± 0.01	3.29 ± 0.07	0.16 ± 0.01
	Establishment	2.73 ± 0.07	0.21 ± 0.01	-0.47 ± 0.12	0.51 ± 0.01	-2.64 ± 0.27	0.59 ± 0.03
1,000	Introduction	3.16 ± 0.06	0.41 ± 0.01	3.13 ± 0.07	0.41 ± 0.01	3.08 ± 0.07	0.42 ± 0.01
	Establishment	1.84 ± 0.06	0.52 ± 0.01	-2.05 ± 0.08	0.82 ± 0.01	-3.39 ± 0.24	0.71 ± 0.01
10,000	Introduction	1.69 ± 0.04	0.73 ± 0.01	1.64 ± 0.04	0.74 ± 0.01	1.63 ± 0.04	0.74 ± 0.01
	Establishment	0.21 ± 0.03	0.84 ± 0.01	-2.88 ± 0.06	0.96 ± 0.01	-3.62 ± 0.25	0.74 ± 0.01

in reality is unknown, although for the British breeding avifauna $K/I \sim 225/1.6 \times 10^8$ or around one tenth that in Figure 6.3A (Musgrove et al., 2013; Blackburn & Gaston, 2018). In general, establishment failure steepened these SAR slopes, so that z -values for established species were generally in the range of 0.5 and above (Table 6.1). This is because, in most cases, failure was proportionally higher on smaller islands. Again, however, slopes were closer to those typically observed in alien SARs when K was low. Introduced alien SARs in general appear more curvilinear on log–log axes than established alien SARs (Figure 6.3), but we did not formally explore this element further.

Our simulations are simple and only scratch the surface of possible parameter space in terms of K , I , the form of the species abundance distribution, and how individuals might be sampled from that distribution. They also assume that alien individuals reach islands in proportion to island area, which is speculative if not unreasonable, and do not address alien population dynamics beyond establishment. That SARs can be derived by sampling from underlying species abundance distributions is well known since the classic work of Preston (1962; see review in McGill et al., 2007), but to our knowledge no one has previously explored how establishment probability might transform introduced SARs into established SARs. It is clear that some simple assumptions allow realistic introduced SARs to be modelled as sampling effects and realistic alien SARs to then arise from introduced population failure. Sampling effects can therefore potentially explain both native and alien SARs and, if native and alien colonists are drawn from underlying species abundance distributions of similar form, why they have very similar slopes (Baiser & Li, 2018).

6.4.3 Other Mechanisms

If the similarity between native and alien SARs is due to a common mechanism, some of the other explanations proposed to underpin native SARs seem likely to be ruled out. For example, MacArthur and Wilson (1963, 1967) proposed that SARs are the result of size-dependent variation in the rates of colonization and extinction across islands. Larger islands intercept more colonists and the species that colonize have lower extinction rates than on small islands. However, for aliens, while the number of colonist species does increase with area, extinction does not seem (on the limited evidence available) to be a negative function of area as MacArthur and Wilson posit – a more or less constant proportion (and

hence a larger number) of introduced aliens goes extinct from larger islands (Blackburn et al., 2008). That element of the Equilibrium Theory of Island Biogeography is not supported, at least by island alien birds. Metapopulation-based explanations also seem unlikely, inasmuch as extinction probability in such models is also a negative function of patch area (Hanski & Gyllenberg, 1997).

One oft-cited mechanism for SARs in native species is that areas with a wider range of habitats can support more species, while habitat diversity is a positive function of area (Williams, 1964; Pyšek et al., 2002). A related idea is that smaller areas may possess different habitats to larger ones as a consequence of their smallness (Whittaker & Fernández-Palacios, 2007). Leaving aside the question of how habitats are defined (which in practice is often in terms of their biological communities, implying a degree of circularity), native and alien SARs could show similar slopes if native and alien species respond to habitat diversity in the same way. Once again, it seems surprising under this mechanism that more of the alien populations introduced to larger areas should go extinct, as one might expect introduced species to be more likely to find suitable habitats in larger areas. However, it is not beyond the bounds of possibility that a fairly constant proportion of species would fail to be translocated to suitable habitats in areas of different sizes, given that more species are translocated to larger areas (i.e. the introduced alien SAR).

In a related vein, Baiser and Li (2018) suggest that, if alien richness is determined by the likelihood of disturbance, aliens and natives may show similar SAR exponents if disturbance scales with area in the same way as habitat diversity. This seems an unlikely coincidence across the range of studies they reviewed. However, disturbance has itself been proposed as a general driver of SARs, either if higher disturbance in small areas makes such areas unsuitable for some species in the source pool (McGuinness, 1984) or, conversely, if greater disturbance in some areas creates opportunities for species that otherwise would not be present (Whittaker & Fernández-Palacios, 2007). Traditionally, species richness is argued to be highest at intermediate levels of disturbance, as this allows the coexistence of species that are good dispersers but poor competitors (and hence that thrive in disturbed areas) with species that are good competitors but poor dispersers, which would come to dominate communities in the absence of disturbance (Connell, 1978). In effect, this is a restatement of the habitat diversity hypothesis, but where diversity is maintained by some areas (but not all) being subject to disturbance. Nevertheless, if some disturbance leads to increased native species richness and allows

alien species to establish, this could in theory lead to similar scaling of native and alien richness with area. We know of no tests of this idea for alien species, although the hypothesis of a relationship between species richness and disturbance is arguably unsupported on both empirical and theoretical grounds (Fox, 2013).

6.5 Conclusions

The species–area relationship is one of the most general patterns in ecology (Chapters 1–3) and it is little surprise to see that alien species also conform to this general pattern (Baiser & Li, 2018). With all else being equal, we would expect to find more species in larger geographic areas even if life were distributed randomly across the surface of the planet. Yet, native and alien species are not just similar in showing positive SARs – the slope values of their respective relationships would seem to be too close to arise by coincidence. Alien species also exhibit other macroecological patterns, including Bergmann’s Rule (Blackburn et al., 2019) and Rapoport’s Rule (Sax, 2001; Dyer et al., 2020), suggesting that drivers of the distribution of native species across the planet also force alien species distributions to adhere to their rules. Given that alien species represent a massive natural experiment, encompassing more or less every habitat on every significant continent and island, this appears to open up an unprecedented opportunity to study the mechanisms underpinning the distribution of biodiversity worldwide.

And yet, alien SARs are the result of a sequential process involving the transportation of individuals beyond their natural geographic range limits, the introduction of some proportion of those individuals to a place where they do not naturally occur and the establishment of a viable population (only) from those introduced individuals (Blackburn et al., 2011). The outcomes of later stages in this process depend on inputs from the earlier stages. In particular, the alien species richness of an area is typically some proportion (<1) of the number of alien species that were introduced to the area; that is, colonization pressure. In the one data set we have, island birds, this proportion is essentially constant across islands of different areas, suggesting that the slope of the SAR for established aliens is a consequence of the slope of the SAR for introduced aliens, with the intercept modified by random extinction. Colonization pressure similarly influences Bergmann’s and Rapoport’s Rules in alien birds (Blackburn et al., 2019; Dyer et al., 2020) and may also explain when alien species do not match the macroecological patterns of native species,

for example in terms of spatial gradients of species richness (Dawson et al., 2017; Dyer et al., 2017b).

That said, there are still many interesting and unresolved questions about the similarities between native and alien diversity patterns. In terms of SARs, for example, we would expect positive relationships if life were distributed randomly across the surface of the planet, which is a state that may at least be approximated by some alien species groups. The non-deliberate transport and introduction of many alien species may well approximate a random sampling process, leading to widespread and abundant native species being more likely to be introduced (Colautti et al., 2006; Leung & Roura-Pascual, 2012); this is also true for deliberate introductions (Blackburn & Duncan, 2001). Yet, this process generally leads to SARs with near-identical slopes to those for the native species in the same taxon and location, once we factor in a biologically realistic establishment process (Figure 6.2C). Can we identify drivers of establishment failure related to any underlying factor? Could native SARs ultimately be a consequence of random sampling of colonists from a species pool, with the same establishment process (driven by founding population size or propagule pressure) whittling the colonists down to the SAR? What would a ‘colonist SAR’ look like for native species? Given that we only really have one dataset underpinning our knowledge of how introduced and established alien SARs might be related (island birds; Blackburn et al., 2008), how representative is the introduced alien SAR in those data? Parallel introduced and established alien SAR slopes seems a less likely outcome of random sampling processes than a steeper alien SAR slope (Figure 6.3), as we would generally expect higher extinction rates on smaller islands. However, our simulations barely begin to explore the possible parameter space of relevant processes.

The similar slopes of alien and native SARs, for the same taxa over the same areas, are also interesting in terms of their implications and consequences for the overall biodiversity of the areas concerned. While areas are losing species to extinction at an elevated rate, as well as gaining species through alien establishment, aliens in general add to the species richness of areas, with gains more or less in proportion to native species richness. Thus, areas with more species tend to gain more species (Stohlgren et al., 2006). What does this mean for the drivers of species richness? Does it mean that areas generally are not saturated in terms of their species richness and can readily gain new species without consequences? Does it mean that human activities in those areas have facilitated higher levels of richness, perhaps through the effects of disturbance

(Kolar & Lodge, 2001)? Or is biodiversity now out of equilibrium in many areas and, in the long term, we can expect more extinctions, perhaps in both the native and alien biotas? Certainly, many species are teetering on the brink (IUCN, 2018). Time will tell. In the meantime, it will be helpful to try to gather more information on the process of invasion by alien species, especially how introduced richness transforms into established richness, both for what it tells us about how colonization processes might operate in practice to generate richness and for mitigating that transformation in the future.

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References

- Baiser, B. & Li, D. (2018) Comparing species–area relationships of native and exotic species. *Biological Invasions*, **20**, 3647–3658.
- Blackburn, T. M. & Duncan, R. P. (2001) Establishment patterns of exotic birds are constrained by non-random patterns in introduction. *Journal of Biogeography*, **28**, 927–939.
- Blackburn, T. M. & Gaston, K. J. (2018) Abundance, biomass and energy use of native and alien breeding birds in Britain. *Biological Invasions*, **20**, 3563–3573.
- Blackburn, T. M., Lockwood, J. L. & Cassey, P. (2008) The island biogeography of exotic bird species. *Global Ecology & Biogeography*, **17**, 246–251.
- Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U. & Richardson, D. M. (2011) A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, **26**, 333–339.
- Blackburn, T. M., Redding, D. W. & Dyer, E. E. (2019) Bergmann's Rule in alien birds. *Ecography*, **42**, 102–110.
- Blackburn, T. M., Scrivens, S. L., Heinrich, S. & Cassey, P. (2017) Patterns of selectivity in introductions of mammal species worldwide. *NeoBiota*, **33**, 33–51.
- Brett, M. T. (2004) When is correlation between non-independent variables 'spurious'? *Oikos*, **105**, 647–656.
- Brown, J. H. (1995) *Macroecology*. Chicago, IL: University of Chicago Press.
- Cadotte, M. W., McMahon, S. M. & Fukami, T. (2006) *Conceptual ecology and invasion biology: Reciprocal approaches to nature*. Dordrecht, the Netherlands: Springer.
- Capellini, I., Baker, J., Allen, W. L., Street, S. E. & Venditti, C. (2015) The role of life history traits in mammalian invasion success. *Ecology Letters*, **18**, 1099–1107.
- Cassey, P., Delean, S., Lockwood, J. L., Sadowski, J. S. & Blackburn, T. M. (2018) Dissecting the null model for biological invasions: A meta-analysis of the propagule pressure effect. *PLoS Biology*, **16**, e2005987.

- CBD (2002) *COP 6 Decision VI/23. Alien species that threaten ecosystems, habitats or species*. www.cbd.int/decision/cop/default.shtml?id=7197.
- Colautti, R. I., Grigorovich, I. A. & MacIsaac, H. J. (2006) Propagule pressure: A null model for biological invasions. *Biological Invasions*, **8**, 1023–1037.
- Connell, J. H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.
- Darwin, C. (1859) *On the origin of species*. London: Murray.
- Dawson, W., Moser, D., Van Kleunen, M., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Winter, M., Lenzner, B., Blackburn, T. M., Dyer, E. E., Cassey, P., Scrivens, S. L., Economo, E. P., Guénard, B., Capinha, C., Seebens, H., García-Díaz, P., Nentwig, W., García-Berthou, E., Casal, C., Mandrak, N. E., Fuller, P., Meyer, C. & Essl, F. (2017) Global hotspots and correlates of alien species richness across taxonomic groups. *Nature Ecology & Evolution*, **1**, 0186.
- Diamond, J. (1986) Overview: Laboratory experiments, field experiments, and natural experiments. *Community ecology* (ed. by J. Diamond and T. J. Case), pp. 3–22. New York: Harper Row.
- Dyer, E. E., Cassey, P., Redding, D. W., Collen, B., Franks, V., Gaston, K. J., Jones, K. E., Kark, S., Orme, C. D. L. & Blackburn, T. M. (2017b) The global distribution and drivers of alien bird species richness. *PLoS Biology*, **15**, e2000942.
- Dyer, E. E., Redding, D. W., Cassey, P., Collen, B. & Blackburn, T. M. (2020) Evidence for Rapoport's rule and latitudinal patterns in the distribution of alien bird species. *Journal of Biogeography*, **47**, 1362–1372.
- Dyer, E. E., Redding, D. W. & Blackburn, T. M. (2017a) The global avian invasions atlas, a database of alien bird distributions worldwide. *Scientific Data*, **4**, 170041.
- Fox, J. W. (2013) The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology & Evolution*, **28**, 86–92.
- Gaston, K. J., Jones, A. G., Hanel, C. & Chown, S. L. (2003) Rates of species introduction to a remote oceanic island. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 1091–1098.
- Hanski, I. & Gyllenberg, M. (1997) Uniting two general patterns in the distribution of species. *Science*, **275**, 397–400.
- HBW & BirdLife International (2017) *Handbook of the birds of the World and BirdLife International digital checklist of the birds of the world. Version 2*. datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v2%20Dec17.zip.
- Hulme, P. E. (2008) Contrasting alien and plant species–area relationships: The importance of spatial grain and extent. *Global Ecology & Biogeography*, **17**, 641–647.
- IUCN (2018) *The IUCN red list of threatened species. Version 2018-2*. www.iucnredlist.org/.
- Jeschke, J. M. & Strayer, D. L. (2005) Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences USA*, **102**, 7198–7202.
- van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Kreft, H., Weigelt, P., Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F.,

- Cabezas, F. J., Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Ebel, A. L., Figueiredo, E., Fuentes, N., Groom, Q. J., Henderson, L., Inderjit, Kupriyanov, A., Masciadri, S., Meerman, J., Morozova, O., Moser, D., Nickrent, D. L., Patzelt, A., Pelter, P. B., Baptiste, M. P., Poopath, M., Schulze, M., Seebens, H., Shu, W., Thomas, J., Velayos, M., Wieringa, J. J. & Pyšek, P. (2015) Global exchange and accumulation of non-native plants. *Nature*, **525**, 100–103.
- Kolar, C. S. & Lodge, D. M. (2001) Progress in invasion biology: Predicting invaders. *Trends in Ecology & Evolution*, **16**, 199–204.
- Lawton, J. H. & May, R. M. (eds.) (1995) *Extinction rates*. Oxford: Oxford University Press.
- Leung, B. & Roura-Pascual, N. (2012) TEASing apart alien species risk assessments: A framework for best practices. *Ecology*, **15**, 1475–1493.
- Lockwood, J. L., Cassey, P. & Blackburn, T. M. (2009) The more you introduce the more you get: The role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions*, **15**, 904–910.
- MacArthur, R. H. & Wilson, E. O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.
- MacArthur, R. H. & Wilson, E. O. (1967) *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- May, F., Gerstner, K., McGlenn, D. J., Xiao, X. & Chase, J. M. (2018) mobsim: An R package for the simulation and measurement of biodiversity across spatial scales. *Methods in Ecology and Evolution*, **9**, 1401–1408.
- May, R. M. (1975) Patterns of species abundance and diversity. *Ecology and evolution of communities* (ed. by M. L. Cody and J. M. Diamond), pp. 81–120. Cambridge, MA: Harvard University Press.
- McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., Dornelas, M., Enquist, B. J., Green, J. L., He, F., Hurlbert, A. H., Magurran, A. E., Marquet, P. A., Maurer, B. A., Ostling, A., Soykan, C. U., Ugland, K. I. & White, E. P. (2007) Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, **10**, 995–1015.
- McGuinness, K. A. (1984) Species–area curves. *Biological Reviews*, **59**, 423–440.
- Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G. B. & Worm, B. (2011) How many species are there on Earth and in the ocean? *PLOS Biology*, **9**, e1001127.
- Moser, D., Lenzner, B., Weigelt, P., Dawson, W., Kreft, H., Pergl, J., Pyšek, P., van Kleunen, M., Winter, M., Capinha, C., Cassey, P., Dullinger, S., Economo, E. P., García-Díaz, P., Guénard, B., Hofhansl, F., Mang, T., Seebens, H. & Essl, F. (2018) Remoteness promotes biological invasions on islands worldwide. *Proceedings of the National Academy of Sciences USA*, **115**, 9270–9275.
- Musgrove, A., Aebischer, N., Eaton, M., Hearn, R., Newson, S., Noble, D., Parsons, M., Risely, K. & Stroud, D. (2013) Population estimates of birds in Great Britain and the United Kingdom. *British Birds*, **106**, 64–100.
- Prairie, Y. T. & Bird, D. F. (1989) Some misconceptions about the spurious correlation problem in the ecological literature. *Oecologia*, **81**, 285–288.

- Preston, F. W. (1962) The canonical distribution of commonness and rarity: Part I and II. *Ecology*, **43**, 185–215, 410–432.
- Pyšek, P. (1998) Alien and native species in Central European urban floras: A quantitative comparison. *Journal of Biogeography*, **25**, 155–163.
- Pyšek, P., Kučera, T. & Jarošík, V. (2002) Plant species richness of nature reserves: The interplay of area, climate and habitat in a central European landscape. *Global Ecology & Biogeography*, **11**, 279–289.
- Pyšek, P., Pergl, J., Essl, F., Lenzner, B., Dawson, W., Kreft, H., Weigelt, P., Winter, M., Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F., Cabezas, F. J., Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Dullinger, S., Ebel, A. L., Figueiredo, E., Fuentes, N., Genovesi, P., Groom, Q. J., Henderson, L., Inderjit, Kupriyanov, A., Masciadri, S., Maurel, N., Meerman, J., Morozova, O., Moser, D., Nickrent, D., Nowak, P. M., Pagad, S., Patzelt, A., Pelsler, P. B., Seebens, H., Shu, W., Thomas, J., Velayos, M., Weber, E., Wieringa, J. J., Baptiste, M. P. & van Kleunen, M. (2017) Naturalized alien flora of the world: Species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. *Preslia*, **89**, 203–274.
- R Core Team (2018) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Richardson, D. M. (ed.) (2011) *Fifty years of invasion ecology: The legacy of Charles Elton*. Oxford: Wiley–Blackwell.
- Rosenzweig, M. L. (1995) *Species diversity in space and time*. Cambridge: Cambridge University Press.
- Sax, D. F. (2001) Latitudinal gradients and geographic ranges of exotic species: Implications for biogeography. *Journal of Biogeography*, **28**, 139–150.
- Sax, D. F. & Gaines, S. D. (2005) The biogeography of naturalised species and the species–area relationship: Reciprocal insights to biogeography and invasion biology. *Conceptual ecology and invasions biology: Reciprocal approaches to nature* (ed. by M. W. Cadotte, S. M. McMahon and T. Fukami), pp. 449–479. Dordrecht, Netherlands: Kluwer.
- Sax, D. F., Stachowicz, J. J. & Gaines, S. D. (eds.) (2005) *Exotic species: A source of insight into ecology, evolution, and biogeography*. Sunderland, MA: Sinauer Associates.
- Scheiner, S. M. (2003) Six types of species–area curves. *Global Ecology & Biogeography*, **12**, 441–447.
- Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., Kartesz, J., Kenis, M., Kreft, H., Kühn, I., Lenzner, B., Leibhold, A., Mosen, A., Moser, D., Nishino, M., Pearman, D., Pergl, J., Rabitsch, W., Rojas-Sandoval, J., Roques, A., Rorke, S., Rossinelli, S., Roy, H. E., Scalera, R., Schindler, S., Štajerová, K., Tokarska-Guzik, B., van Kleunen, M., Walker, K., Weigelt, P., Yamanaka, T. & Essl, F. (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications*, **8**, 14435.
- Sherratt, T. N. & Wilkinson, D. M. (2009) *Big questions in ecology and evolution*. Oxford: Oxford University Press.

- Stohlgren, T. J., Barnett, D., Flather, C., Fuller, P., Peterjohn, B., Kartesz, J. & Master, L. L. (2006) Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biological Invasions*, **8**, 427–447.
- Tarasi, D. D. & Peet, R. K. (2017) The native–exotic species richness relationship varies with spatial grain of measurement and environmental conditions. *Ecology*, **98**, 3086–3095.
- Whittaker, R. J. & Fernández-Palacios, J. M. (2007) *Island biogeography: Ecology, evolution, and conservation*, 2nd ed. Oxford: Oxford University Press.
- Whittaker, R. J., Rigal, F., Borges, P. A. V., Cardoso, P., Terzopoulou, S., Casanoves, F., Pla, L., Guilhaumon, F., Ladle, R. J. & Triantis, K. A. (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.
- Williams, C. B. (1964) *Patterns in the balance of nature*. London: Academic Press.
- Williamson, M. (1996) *Biological invasions*. London: Chapman and Hall.
- Wilson, D. E. & Reeder, D. M. (eds.) (2005) *Mammal species of the world. A taxonomic and geographic reference*, 3rd ed. Baltimore, MD: Johns Hopkins University Press.