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Chapter · April 2011

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# **CONSERVATION BIOGEOGRAPHY**

Edited by  
**Richard J. Ladle and Robert J. Whittaker**



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## CHAPTER 8

# APPLIED ISLAND BIOGEOGRAPHY

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### 8.1 INTRODUCTION

When a nature preserve is set aside, it is destined to become an island in a sea of habitats modified by man.

(Wilson & Willis, 1975, p. 525)

Islands have played a central part in the development of conservation theory. In particular, the Equilibrium Theory of Island Biogeography (ETIB) (MacArthur & Wilson, 1963, 1967; Wilson, 1969) has played a pivotal role in diverse areas such as protected area network design theory and predicting extinction rates. The ETIB is a dynamic equilibrium model which postulates that the number of species of a given taxon found on an island will be the product of opposing forces leading respectively to the gain and loss of species, and resulting in a continual turnover of the species present on each island through time.

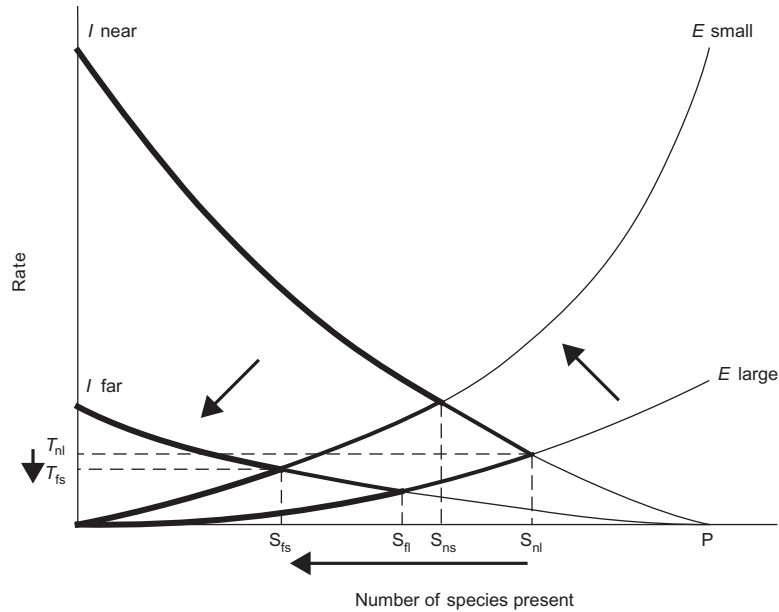
This is captured in MacArthur and Wilson's famous graphical model, in which immigration rate declines exponentially and extinction rate rises exponentially as an initially empty island fills up towards its equilibrium richness value (shown by the intersection; Figure 8.1). The immigration rate curve flattens with increasing island isolation and the extinction rate curve flattens with increasing area, thereby generating a family of curves providing unique combinations of richness and turnover for each combination of area and isolation.

The influence of the ETIB is marked not just by the research it has inspired, but also by the theories and

applications it has spawned and influenced (e.g. species–energy theory, metapopulation theory, island assembly theory, neutral theory and stochastic niche theory; reviewed in Whittaker & Fernández-Palacios, 2007). Within a few years of publication, the application of the ETIB to the field of conservation was being vigorously debated by academics. One of the key insights was the realization that terrestrial reserves and national parks could be viewed as simply another type of island ('habitat islands') surrounded by a 'sea' of human-altered landscapes. It logically followed that these reserves would behave like islands cut off from the mainland by rising sea levels, i.e. they would lose species as they 'relaxed towards equilibrium' (Figure 8.1; Diamond, 1975a; Wilson & Willis, 1975).

In the context of the 'crisis' discourse of conservation science from the 1970s onwards, several prominent conservation scientists turned to island theory in the search for an 'off the shelf' general scientific guide on protected area system design to assist in both advocacy and implementation. If each protected area might become, in time, an island surrounded by habitats modified by man (Wilson & Willis, 1975, p. 18), and given a finite total area that can be set aside for conservation as a natural landscape is being converted to other uses, one of the basic questions is, 'What configuration of reserves should conservationists advocate?'

According to Margules & Pressey (2000), reserves have two main roles: they should sample or represent the biodiversity of each region and they should



**Figure 8.1** The equilibrium model of island biogeography and the implications of habitat fragmentation (bold arrows). An equilibrium number of species ( $S$ ) is set by two opposing processes, immigration ( $I$ ) and extinction ( $E$ ). The rate of immigration decreases and the rate of extinction increases with increasing richness; the rate of immigration reaches zero when the entire pool ( $P$ ) of potentially immigrating species have arrived. Immigration rates on islands far ( $I_f$ , far) from the source pool are expected to be lower than those on near ( $I_n$ , near) islands. Extinction rates are expected to be higher on small ( $E_s$ , small) islands than on large ( $E_l$ , large) islands. Hence, different equilibrium numbers of species are established based on the area and the isolation of the islands ( $S_n$ ;  $S_f$ ;  $S_m$ ;  $S_{nl}$ ); and both equilibrium species richness and rates of species turnover ( $T$ ) are expected to vary with the combination of immigration and extinction rates that characterize any given island (e.g.  $T_n$ ;  $T_f$ ). Bold arrows show the direction of the changes predicted by the model upon fragmenting a more or less contiguous tract of habitat into small, isolated patches. Figure modified from MacArthur and Wilson, 1967, Figure 8, p. 22.

separate this biodiversity from processes that threaten its persistence. The extent to which protected areas fulfil this role depends on how well they meet two objectives of reserve design.

The first is *representation*, a long-established goal referring to the need for reserves to incorporate the full variety of biodiversity in the region, ideally at all levels of organization (Chapters 2, 5, 6).






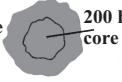









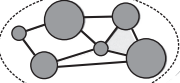


The second is *persistence*. Reserves, once established, should promote the long-term survival of the species and other elements of biodiversity that they contain by maintaining natural processes and viable populations, and by excluding threats (Chapter 7).

To meet these objectives, conservation planners must not only design systems of reserves that take into consideration natural physical and biological patterns,

they must also make decisions about reserve size, connectivity, replication and the alignment of boundaries (Margules & Pressey, 2000; Whittaker *et al.*, 2005). All of this needs to be done while conforming to budgetary constraints and, typically, strong political and socio-economic constraints on the size and location of reserves.

Island biogeography theory provides the theoretical framework for much fragmentation research and has been invoked as the source of general principles of reserve network design (Diamond, 1975a; Wilson & Willis, 1975; Haila, 2002; see Figure 8.2). Examples include:

- a large reserve is superior to a small one;
- a single large reserve is better than several small reserves with the same total area;

WORSE		BETTER	
a)	Small reserve 	 Large reserve	
b)	Fragmented reserve 	 Unfragmented reserve	
c)	Higher edge effects 	500 ha reserve  Lower edge effects	
d)	Isolated reserves 	 Increased connectivity (corridors)	
e)	Isolated reserves 	 Increased connectivity (stepping stones)	
f)	Partial protection 	 Complete protection	
g)	Uniform habitat 	 Increased habitat diversity	
h)	Local perspective 	 Regional perspective	
i)	Humans excluded 	 Human integration (buffer zones)	

**Figure 8.2** Design guidelines for reserves, as derived initially from the theory of island biogeography and extended by subsequent contributions to theory (e.g. see Harris, 1984; Shafer, 1997). Re-drawn from Huggett (2004, Figure 18.3, p. 362).

- when two or more reserves are inevitable for some specific habitat or species, the inter-reserve distance should be as short as possible;
- corridors between reserves are recommended to increase inter-reserve migration/dispersal;
- a circular reserve is superior to a linear one because of the potential problems created by biotic and abiotic edge effects, i.e. the changes in biological and physical conditions that occur when for example a woodland

reserve is surrounded by a non-woodland matrix (see Diamond, 1975a; Wilson & Willis, 1975; Diamond & May, 1981).

Many of these ETIB-derived 'principles' have been the subject of intense debate. For example, while corridors between reserves (increased connectivity) certainly may increase immigration, facilitate gene flow and reduce local extinctions through the rescue effect, they may also facilitate the spread of disease, fires and exotic

species. Hence, decisions about corridors should be case-specific (see Whittaker & Fernández-Palacios, 2007)<sup>1</sup>.

One of the most hotly discussed conservation topics of the 1970s and 1980s was the so-called SLOSS debate, which posed the question: 'Given the opportunity to put a fixed percentage of land into conservation use, is it better to opt for a Single Large Or Several Small reserves?' At one extreme is the creation of a single large reserve; the alternative is to opt for several smaller reserves that amount to the same area but which are scattered across the landscape.

The answer to the SLOSS question is by no means simple. Crucially, it depends on the slope of the species–area curve, the proportion of common species in the small reserves and the gradient of colonizing abilities among species in the available pool of species. Indeed, both theoretical analyses and empirical evidence suggest that, in some circumstances, several small reserves may contain more species than a single large one. This is due to compensating advantages such as: greater overall representation of rare habitats; more effective representation of differing biogeographical elements across a region; competitive effects involving there being different 'winners' in different patches; less effective spread of disease and exotic species; and more habitat for edge species (e.g. Soulé & Simberloff, 1986; Zimmerman & Bierregaard, 1986; Godefroid & Koedam, 2003).

Moreover, the initial debate over SLOSS generally overlooked the complexity of species diversity dynamics. Factors such as the minimum viable population (MVP) for rare/ecologically important species, the minimum area needed in order to sustain an MVP and the minimum dynamic area to maintain the ecosystem integrity must also be considered in questions concerning nature conservation (Soulé & Simberloff, 1986; Shafer, 1990; Wu & Vankat, 1995). It is now generally accepted that the species–area relationship and the equilibrium theory of island biogeography – in part an attempt to explain systematic variations in the form of the species–area relationship – are unable to provide final resolution to the SLOSS question.

There are several broad explanations for the difficulty of extracting generalities from the study of habitat islands, and perhaps the most important is that

answers to questions like SLOSS are likely to exhibit scale dependency. For example, large mammals, with their large home ranges or territories and their vulnerability to human hunting, are likely to require vastly larger reserves than are needed to capture viable populations of butterflies. The former are also likely to have less specific habitat requirements than the latter, so reserve systems designed for one are likely to be suboptimal for the other.

Another aspect of scale is the range of sizes and inter-reserve distances. Imagine that you were distributing reserves across East Lincolnshire (a low-lying and rather flat part of the UK). The range in reserve sizes and distances involved in these generally agricultural landscapes would be small, and one would not expect to encounter different species pools. Imagine, by way of contrast, that you were distributing reserves across a large-scale biogeographical gradient such as the Mexican transition zone, i.e. the transition zone between the Nearctic and Neotropical regions. Here we might be contemplating rather larger reserves and potentially very large distances between them, and different reserves might contain contrasting proportions of species ultimately derived from different biogeographical regions/provinces.

The falsification of the assumption of a single species pool that is inherent in the ETIB undermines the application of this theory to resolve SLOSS at such a scale. Instead, we may turn to the direct analyses of species' distributional data discussed in the previous two chapters for reserve network planning in such a context. Hence, although some authors have attempted to apply the island analogy on these very coarse scales (e.g. Brooks *et al.*, 1997, 2002), as we demonstrate below, applied island biogeography is essentially a framework for application at local to landscape scales (Whittaker & Fernández-Palacios, 2007).

The SLOSS debate illustrates that although ETIB provides a basic conceptual model for understanding habitat fragmentation, apart from a number of broad generalizations that are largely ecological 'good sense' anyway (e.g. many large refuges hold important species that small ones do not, ecologically heterogeneous refuges tend to hold more than homogeneous ones, habitat connectivity can often be beneficial in terms of species richness), generating policy-relevant guidance from a broad-brush macroecological theory is not straightforward.

In this chapter, we review some of the more interesting themes within applied island biogeography, starting with the most basic general question: is it realistic

<sup>1</sup>While in traditional biogeography the term corridor is given to a connection that allows essentially free passage of a particular biota (cf. Chapter 7; and see also: Lomolino *et al.*, 2006), research within the present frame of reference on ecological habitat corridors can refer to very narrow connecting features, which may be highly selective in terms of the species that can move along them.

to expect habitat islands to behave according to the same principles as real islands? In answering this question, we critically review the application of ideas derived from island ecological biogeography to conservation problems and suggest a number of future directions where island theory can potentially inform applied conservation questions.

## 8.2 IMPLICATIONS OF HABITAT LOSS AND FRAGMENTATION: FROM THEORY TO EVIDENCE

A theory is more impressive the greater the simplicity of its premises, the more different the kinds of things it relates and the more extended its range of applicability.

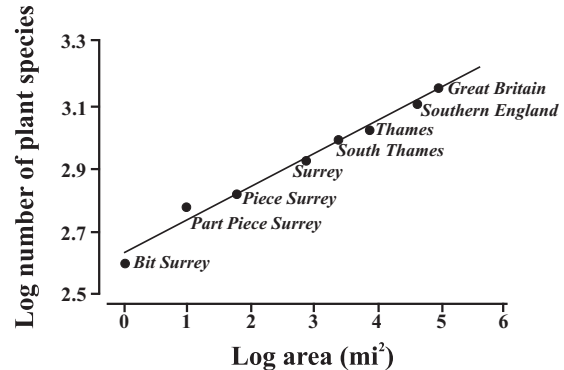
(Albert Einstein, 1949, from Schlipp (1973, p. 33).

### 8.2.1 The use of species–area relationships in conservation

A basic rule of thumb derived from island theory is that if a habitat is reduced by 90 per cent, then some 50 per cent of species are expected to go extinct. In this and the following section, we explore this rule of thumb and consider the extent to which we can rely upon such simple generalizations.

The species–area relationship (SAR) is not simply one of ecology's most general patterns but was also one of the first to be discovered. It also has a profound importance for conservation biogeography. Descriptions of the SAR are known from as early as 1778 (Johann Reinhold Forster) and 1820 (Augustin de Candolle) (see Lomolino, 2001, for further details). The first known plot relating species with area was made by Hewett Cottrell Watson in 1859 (see Rosenzweig, 1995), the same year that Darwin published his magnum opus *On the Origin of Species*. Watson presented the relationship between plant species and area, beginning with the richest county, Surrey, and then built up to the whole island (see Figure 8.3). According to Rosenzweig (1995, p. 9), 'it is the world's oldest known empirical example of an ecological pattern'.

It was not until the 1920s that two botanists, Olof Arrhenius (1921) and Henry Allan Gleason (1922), expressed this relationship in mathematical terms. Arrhenius introduced the relationship as a power



**Figure 8.3** The first known species–area curve, based on the number of plant species of England (Watson, 1859). Re-drawn from Rosenzweig (1995, pp. 9).

model:  $S = cA^z$ , while Gleason (1922) suggested a semi-logarithmic model  $S = k + d \log A$ , where  $S$  is the number of species,  $A$  is (island) area, and  $c$ ,  $z$ ,  $k$  and  $d$  are constants. Quantification was a critical, long-awaited advance, primarily because it enabled scientifically rigorous investigations of species–area curves, therefore allowing biogeographers and ecologists to use comparative methods to search for and evaluate causal explanations. Ultimately, this breakthrough allowed modern-day conservation biogeographers to apply species–area models to make predictions and develop strategies for conserving biological diversity (see Lomolino, 2001).

Today, more than 20 mathematical models have been proposed for the description of the SAR, with the power model of Arrhenius being still the most commonly applied and frequently the most effective (see Connor & McCoy, 1979; Tjørve, 2009; and see Williams *et al.*, 2009, for a comprehensive review of all the available models and their appropriate usage).

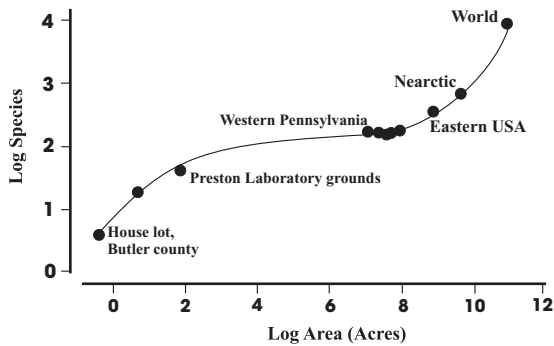
The next key breakthrough was by Frank Preston, an engineer and naturalist, who proposed a mechanistic explanation of the species–area pattern and for the values that the slope of the relationship in a logarithmic space should take. His starting point was a theoretical consideration of the species abundance distribution, which he argued typically followed a log-normal distribution (Preston, 1948, 1962).

The theory states that the most numerous species are those of middling abundance, while species with very few individuals are as rare as species with a very large number of individuals, giving rise to a log-normal



curve. Preston showed that a log-normal series of abundance should give rise to a SAR with a slope ( $z$ ) value of approximately 0.263 – towards the low end of the range of values known at that time from islands and above those of continental patches (for details see Rosenzweig, 1995, pp. 268–276). These differences pointed to a role for isolation via population migration.

Preston was also one of the first to notice that the slope of the species–area relationship ( $z$ ) changes with geographical scale. He published a figure tracing bird diversity increase from a house lot to the entire world, showing how the relationship changes in form from fine to coarse spatial scales (Figure 8.4; Preston, 1960). This idea was further elaborated by Rosenzweig (1995, 2001, 2004), who suggested that the ‘species–area pattern’ is actually comprised of three different species–area relationships, whereby processes operating at different spatial and temporal scales (Schmida & Wilson, 1985; Crawley & Harral, 2001) lead to different  $z$ -values (Figure B8.1a; Table 8.1).



**Figure 8.4** Species–area curve for birds commencing within north-eastern USA, across three different spatial scales. Modified after Preston (1960) and Rosenzweig (1995).

At local scales, within and among habitats within regions (‘sample areas’), species accumulation is a function of relative abundance distributions and beta diversity (encompassing aspects of habitat heterogeneity and species turnover among sites). The  $z$ -values typically observed for sample areas fall between 0.1 and 0.2. Across islands or disparate habitats within a region (the ‘archipelagic category’), species richness per island/habitat is affected by increased dispersal limitation, due either to spatial distances between similar habitat patches (e.g. islands in an archipelago) or to ecological differences between habitats (e.g. where frequency distributions of species differ greatly across habitats within the region). The  $z$ -values typically observed for intra-provincial/archipelagic areas fall between 0.25 and 0.55. At the largest scales, the accumulation of species with increasing area is due to the addition of species from separate biotic provinces (the ‘inter-provincial species–area relationship’). The  $z$ -values typically observed for inter-provincial areas have a lower margin of  $z = 0.6$  and range upwards, with most lying around 0.9–1.0 or even higher (Table 8.1; Rosenzweig, 1995, 2001, 2004; Figure B8.1a).

Rosenzweig’s work (1995; see also 2001, 2004) offered a more nuanced dynamic perception of the SARs and the biological meaning of their slopes. Fundamentally, the  $z$  is not just an indication of the isolation of the system under study – a perception that dominated the field of island biogeography for more than 40 years (Preston, 1962; MacArthur & Wilson, 1967) – but reflects the dominant processes establishing species richness patterns. As Rosenzweig (1995, p. 278) succinctly states: ‘the slope of the species–area curve reflects the timescale that determines it’. These timescales range from hours/days for curves from small sample areas, to the millennia of evolutionary time for the curves among different biotic provinces (Box 8.1).

**Table 8.1** Three biological scales of species–area curves, the dominant process of species addition at each scale and the respective range of the slope ( $z$ ) values, as proposed by Rosenzweig (e.g. 2004). For further discussion, see Box 8.1.

Scales of SAR	Dominant process(es) of species addition	$z$ -values range
Intra-provincial	Habitat heterogeneity, species abundance	0.1–0.2
Archipelagic	Dispersal	0.25–0.45
Inter-provincial	Speciation	Higher than 0.6 (0.8–0.10)



### Box 8.1 Scale and the species–area relationship (SAR)

Box prepared by R.J. Whittaker and K.A. Triantis – excerpted and modified slightly from Triantis, Mylonas and Whittaker (2008).

#### Scales and types of SAR

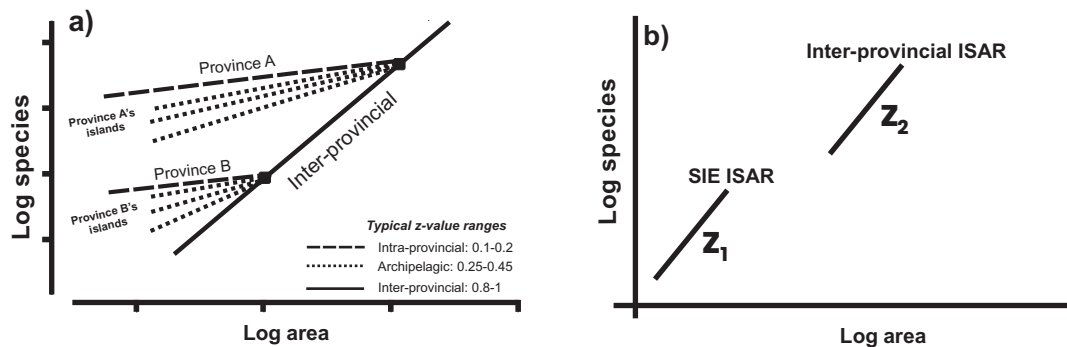
The species–area relationship (SAR) – the increase in species number with increasing area – is one of the best-documented general patterns in biogeography and ecology, yet controversy persists about the best means of describing the relationship and about the precise form of different types and/or scales of SAR.

SARs are typically described using power functions where the exponent (i.e. the slope of the log-area/log-richness relationship) is commonly referred to as the  $z$ -parameter. The  $z$ -parameter has a simple mathematical interpretation: it is the rate at which species accumulate with increasing area. However, there is no consensus on the biological interpretation and scale dependency (e.g. at which spatial scales particular evolutionary and ecological processes predominate) of SARs.

As discussed in the text, Rosenzweig (1995, 2003, 2004), has argued that the ‘species–area pattern’ is comprised of three different species–area relationships (or four if the point scale, which depends on sampling effort, is included), whereby processes operating at different spatial and temporal scales lead to different  $z$ -values (Figure B8.1a). In practice, Rosenzweig’s scheme encompasses data sets of two different structures. The first form employs a nested sampling structure and results in species accumulation curves (SACs) at two scales: the point (i.e. local) scale and the intra-provincial (i.e. regional) scale. The second form is where the independent variable is the area of (to varying degrees) geographically discrete and isolated land masses, and the dependent variable is the number of native species found within each area. Again there are two scales in his scheme: the archipelagic (i.e. a set of geographically clustered islands) and the inter-provincial (i.e. between regions).

Whittaker and Fernández-Palacios (2007, Box 4.4, p. 94) term these archipelagic and inter-provincial relationships ‘true’ island species–area relationships (ISARs) to distinguish them from the phenomenologically distinct SACs arising from the nested sampling designs. It is on these  $z$ -values of true ISARs that we now focus.

For real islands, MacArthur and Wilson (1967) reported archipelagic ISAR  $z$ -values as typically falling within a range of 0.2 to 0.35, while Williamson (1988) reported a much wider range in  $z$ , from 0.05 to 1.132. In his review,



**Figure B8.1a** Three biological scales of species–area curves, as proposed by Rosenzweig (e.g. 2004).

(a) Rosenzweig’s species–area pattern includes four scales, but the point scale is not illustrated in the graphic. The point and intra-provincial scales comprise species accumulation curves from a nested sampling system, whereas the inter-provincial and archipelagic scales (termed ISARs herein, for island species–area relationships) are plots of the number of species found in discrete units of space. (b) The inter-provincial ISAR and the SIE (single-island endemics)–area relationship exhibit similar  $z$ -values (slopes) according to results reported herein. Despite the differences in the spatial scale and the number of species involved, the two systems exhibit analogous trends of increasing species number with area, as in both speciation is the major process of species addition.

Rosenzweig (2004) essentially supports MacArthur and Wilson, reporting that values typically fall between 0.25 and 0.45. By contrast,  $z$ -values typically observed for inter-provincial ISARs have a lower margin of  $z = 0.6$  and range upwards, with most lying around 0.8–1.0 (Rosenzweig, 2004) and some exceeding 1.0 (Rosenzweig, 1995, 2004). These observations have very considerable significance for conservation science as humans continue to alter the extent and connectivity of habitats both locally and globally. It is thus important to test the robustness and explore the properties of Rosenzweig's species–area pattern model.

### A test of the form of inter-provincial ISARs from strongly isolated islands

Archipelagic ISARs have been studied for real and habitat islands for many taxa in numerous studies over several decades, and their properties are thus reasonably well known. By contrast, generalizations on the form of inter-provincial ISARs derive from relatively few data sets. Biotic provinces/regions can be defined as self-contained areas that, for the target taxon, are relatively independent from an evolutionary perspective (i.e. wherein most species are endemic to these provinces).

In this analysis, we focus on the form of ISARs for single-island endemics (SIEs), exploring the idea that for those species restricted to single islands, the islands in question can be regarded as provinces. Using this approach, and by focusing on these systems, we can study the evolutionary contribution to ISARs and gain significant insights regarding the patterns that arise when speciation is a significant or the major source of diversity, as happens in the case of continental biotic provinces/regions.

Our first aim is therefore to explore the consistency in form of SIE–area relationships across taxa and archipelagos of varying proportion of SIEs. Our second aim is to use SIE data to test the robustness of the generalization that inter-provincial ISARs are significantly steeper than archipelagic ISARs, producing  $z$ -values typically falling between 0.8–1.0, and 0.25–0.45, respectively. We do so by comparing  $z$ -values for SIE with those for 'all native species' for the same taxa, using 13 different data sets from the Caribbean, Fiji, Hawaii, Canary Islands and Great African Lakes, and using the power (log–log) model.

For further details of data set properties and methods of analysis, see the source paper. The key findings of the analyses were as follows:

Eleven of the SIE–area relationships were statistically significant, explaining high proportions of the variance in SIE numbers ( $R^2$  0.57–0.95), the two exceptions being for the Canary Islands, whereby inclusion of the two oldest islands greatly reduces the fit of traditional species–area models (see Whittaker *et al.*, 2008). The  $z$ -values of the statistically significant SIE–area relationships ranged from 0.47 to 1.13, with a mean value of 0.80 ( $SD \pm 0.24$ ). All the island systems in which SIE represent >50 per cent of species exhibited  $z$ -values for the SARs of native species higher than those deemed typical of archipelagic SARs. Moreover, for the three cases in which the percentage of SIE equals or exceeds 90 per cent, the mean  $z$ -value is unity ( $1.00 \pm 0.21$ ). The findings thus approximate the schematic shown in Figure B8.1b.

Hence, the results of the present work provide significant support for Rosenzweig's proposition that  $z$ -values from inter-provincial ISARs should be very high, approaching unity. This should hold not only for the scale of recognized global biogeographical regions, but also for any system in which speciation is the major process. Of course, the timescales in which species evolve and go extinct may differ between island systems and global biogeographical provinces. Nevertheless, it seems that the two system types exhibit analogous patterns of species accumulation with area.

Therefore, studies of evolutionary dynamics in relation to area, employing data for single island endemics, would be well worth pursuing in other taxa and regions, as they could be used as model systems to test:

- 1 variation in critical island sizes below which within-island diversification does not occur;
- 2 how these thresholds vary with taxa and island groups;
- 3 how consistent the form of inter-provincial ISARs are;
- 4 their capability for predicting future diversity;
- 5 and they may also be used to recognize and examine the influence of additional factors such as climate, productivity, etc.

Such studies can offer great insights into basic questions of conservation biogeography, such as the potential impact of habitat fragmentation and loss and homogenization on biological diversity.

These macroecological approaches to island data, generated by the stimulus of the MacArthur–Wilson theory, have promoted the wide use of species–area curves for conservation purposes. These include predicting species endangerment globally, regionally and locally (McDonald & Brown, 1992; Tilman *et al.*, 1994; Pimm & Askins, 1995; Brooks & Balmford, 1996) as functions of habitat loss and fragmentation; devising general reserve-design principles (Diamond, 1975a; Wilson & Willis, 1975); and identifying conservation targets for specific habitat types (Desmet & Cowling, 2004). Among the most controversial uses of the species–area relationship based implicitly on ETIB is its application in the forecasting of future species extinctions as a function of habitat loss due to factors such as deforestation (e.g. Brooks *et al.*, 1997, 2002) or future climate change (e.g. Thomas *et al.*, 2004 – see Box 7.3).

Projected extinctions based on species–area models involve several uncertainties (Heywood *et al.*, 1994; Whittaker & Fernández-Palacios, 2007) and can never completely replace species-level assessments for the identification of extinction threat (e.g. Kotiaho *et al.*, 2005). However, for many species of conservation concern, the collection of appropriately detailed information is an unrealistic target. It is vital, therefore, that conservation biogeographers develop more realistic indirect measures and theoretical projections of extinctions, based on as pragmatic a set of assumptions as possible (May *et al.*, 1995; Laurance, 2007).

The wide variations in outcomes can be seen from efforts to estimate likely extinctions arising from tropical deforestation. Results of current and future rates of deforestation have varied dramatically, ranging from the alarming (e.g. Ehrlich & Wilson, 1991) to more modest (but still significant) losses (Wright & Muller-Landau, 2006), thus strongly affecting projections of future species losses.

Recently, Wright & Muller-Landau (2006) noted that the estimates of net tropical deforestation rates during the 1990s differ by 250 per cent (see their Table 2). Using a number of criteria, they considered 45 humid tropical countries that support 89.6 per cent of all extant closed tropical forest and 89.9 per cent of all potential tropical forest cover. They concluded that deforestation rates will decrease as population growth slows, and that a much larger area will continue to be forested than previous studies suggest.

Such uncertainties, along with differences arising from choice of assumptions about species persistence

in degraded habitats, from the high sensitivity of predictions to uncertainty or errors in species–area slopes and from large uncertainties about both the global species totals and the geographical distribution of biodiversity, mean that all currently available predictions of future losses inherently possess great uncertainty (see Table 8.2, and Chapter 7 and see Laurance, 2007, 2008; Willis & Bhagwat, 2009, for general discussion). Although the most recent of the estimations presented in Table 8.2 was made in 1992, we consider the information to be useful in pointing out the problems in predicting global extinctions that can arise through different assumptions on a number of critical issues.

In short, extinction rate estimates based on species–area projections involve many uncertainties (Heywood *et al.*, 1994). The precise form of the relationship describing the loss of species from an original habitat as a function of the remaining habitat area is still an open question. There are two main associated issues. First, many species are not restricted to their ‘native’ habitat and can persist in certain anthropogenic habitats. Second, the slope of the species–area relationship used for the loss of total area of a habitat is still uncertain; there is no strong theoretical or empirical justification for the use of a ‘global’ slope value of  $z = 0.25$  (or any other single value).

Whittaker & Fernández-Palacios (2007) have criticized the use of SAR as a means of forecasting species threatened by, or committed to, extinction, noting ‘the way in which the species–area models are used ... is conceptually decoupled from the island theory from which it seemingly derives’. They argue first that, a  $z$  of 0.25 is a subjective ‘middle’ value to take (see discussion above about the  $z$ -values of the different SAR categories). Second, and more crucially, this  $z$ -value has been derived from analyses of true isolates. It describes approximately how many species are held in each of a series of isolates/islands of different size. Yet, in several recent studies the  $z$ -value is applied not to separate fragments but to an entire region (e.g. Brooks & Balmford, 1996; and see also Box 10.2, pp. 272–273 in Whittaker & Fernández-Palacios, 2007).

As will be discussed in the section on nestedness below, depending on the degree of shared species between different habitat islands, it is possible for relatively low or very high proportions of the original species found in a region to be represented in a

**Table 8.2** Some estimates of global species loss due to tropical deforestation and the key assumptions made (adapted from Krishnamurthy, 2003; see therein for references).

Extinction estimate	Total species (millions)/ per cent tropical	Tropical forest loss	Extinction/ area lost	Source
1 species/hour by 2000	5–10/40–70%	245,000 km <sup>2</sup> /year	50% species extinct when 10% area left	Myers, 1979
33–50% of all species between 1970 and 2000	3–10/25%	50% deforestation by 2000	Species–area, concave curve	Lovejoy, 1980
1 million species by 2000	4/40%	33% of remaining forest destroyed	50% species in area will go extinct	Myers, 1985
10% of all species by 2000; 25% by 2015	4–5/ 50%	2% deforestation/ year	50% species in area will go extinct	Raven, 1988
17,500 species/year	10/50%	0.7% deforestation/ year	50% species in area will go extinct	Wilson, 1988b
8.8% of all species by 2000	3–10/25%	12.3% deforestation between 1980 and 2000	Species–area, concave curve	Lugo, 1988a, b
5–38% of all species between 1990 and 2000	10/>50%	0.8–1.6 % deforestation/year	Species–area; $z = 0.15, 0.35$	Reid & Miller, 1989
27,000 species/year	10 in tropical rain forests	1.8% deforestation/ year	Species–area; $z = 0.15$	Wilson, 1992

series of habitat islands. Therefore, treating what are actually archipelagos of habitat islands as though they were a single island in analyses of extinction threat is a potentially crucial oversimplification – and it is one reason why we cannot rely upon the ‘90 per cent area loss = 50 per cent species loss’ generalization with which we began this section.

As a further note of caution, it is important to emphasize that while the species–area relationship is indeed a very general pattern, area rarely explains all interpretable variation in species richness, with some residual variation being attributable not only to system isolation but to other variables such as habitat diversity, elevational range, disturbance regime, etc. (Whittaker & Fernández-Palacios, 2007; Triantis *et al.*, 2008). It follows that SARs can only provide a crude approximation for use in conservation planning. Hence, as noted by Whittaker *et al.* (2005), the application of the species–area relationship for informing conservation sciences is one area within conservation biogeography where the theory appears to require further work.

### 8.2.2 Relaxation and the extinction debt

Newly emerged islands present new habitat and accumulate species through time via immigration. In contrast, habitat islands created through isolation by rising water levels or by habitat destruction (e.g. deforestation) are typically assumed to support something approximating a full complement of local species at their formation. That is, they are expected to contain both source populations (having positive population growth within the area itself) and sink or casual populations that happened to be present at the time of isolation, but which do not exhibit positive population growth within the area itself. Upon isolation these islands are thus ‘supersaturated’ for a patch of their newly reduced area and increased isolation.

With time, these islands lose species, a phenomenon called *species relaxation* (Diamond, 1972; Wilcox, 1980). Immigration (at a lower rate than before) and extinction (at a higher rate than before isolation) should both continue during the relaxation period and subsequently they come back into balance; at this

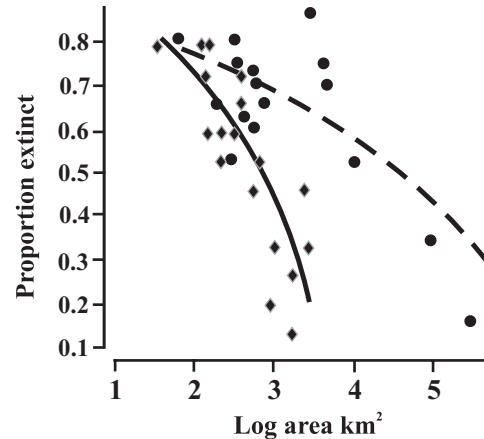
point, the island has found its new, lower equilibrium richness level (Figure 8.1). The time taken for relaxation to occur is referred to as the 'lag time' and the anticipated eventual species loss is termed the 'extinction debt' (see Ewers & Didham, 2006).

Two classic examples of relaxation are presented in Figure 8.5. The first example takes the form of a data set for the mammals living in isolated high mountains forests of the south-western USA (Brown, 1971). The radical shift in climate following the end of the latest glacial period resulted in these mammalian populations becoming isolated from each other by the increasing aridity of the valleys surrounding them. The second example is for the mammals of the Sunda Islands of Indonesia (Wilcox, 1980). These islands, interconnected during the last glacial period, were isolated by the ocean as the glaciers melted and raised the sea level. Thus, both these systems became isolated around the start of the Holocene (c. 10 ka) and since then are thought to have gradually been losing species.

Biogeographers and conservationists have been interested in three general questions related to species relaxation. First, how does relaxation proceed? In other words, what is the shape of the curve of species loss over time? Second, how much time is needed between fragmentation and extinction (the lag time)? Third, and critically, how many species will be left after relaxation is complete? Conversely, how many and which species will eventually go extinct?

Relaxation after habitat loss and fragmentation is typically expected to proceed in a sequence of stages (after Wilcove, 1987):

- **Stage 1.** Initial exclusion. Some species will be lost from the landscape simply because their original ranges did not include any of the remnant patches.
- **Stage 2.** Extirpation due to lack of essential resources. Species vary greatly in their resource requirements and many require very large areas and/or very rare resources. Thus, the likelihood that all of a species' resource requirements can be met decreases as the remaining area decreases.
- **Stage 3.** Perils associated with small populations. Small populations are much more susceptible to a host of genetic, demographical, and stochastic problems. As the total area of the remnant patches decreases, and the ability to sustain large populations decreases, these problems become increasingly severe (e.g. Frankham *et al.*, 2002).



**Figure 8.5** Mammal diversity on Sunda Islands (circles) and south-western US mountaintops (diamonds). These isolates started forming about 10,000 years ago at the end of the Pleistocene. In both archipelagos, larger islands have experienced proportionately fewer extinctions. The above estimations are based on two general assumptions. First, it is assumed that the extinction rates are comparable. Rosenzweig (1995) considered that, as the same taxon is studied and given that the two systems have been formed due to the same event (the switch into the current interglacial) and thus began losing species at approximately the same time, we can hypothesize a similar rate of extinctions. Second, it is assumed that the original number of species for each island can be estimated from a mainland area (Malaysian mainland for Sunda Islands and Sierra Nevada for US mountaintops) of the same size as the island. Re-drawn after Rosenzweig (1995, his Fig. 6.5).

- **Stage 4.** Deleterious effects of isolation. Some populations may be rescued from extinction by migration and recruitment of individuals from other populations. The likelihood of such rescue effects decreases as isolation increases.
- **Stage 5.** Ecological imbalance. Most species are strongly influenced by interactions with other species. Loss of one species during any of the aforementioned stages of relaxation may result in the subsequent loss of its predators, parasites, mutualists, or commensals (e.g. Koh *et al.*, 2004). In addition, habitat disturbance and reductions in community diversity during the earlier stages of relaxation may facilitate the establishment of introduced species, triggering a cascade of subsequent extirpations.



It has been argued that it may take several generations for the processes causing relaxation to play out following habitat destruction and fragmentation, meaning that there is a substantial lag time between the initial stimulus and the end of the process of species losses (Tilman *et al.*, 1994; Ewers & Didham, 2006; Vellend *et al.*, 2006). This creates an 'extinction debt' – a future ecological cost of habitat destruction that may not be initially apparent in studies made shortly after habitat fragmentation has occurred. Indeed, Brown's (1971) mammal assemblages were hypothesized to still be in the process of relaxation from their relatively large mountain top habitat islands thousands of years after isolation (Figure 8.5; and see further discussion in Lomolino *et al.*, 2006).

Whether such protracted response times are typical is unknown, but it does seem highly likely that the true ecological costs of the historically recent spate of anthropogenic habitat disturbance, destruction and fragmentation across the globe are yet to be realized (see, for example, Figure 8.6). It is also noteworthy that, although the majority of recorded species extinctions since AD 1600 have occurred on oceanic islands, predictions of increasing numbers of future extinctions suggest a significant shift to continental areas (Millennium Ecosystem Assessment, 2005).

Developing methods to quantify the magnitude and taxonomic distribution of the extinction debt is clearly vitally important for effective conservation planning and prioritization. However, this objective is by no means simple to attain. Accurate assessment of extinction rates and their extrapolation into the future requires good quality long-term data on species occurrences – data which are generally lacking, especially for less conspicuous and/or numerically much more species rich taxa.

This lack of appropriate knowledge (Chapter 4) has led to an inevitable reliance on indirect measures and theoretical projections of extinction debt. These include: species–area models; rates at which well-known species are shifting to increasingly more threatened categories of conservation concern; extinction probabilities associated with the IUCN categories of threat; impacts of projected habitat loss on species currently threatened with habitat loss; and the extrapolation of correlations of species loss with climate change (e.g. McDonald & Brown, 1992; Mace & Kunin, 1994; Pimm & Askins, 1995; Thomas *et al.*, 2004 – for further discussion see Ladle, 2009).

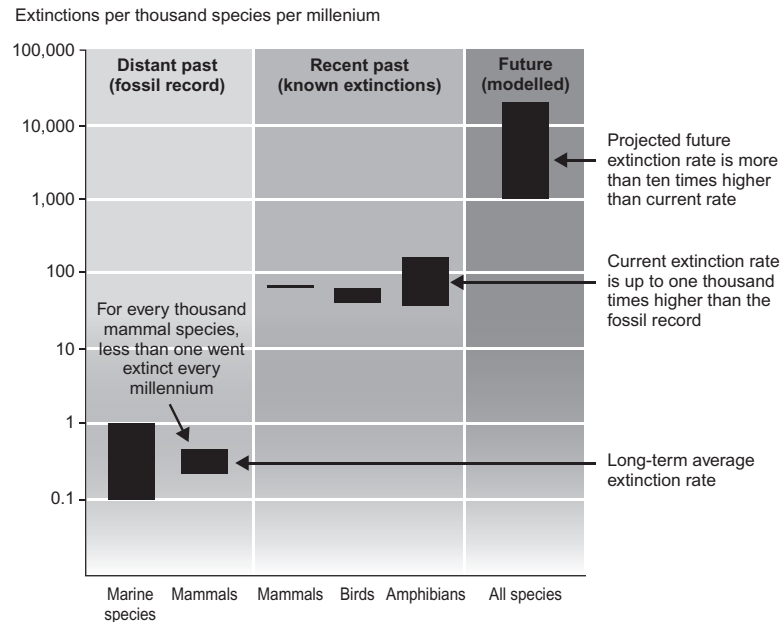
One of the best-known empirical examples of relaxation on an ecological timescale is the loss of bird species from Barro Colorado Island in Panama. The island was formerly a hilltop in an area of continuous neotropical lowland rain forest, but abruptly became a 15.7 km<sup>2</sup> island when the central section of the Panama Canal Zone was flooded to make Lake Gatun in 1914.

Of about 208 bird species estimated to have been breeding on Barro Colorado island immediately following isolation in the 1920s and 1930s, 45 were no longer present by 1970 (Wilson & Willis, 1975). However, only a minority of these losses were directly attributable to stochastic processes of relaxation. The others could be attributed to ecological changes such as forest regeneration following abandonment of farming activity, which reduced the availability of open habitats, or predation by terrestrial mammals (see review in Whittaker & Fernández-Palacios, 2007).

For example, many of the birds lost were typical of second growth or forest edge, suggesting that the regeneration of the forest following abandonment of farming activity must have reduced the availability of these more open habitats. Additionally, some ground-nesting species were probably eliminated by their terrestrial mammalian predators, which became abundant after the disappearance of top carnivores with large area requirements. This effect, of increasing numbers of smaller omnivores and predators due to the absence of large ones, has been termed mesopredator release (Soulé *et al.*, 1988) and has been documented to occur in several other similar contexts (e.g. Laurance, 2002).

A later avifaunal survey of Barro Colorado Island reported sightings of 218 species from the island or the waters immediately around it between 1994 and 1996, including five new records, none of which were thought to be of breeding species (Robinson, 1999). As anticipated from the island theory (Figure 8.1), the rate of species loss appears to have declined over time, especially for forest-interior birds. However, overall, species extinctions do appear to have continued to exceed colonizations.

So, in summary, the isolation of the hilltops to form this lake-bound island has been followed by around a century in which the process of relaxation has been the dominant trend. Future changes in avifaunal species richness and composition on the island are likely to be dependent on the extent to which the



**Figure 8.6** Past and future extinctions. 'Distant past' refers to average extinction rates as calculated from the fossil record. 'Recent past' refers to extinction rates calculated from known extinctions of species (lower estimate) during the last 100 years or known extinctions plus 'possibly extinct' species (upper bound). 'Future' extinctions are model-derived estimates using a variety of techniques and, in general, refer either to future loss of species based on the level of threat that exists today or to current and future loss of species as a result of habitat changes. The techniques involved for modelling future extinctions are: species–area models; rates at which species are shifting to increasingly more threatened categories; extinction probabilities associated with the IUCN categories of threat; impacts of projected habitat loss on species currently threatened with habitat loss; and correlation of species loss with energy consumption. According to the authors of the assessment, the lower bound estimates for future modelled extinctions are low certainty estimates, and the upper bound estimates are speculative (i.e. even lower certainty). Adapted from Millennium Ecosystem Assessment (2005).

nearby mainland forest cover is retained, as these forests provide the source of the transient birds and occasional new colonists (those that stay to breed) observed on Barro Colorado Island.

The most significant problem with predicting future extinctions in such systems is that we have an inadequate theoretical and empirical basis by which to estimate the rate at which species will be lost over time or the total time period required for a new (dynamic) equilibrium to be achieved. Precise estimates of the 'time to extinction' of each species under threat remains an unrealistic aim for both true and habitat islands, as it will largely be species- and system-specific.

A classic illustration of this problem is provided by the tropical moist forests of the Atlantic seaboard of Brazil, known as the Mata Atlantica, which have been reduced over the past few centuries to only about 7 per cent of their estimated former cover (Ribon *et al.*, 2003). This is a large region and the remnants are numerous and widely distributed, so the '90 per cent habitat loss = 50 per cent species loss' rule of thumb (above) should not really be expected to apply. Nonetheless, such habitat loss and insularization should have driven significant losses.

To date, however, no extinctions have been documented with any degree of certainty, although many species appear on IUCN 'Red Lists' as 'vulnerable',



'endangered' or 'critically endangered', largely based on reductions in range or population estimates (Ribon *et al.*, 2003). Despite the criticism, especially of methodology and taxonomic bias (e.g. Régnier *et al.*, 2009), the IUCN Red List has become an essential source of information for conservation action and is widely recognized as the most comprehensive compilation of extinct and threatened species (Mace & Lande, 1991; Rodrigues *et al.*, 2006).

Brooks and Balmford (1996) compared losses of birds in the region, projected using a species-area model, with those listed by the IUCN as 'threatened', and they found congruence. They concluded that the forecasts of looming extinction are basically correct, but that there is a substantial lag between the habitat loss/fragmentation process and global extinction of the species. There is, moreover, good evidence of local extirpation within the existing range of many bird species that live in devastated habitats such as the Mata Atlantica.

Thus, within the Viçosa region (a 120 km<sup>2</sup> area in south-eastern Brazil) over the last 70 years, it appears that at least 28 bird species have become locally extinct, with 43 being classified as 'critically endangered' and 25 'vulnerable'. In total, 61 per cent of the original avifauna has been significantly reduced in incidence (Ribon *et al.*, 2003). Nectarivorous species appear to have been affected least, followed by omnivores and carnivores, with frugivores and insectivores hit the hardest. Assuming relaxation to be well under way in these fragmented systems, the questions of estimating the time lag between habitat loss and eventual species losses, and of predicting the identities and numbers of these losses, remain unanswered.

In this context, as noted by Raheem *et al.* (2009), it is surprising that fragment age (i.e. the time of isolation/creation of a fragment) has received little attention from ecologists and conservationists. In most landscapes, it is the productive and/or most accessible areas that are deforested first, thus producing a non-random spatial and temporal distribution of habitat fragments (Laurance *et al.*, 2002; Ewers *et al.*, 2006). A topographically diverse landscape, such as on most oceanic islands, will therefore typically contain an assortment of older, smaller and more degraded fragments at lower elevations and younger, larger and less degraded fragments at higher elevations (see for example Box 8.2).

The above example illustrates the difficulties of untangling causal processes underlying species

relaxation within real landscapes. Part of this complexity is generated by the operation of two overlapping temporal scales that are critical in determining net rates of species loss across fragments: the rate at which habitat is being lost from a region (considering also the possible recovery of habitat; see Wright & Muller-Landau, 2006); and the age of the habitat fragments created within that region. Untangling the contribution of these two interlinked age-dependent factors may be critical to a better understanding of the relaxation process and thus for more accurate predictions of species losses and relaxation lag time.

Recently, Raheem *et al.* (2009), studying the land snails assemblages in fragments of natural rain forest in Sri Lanka's wet zone, concluded that fragment age, along with fragment shape complexity, were the only two significant determinants of fragmentation-related changes in community composition. Attributes of fragments such as area, distance-to-edge and matrix quality, which have been traditionally linked to species losses, exhibited no obvious effect (see also below). In practice, review of the literature on such effects reveals many such idiosyncrasies between studies. At least some part of the differences in findings from one case study to the next reflects differences in the 'experimental design' of the fragmented systems analysed and, in particular, the range in values of properties such as area, age, distance from source, habitat complexity, etc. that each study encompasses.

### 8.2.3 Ecosystem collapse and threshold responses in habitat islands

Reduction of habitat area can cause super-saturation as immigration rate declines and extinction rate rises (above). In the most extreme scenario, where the loss of habitat is so extreme that immigration into a patch virtually ceases, species richness may, in theory, collapse catastrophically (see Whittaker & Fernández-Palacios, 2007, their figure 10.5; and also Vandermeer & Lin, 2008). Although the process of species richness collapse and associated loss of ecosystem function is not presently well-defined or understood, it is thought to be linked to extreme impoverishment of the available resources that are required for a system to sustain its functionality (e.g. Dobson *et al.*, 2006).

One of the most emblematic examples of an ecosystem collapsing comes from the island literature. Easter Island (Rapa Nui) was once one of the most isolated

### Box 8.2 Extinction debt in the Azores

Box prepared by K.A. Triantis and R.J. Whittaker – excerpted and modified slightly from Triantis *et al.* (2010). See the source paper for a full analytical presentation of the materials and methods used.

Habitat destruction is considered to be the leading cause of terrestrial species extinctions. However, there is typically a time lag between the reduction in habitat area and the eventual disappearance of the remnant populations. These ‘surviving but ultimately doomed’ species represent an extinction debt. Calculating the magnitude of such future extinction events has been hampered by potentially inaccurate assumptions about the slope of species–area relationships, which are habitat- and taxon-specific [see text]. We have overcome this challenge by introducing a novel method that uses the historical sequence of deforestation in the Azorean Islands to calculate realistic and ecologically-adjusted species–area relationships.

The Azores constitute an ideal model system for assessing extinction debt because:

- 1 they have lost more than 90 per cent of their original native forest during the five centuries of human occupation;
- 2 being one of the most isolated archipelagos on Earth they support a significant number of single island endemics (SIE);
- 3 the history of human settlement and deforestation is well known;
- 4 extensive biogeographical data exist for a range of taxa.

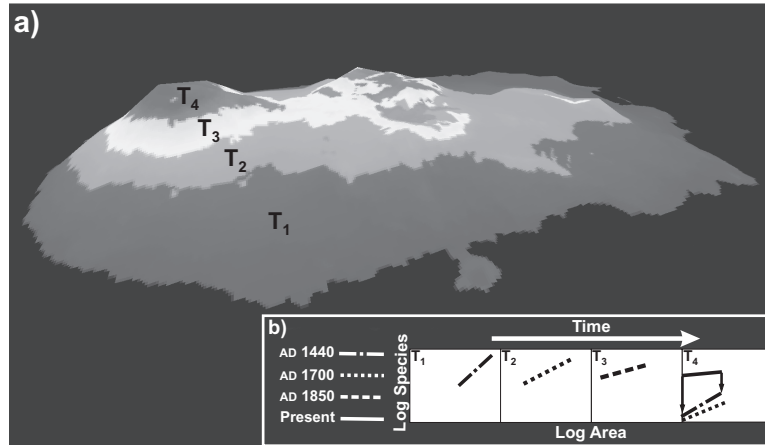
The Azorean Islands were discovered in AD 1432 by Portuguese explorers, and more than 500 years of human settlement have taken their toll on the local fauna and flora, 420 species of which are endemic to the archipelago. Today, approximately 70 per cent of the vascular plants and 58 per cent of the arthropods found in the Azores are exotic, many of them invasive.

The destruction of the native ‘laurisilva’, a humid evergreen broadleaf laurel forest, in the Azores has followed a clear temporal sequence. At the time of human colonization (c. AD 1440), the archipelago was almost entirely covered by forest. By 300 years ago (c. AD 1700) human activities had restricted the native forest in most islands to areas above 300m a.s.l. and, by c. AD 1850, areas with native forest were present only above 500m a.s.l. The development of an economy dependent on milk production during the last decades of the 20th century drove a further reduction of native forest area, to 2.5 per cent of the total area of the archipelago (Figure B8.2a).

The Azorean arthropod fauna has been intensively sampled during the last ten years. The Borges *et al.* (2005) checklist includes virtually all arthropod species native to the Azores, as well as an accurate description of their presence or absence in all the islands of the archipelago. The endemic arthropods belonging to three groups – Araneae, Hemiptera and Coleoptera – were classified as native forest dependent and non-forest dependent species, and only the forest dependent species endemic to the archipelago were considered for further analyses.

We used four different ‘habitat areas’ to calculate our species–area relationships: these were chosen to correspond to the extent of native forest at four known points in time before and since human colonization (≈AD 1440, AD 1700, AD 1850, AD 2000; Figure B8.2a). Although the historical estimates of forest cover are crude approximations, we consider that they are accurate enough to provide a baseline for estimating the present extinction debt.

Our analyses follow the rationale that if species ‘relaxation’ has not yet taken place or is incomplete (i.e. the extinction debt has not yet been paid), then the best fitting species–area model will correspond not to present forest area but to a past baseline – a hypothetical dynamic equilibrium from which the system has since departed. However, there is a complication in dealing with a system of endemic species on oceanic islands of varying age, namely that the dynamics of colonization, speciation and extinction may be at different points, depending on the age of the island. Accordingly, we fitted and compared both species–area and species–area–time models.



**Figure B8.2a** The sequential reduction of the native forest and the respective species–area relationships. **(a)** The elevational occupancy of native forest in historical times for the island of Terceira (Azores).  $T_1$ : Before human occupation (almost complete coverage of island's area);  $T_2$ : approximately 300 years ago (300–500 m);  $T_3$ : approximately 160 years ago (above 500 m);  $T_4$ : current distribution. **(b)** A schematic representation of the effects of the sequential reduction of the native forest on the species–area relationships of endemic forest arthropods. The dashed lines in  $T_4$  represents the future species–area relationships, extrapolated from  $T_1$  and  $T_2$  (see text). The magnitude of the extinction debt is represented by the difference between current species richness (solid line) and the future predictions (dashed lines). From Triantis *et al.* (2010).

For the total island area and the habitat area above 300 m, the species–area–time model applied was significant ( $P < 0.05$ ) for the arthropod taxa considered, with most of the explained variance attributable to area. However, for the area above 500 m and the present area covered by native forest, neither the species–area–time relationships nor the respective species–area relationships were statistically significant. We thus used the first two benchmark relationships, for total area ( $\approx$  AD 1440) and area above 300 m ( $\approx$  AD 1700), to represent the baseline conditions for estimation of current extinction debt. Hence, we used the parameters estimated for the total area of the islands (Prediction 1 in Table B8.2a) and that of the area above 300 m (Prediction 2 in Table B8.2a) to estimate the number of endemic forest arthropods that 'should' be present and, by direct comparison with the number of extant species, to derive the number of future extinctions (i.e. the extinction debt) (Table B8.2a).

For the arthropod taxa considered, our results clearly indicate that the majority of the endemic forest-inhabiting species (>50 per cent) are expected to go extinct in time, especially on those islands on which the native forest has been restricted to small areas or has been totally removed. Terceira, the island with the largest remnants of native forest, has the smallest number of predicted future extinctions.

At face value, these figures constitute a powerful warning to island conservationists that the worst of the extinction crisis is by no means over. Furthermore, in spite of the fact that some archipelagic endemic species may benefit from a degree of population reinforcement between habitat fragments or islands, the parallel reduction of the native forest across all islands in the last 600 years has greatly diminished the probability of such source-sink dynamics rescuing species from global extinction. Hence, we would also anticipate a correspondingly large number of archipelagic-scale species extinctions for Azorean endemic arthropods in the future as the extinction debt is settled. In point of fact, at least five SIE species of beetles recorded early in the 20th century have not been recorded since 1965 and might therefore be considered extinct.

In the paper, we argued that the figures reported above are likely to be more accurate than previous predictions because we have focused our attention on endemic forest species that have evolved in,

**Table B8.2a** Number of forest-dependent archipelagic endemic arthropods for the nine Azorean Islands and the respective predicted number of species that should be found based on the species–area–time models from the total area (Prediction 1) and the area above 300 metres (i.e. area occupied by native forest c. 300 years ago; Prediction 2). Currently there is no native forest on Graciosa and Corvo islands. Note that the results remain similar when the different groups, i.e. Coleoptera, Araneae and Hemiptera, which have been lumped together in the table, are analysed separately.

Island	Arthropods	Prediction 1 (total area)	Prediction 2 (area >300 m)	Species loss
Graciosa	8	1.14	2.42	86–70%
Corvo	3	1.00	1.34	66–55%
Flores	24	4.01	8.04	83–67%
Faial	17	1.11	2.59	93–85%
Pico	28	2.55	4.66	91–83%
São Jorge	21	1.28	2.83	94–87%
Terceira	29	5.79	12.10	80–58%
São Miguel	34	1.84	5.28	95–84%
Santa Maria	24	0.29	1.93	99–92%

and are only found in association with, the native forest. At the same time, we avoided additional ‘noise’ caused by generalist species that may well be able to survive in other (i.e. anthropogenic) habitats. If this logic is correct, then the implication is that large-scale conservation efforts need to be implemented if the high extinction debt we have identified is to be deferred or avoided. Human-induced fragmentation, land-use changes and invasive species have already been identified as important threats to Azorean biodiversity.

This paper argues that the conservation of the Azorean natural heritage, and that of many other oceanic islands, will largely depend on establishing an integrated large-scale strategy to manage both indigenous and non-indigenous species, while simultaneously protecting the remnants of native habitat and, ideally, increasing their extent. However, as appreciated by the authors (and pointed out by the journal’s reviewers), there are a number of key assumptions embedded in this study that may undermine the power of the analyses and which may serve as points for class discussion. These include:

- 1 the reliance on an assumption of a dynamic equilibrium, or something approximating to it, prior to human interference;
- 2 that the endemic species identified as forest-dependent can persist only in the native forests; and
- 3 that the remaining forest area, although in most cases fragmented, can be treated as if occurring in a single block, with the degree of fragmentation being insignificant.

fragments of inhabited land in the world. When the first Europeans arrived there on Easter Day AD 1722, they found a fascinating enigma: how could this impoverished, nearly treeless island, with its sparse and impoverished population, have supported the construction of the remarkable giant statues (moai) that could be found all over the island. How, and why, had it all gone so terribly wrong?

The flora of Easter Island currently consists of over 200 vascular plant species, of which only 46 are native. However, the native flora was once rather richer, containing several native tree and shrub species (Diamond, 2007). The forests are now known to have contained a giant palm tree and a number of other trees, some reaching over 30 m in height. These forests persisted for at least 33,000 years (as far back as the

palaeoecological record goes) and survived the major climatic shifts of the late Pleistocene and early Holocene. We can thus be certain that deforestation caused directly or indirectly by humans was responsible for the treeless state of the island observed by the first Europeans (Diamond, 2007).

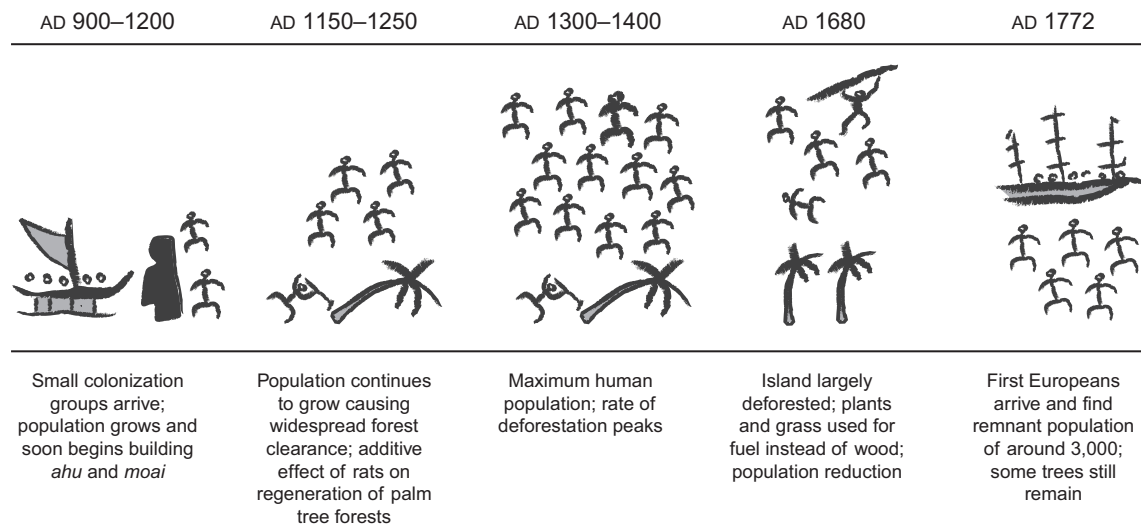
Recent studies have recorded that more than 20 tree and woody plant species were exterminated as an eventual outcome of Polynesian settlement. The palm was almost completely gone by AD 1450 and the other large trees by AD 1650. What is not known with any certainty is exactly how long this almost suicidal environmental destruction took.

The date of the first settlers arriving on the island is still debated. Estimates range from AD 300 to 1200, with the most recent date considered as the most reliable earliest date of occupation (Hunt, 2006; Hunt & Lipo, 2006). Their effect on the forest was soon detectable in the pollen record and it had been entirely eliminated for some time by the end of the 17th century (Figure 8.7; Hunt & Lipo, 2006; Diamond, 2007). The human population reached its peak around AD 1600, but subsequently was intensely reduced, along with the megalithic culture that had sustained the quarry-

ing, sculpting, transport and erection of the remarkable giant statues.

The loss of trees and other plant species is matched by a more complete loss of native birds than on any comparable island in Oceania (Steadman, 1997, 2006). Bird bones associated with Polynesian artefacts 600–900 years old showed that Easter Island once sustained at least 22 species of seabird, of which only seven now occur on one or two offshore islets, and just one of which still nests on Easter Island. Bones also provide evidence for the existence of six endemic land bird species, a heron, two rails, two parrots, and an owl, none of which survive.

Embodied in ecosystem collapse is the concept of trophic cascade, i.e. the chain of knock-on extinctions following the loss of one or a few species that play a critical role (e.g. as a pollinator) in ecosystem functioning. A perturbation at one trophic level propagates through lower levels with alternating positive and negative effects, as highlighted in the phenomenon of mesopredator release, outlined earlier. Thus, the removal or absence of large predators would be expected to lead to increased densities of consumers, which, in turn, would be predicted to have negative



**Figure 8.7** Major events in the sequential collapse of the Easter Island ecosystem. Adapted from Hunt (2006) and modified according to the account provided by Diamond (2004, 2007).

consequences for producers (Oksanen & Oksanen, 2000).

Terborgh *et al.* (2001) studied a set of large predator-free islands created by a hydroelectric impoundment in Venezuela. The small area of the islands restricted the predator community to species predating invertebrates (e.g. birds, lizards, anurans and spiders) and seed predators (rodents), alongside herbivores (howler monkeys, iguanas, and leaf-cutter ants). Predators of vertebrates were absent, and densities of rodents, howler monkeys, iguanas and leaf-cutter ants were found to be 10 to 100 times greater than on the nearby mainland, suggesting that larger predators normally limit their populations.

Moreover, the densities of seedlings and saplings of canopy trees are severely reduced on herbivore-affected islands. Terborgh *et al.* (2001) found support for the idea that hyper-abundant folivores could reduce species-rich forests to an odd collection of herbivore-resistant plants. The endpoint of such a process is likely to be a biologically impoverished system.

All of the above examples suggest the existence of taxon- and system-dependent thresholds, beyond which species losses accelerate (Ewers & Didham, 2006; Whittaker & Fernández-Palacios, 2007). Such thresholds are highly pertinent to understanding relaxation as a result of habitat loss and fragmentation. The most dramatic changes seem to be those following the loss of a trophic tier, typically the loss of top predators. However, similarly dramatic changes can follow the addition of a trophic tier, as seen when terrestrial vertebrate predators are introduced to remote islands previously lacking them (Terborgh, 2010).

Given the central importance of the topics of habitat fragmentation and species relaxation in predicting current and future extinction rates, it is surprising that more attention has not been given to experimental analyses of threshold effects and to studies of the timescales over which the 'extinction debt' persists (see Simberloff & Martin, 1991; Brooks *et al.*, 1999; Laurance, 2002). Although restricted to metapopulation model simulations (of which, more follows below), Keymer *et al.* (2000) have shown that persistence in dynamic landscapes depends on the interaction between three factors: the amount of habitat in the landscape; the rate of change of the amount of habitat; and the life history of the species living in the landscape. More generally, they suggest that including temporal considerations into models of landscape

structure changes the extinction threshold – the amount of habitat destruction a population can tolerate – by making the threshold sensitive to the rates of destruction.

## 8.3 SPECIES INCIDENCE

### 8.3.1 Minimum viable populations, minimum areas and incidence functions

In his seminal paper, Caughley (1994) identified two prevailing paradigms in conservation biology: the 'declining population paradigm' and the 'small population paradigm'. The declining population paradigm is the identification and management of the processes that depress the demographical rate of a species and cause its populations to decline deterministically, whereas the small population paradigm is the study of the dynamics of small populations that have declined owing to some (deterministic) perturbation, and which are more susceptible to extinction via chance (stochastic) events. These concepts underpin the formulation of extinction-risk criteria.

Theoretical and empirical work has repeatedly shown that, once reduced in size and geographical range, populations face a considerably elevated risk of extinction (MacArthur & Wilson, 1967). Or, as Darwin (1872, p. 133) put it: 'Rarity ... is the precursor to extinction'.

There are actually several different forms of rarity (Box 4.1), the most extreme form of which is when a species is reduced to a small population entirely isolated from supplementary immigration, or indeed to the very last such population of the species. In the late 1970s, researchers identified the need to characterize quantitatively the long-term viability of such small and entirely isolated populations (Soulé & Wilcox, 1980). This led to the concept of the minimum viable population (MVP), the smallest number of individuals required to provide a specified probability of persistence over a given period of time (Shaffer, 1981). For instance, the MVP could be operationalized as 'the population size required to ensure a 99 per cent probability of the species' population persisting for 40 generations or for 1,000 years' (see, e.g. Reed *et al.*, 2003).

Theoretical estimates of MVPs typically vary from as few as 50 to as many as 10,000 individuals, based on the postulated effects of demographical, genetic and



environmental variation (Reed *et al.*, 2003; Brook *et al.*, 2006), with the available empirical evidence pointing to the upper end of this range (e.g. Reed *et al.*, 2003). It has been estimated that the maximum tolerable rate of inbreeding is 1 per cent per generation, which has in turn been translated to approximately 50 individuals to ensure short-term fitness (see Shafer, 1990). However, typically only a proportion of the adult population participates in breeding and it is these animals that form the effective population size, which is often substantially smaller than the total population size (Shafer, 1990; see Crandall *et al.*, 1999, for discussion on the concept).

A study of grizzly bears in the Yellowstone National Park showed that to prevent inbreeding rates exceeding 1 per cent required an overall population size of at least 220 rather than 50 animals (Shafer, 1990). Further rule of thumb estimates have been collated by Frankham *et al.* (2002; their Table 14.1, p. 339) as follows: the population numbers required to avoid inbreeding depression and to retain fitness in the short term, >50; to retain evolutionary potential, 500–5,000; and to avoid the accumulation of deleterious mutations, 12 to 1,000 individuals.

Attempts to calculate the viability of single populations (i.e. whether the population is likely to persist for a given period of time) are referred to as population viability analyses (PVA) (see Reed *et al.*, 2003). PVA can take into account the combined impacts of stochastic factors (demographical, environmental and genetic stochasticity) and deterministic factors (e.g. habitat loss, over-exploitation). According to Brook *et al.* (2006), PVA and the threat categories of IUCN (Box 4.1) each offer an assessment of a species' probability of extinction based on its current population size and structure and the characteristics of the threatening processes it faces. On the other hand, the main feature of MVP analysis is that the risk of extinction is fixed and the critical question asked is how large a population must be to avoid this risk.

Demographical stochasticity of initially small populations can lead to losses from a series of isolates without a need to invoke any specific mechanism such as predation or loss of fitness. However, where small populations persist for a reasonable length of time (e.g. several generations), they may also lose genetic variability as they pass through bottlenecks. They may then lose fitness by lacking the genetic flexibility to cope with either the normal fluctuations of environment or an altered environment, and they may also

accumulate so-called deleterious genes, i.e. genes that reduce survival or fertility (see Caughley, 1994).

A further complication in assessing genetic effects of fragmentation is that where a species is split into numerous separate populations in fragmented habitats, there may be multiple bottlenecks involved. This may result in reduced variation within each population, but increased genetic differentiation between populations (see Leberg, 1991). The viability of an isolated population may also be influenced by the occurrence of environmental change or disturbance, and indeed it has been argued that it is critical to take such environmental catastrophes and fluxes into account when estimating the MVP and designing conservation measures based around protecting such small, endangered populations (Mangel & Tier, 1994).

An example of synergetic effects of a catastrophic event and inbreeding is provided by song sparrows (*Melospiza melodia*) living on Mandarte Island in western Canada. The inbred birds died at a much higher rate during a severe storm than did outbred birds (Keller *et al.*, 1994). Although the severe weather was what caused this mortality, it appeared that inbreeding determined, in part, which individuals survived the storm.

Recently, Reed *et al.* (2003) considered the effects of age structure, catastrophes, demographical and environmental stochasticity, and inbreeding depression, to derive MVP estimates for 102 vertebrate species. They defined an MVP as 'one with a 99 per cent probability of persistence for 40 generations'. Across this data set, mean and median estimates of MVP were 7,316 and 5,816 adults, respectively. The estimated values did not differ systematically between major taxa, or with trophic level or latitude, but were negatively correlated with population growth rate. Reed *et al.* (2003) stress that although MVPs provide a useful rule of thumb for species conservation (which is that the size of vertebrate populations needed for successful long-term conservation is about 7,000 adults), MVPs should not be used as precise conservation targets. For further discussion see also Brook *et al.*'s (2006) study on the MVP of 1,198 species.

Closely related to the concept of MVP is the idea of the minimum viable area (MVA). For some species, e.g. snail populations, a fairly small area may suffice to maintain the requisite number of individuals. Species of higher trophic levels generally require more area or space to ensure good survival prospects. It has been



calculated that a single pair of ivory-billed woodpeckers (*Campephilus principalis*), a species generally considered extinct, may have required 6.5–7.6 km<sup>2</sup> of appropriate forest habitat; that the European goshawk (*Accipiter gentilis*) has a home range of about 30–50 km<sup>2</sup> (Wilcove *et al.*, 1986); and that populations of North Island brown kiwi (*Apteryx mantelli*) in New Zealand are unlikely to be viable in protected areas of less than 100 km<sup>2</sup> (Basse & McLennan, 2003).

Even some plant and insect species may need surprisingly large areas if they typically occur at very low population densities (Mawdsley *et al.*, 1998). Thus, for many species, reserves must be really rather large if their purpose is to maintain a MVP entirely within their bounds. For instance, it has been estimated that the minimum viable area for some large mammals during a time span of 1,000 years exceeds 100 times the area of Yellowstone National Park (Shafer, 1995).

The MVA approach, if focused on large-bodied flagship species and converted into policy recommendations, may have benefits for the preservation of entire ecosystems, since many other species with lesser area requirements may benefit from protection within the MVA of the flagship species. However, one limitation of the MVA approach is that it is predicated on the idea that each area is discrete and has no biotic (genetic) exchange with other surrounding areas. If there is such exchange taking place, such that the population is actually part of a network (or metapopulation), then the estimated MVA may be larger than is strictly necessary (see discussion in Whittaker & Fernández-Palacios, 2007).

Another way of examining area requirements of particular species is by means of incidence functions estimating the probability of a species occurring as a function of a key controlling variable, such as island species richness, area, isolation, or sometimes a combination of two key variables (Diamond, 1975b; Wilcove *et al.*, 1986; Watson *et al.*, 2005; and see Figure 8.8).

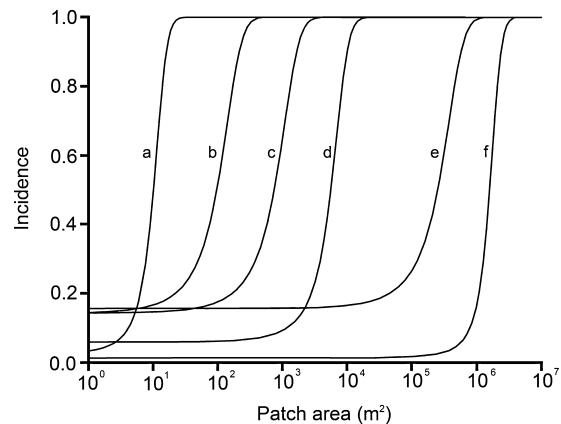
In 1994, Hanski introduced the incidence function model (see also Hanski, 1999; Moilanen & Hanski, 2006). The simplest form uses a snapshot of species presences and absences and predicts extinctions based on patch size and colonizations based on isolation (see MacKenzie *et al.*, 2006, for discussion on the concept).

Moilanen (2002) has drawn attention to three main types of errors likely to occur in data used for incidence functions analyses:

- 1 inaccurate measurements of the patch areas;
- 2 the existence of patches that are unknown within or around the study area ('missing patches');
- 3 patch occupancy is incorrectly observed, with patches considered to be empty actually containing a population of the focal species (the 'false zero' problem).

Perhaps more fundamental a problem is that species incidence functions tell us, of course, the properties of 'islands' on which a target species currently occurs, but not those on which it may persist in the long term or in an altered ecological conditions. Thus, they are not equivalent to estimating MVAs.

Biedermann (2003) provides an interesting analysis of area–incidence relationships of 50 species of vertebrates and invertebrates from 15 different fragmented landscapes, ranging from Central European grassland to Asian tropical forest, in which he demonstrates that area requirements increase essentially linearly with increasing body size on a log–log scale. Biedermann



**Figure 8.8** Examples of species incidence functions based on logistic regression models across different landscapes and ecosystems, ranging from Central European grassland to Asian tropical forest:

- (a) *Kelisia haupti* (planthopper);
- (b) *Arytaina genistae* (psyllid);
- (c) *Neophilaenus albipennis* (spittlebug);
- (d) *Chazara briseis* (butterfly);
- (e) *Dendrocopos minor* (lesser spotted woodpecker);
- (f) *Accipiter gentilis* (goshawk).

Re-drawn from Biedermann (2003).

cautions that the relationship was based on analyses for species more or less restricted to the habitat patches considered, and that we should not consider as granted a similar relationship for generalist species.

If incidence functions really reflect key controlling variables, then they might be of great value in designing reserve networks but, if they are found to be inconsistent across the range or through time, they will need more careful interpretation. Empirical work suggests that, in practice, they do vary in both time and space. In illustration, Hinsley *et al.*'s (1996) study of 31 woodland bird species in 151 woods in a lowland arable landscape in eastern England over three consecutive years has shown that the incidence functions vary through time in relation to density-independent mortality (extremes of weather conditions). Additionally, Hinsley *et al.* (1996) showed that specialist species were more likely to disappear from small woods after severe winter weather than were generalists, and that they could take more than a year to recolonize. We may interpret these patterns as reflecting underlying metapopulation dynamic processes, discussed in the following section.

An illustration that incidence functions might vary across the range of a species comes from another study of woodland birds, this time undertaken in Australia and based on data from three different landscapes located quite near one another (and thus within the same biogeographical context and climate regime). The study, by Watson *et al.* (2005), demonstrated that area- and isolation-based incidence functions differed significantly, seemingly as a function of differences in properties of the landscape matrix within which the woodlands were embedded. The three landscapes were an urban area, a peri-urban area and a rural (agricultural) landscape.

Interestingly, it was evident that while some species were able to occupy smaller woodlands within the rural landscape, others actually showed a higher incidence in small woods in the urban area (within the city of Canberra itself). This provides some indication of the difficulty of designing a reserve network system optimized for all members of the community of interest (see also Magle *et al.*, 2009).

Recently, Prugh *et al.* (2008) compiled occupancy data for 1,015 bird, mammal, reptile, amphibian and invertebrate populations from 89 case studies, including in total 12,370 habitat patches that were embedded within unsuitable matrix of land cover on six continents. Using incidence functions, they evaluated

the predictive ability of patch area and isolation for species occupancy. Surprisingly, both area and isolation performed poorly as predictors. Prugh *et al.* (2008) concluded that is the type of land cover separating patches that most strongly affects the sensitivity of species to patch area and isolation. Thus, although patch size and isolation are indeed important for the occupancy of many species, they find, as do Watson *et al.* (2005) in their study, that it is crucial to take account of the properties of the intervening matrix.

Hence, a key conclusion of this work is that improving the quality of matrix may result in 'higher conservation returns than manipulating the size and configuration of remnant patches for many of the species that persist in the aftermath of habitat destruction' (Prugh *et al.*, 2008, p. 20,770).

### 8.3.2 Metapopulation dynamics

Plant and animal species are typically patchily distributed; indeed all species' ranges involve discontinuities, and especially so at finer scales of analysis. It is frequently possible to discern that within a landscape, a particular species occupies geographically separated patches that are interconnected by occasional movements of individuals and gametes. The name for this network of local populations is a *metapopulation*.

The first metapopulation models were constructed by Richard Levins in papers published in 1969 and 1970 (Gotelli, 1991). The basic idea can be understood as follows: imagine that you have a collection of populations, each existing on patches of suitable habitat. Each patch is separated from other nearby habitat patches by unsuitable terrain. Although these separate populations each have their own essentially independent dynamics, as soon as one crashes to a low level, or indeed disappears, that patch will provide relatively uncontested space for 'surplus' individuals from one of the nearby patches, which will soon colonize the now-unpopulated patch.

For example, Lei and Hanski (1997) studied metapopulation structure in a threatened species of butterfly, *Melitaea cinxia*, and its specialist parasitoid, *Cotesia melitaeaeum*, in a large network of small habitat patches. They observed that the incidence of the parasitoid in host populations was positively correlated with the size of the host population and the area of the habitat patch. *C. melitaeaeum* is thus expected to have a substantial risk of extinction from patches in which

the number of host populations is small, meaning that the parasitoid may well go entirely extinct from certain patches. However, the network of patches provides the possibility of recolonization.

Metapopulation theory, therefore, examines the dynamics of sets of semi-independent populations connected by dispersal (Hanski & Gilpin, 1991). In Levins's (1970) model, a metapopulation is a network of extinction-prone subpopulations of a species occupying a variety of habitat patches. These subpopulations inhabit identical patches and are subject to equal but independent probabilities of extinction and recolonization.

In practice, habitat patches and the landscapes in which they are embedded are very much more complex and heterogeneous than this, so a key challenge for metapopulation modellers is to develop models that are balanced between the attractive simplicity of the general model and fine-tuning to such a degree that models are restricted in application to a single system (see case studies in Whittaker & Fernández-Palacios, 2007).

Sometimes, conservation scientists have suggested managing endangered species via policies that encourage the populations to function as metapopulations, thus allowing for the idea that a mixed-use landscape could be worth conserving, as opposed, for example, to insisting that a large area should remain as, or be restored entirely to, a forest cover.

However, a spatial model created by Lamberson *et al.* (1992), in order to predict how the populations of the northern spotted owl (*Strix occidentalis caurina*) will survive in patches surrounded by logged forest, eventually failed to predict realistic minimum viable populations of the bird (Harrison *et al.*, 1993). The populations of the bird declined in a pattern not predicted by the metapopulation models. On the other hand, some butterfly species have been found to behave according to the predictions of metapopulation models (Thomas & Hanski, 1997). Therefore, the more basic question is: how broadly and to which species does the metapopulation theory apply in habitat fragments?

According to Harrison & Taylor (1997) and Hoopes & Harrison (1998) four scenarios of landscape structure are common in fragmented landscapes (Figure 8.9):

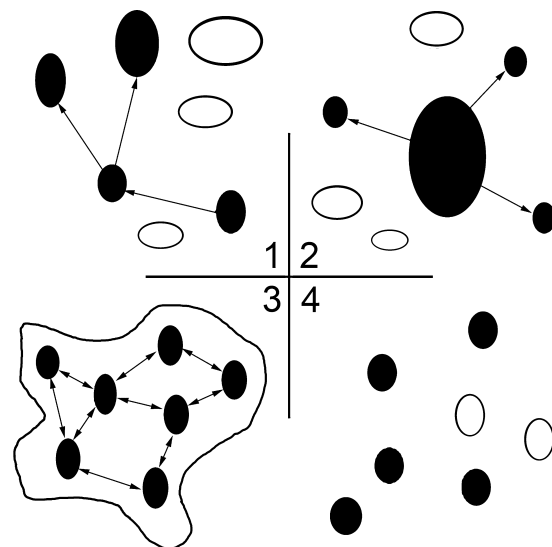
**1** where patches are roughly of equal size and dispersal distances are comparable to the distances between patches (classic metapopulation models may apply);

**2** where patches are so unequal in size and/or habitat quality that most immigrations are in one direction (from large to small patches); extinctions and recolonizations that occur in very small populations are inconsequential (mainland/island metapopulation models may apply);

**3** where patches are so close together relative to dispersal distances that they support a single population and not a metapopulation (patchy populations);

**4** where patches are so far away relative to dispersal distances that the populations are not interconnected and the assembly ceases to be a metapopulation (non-equilibrium metapopulation models may apply).

Thus, whereas patches of tall forest in a savanna landscape may be treated within the framework of metapopulation theory, the concept may not be suitable for forest patches in a highly tree-covered landscape. This is because ecological boundaries between forest and savanna are clear-cut, whereas those between forest and highly tree-covered landscape are fuzzy. Furthermore, an insurmountable barrier for one group of organisms may be easily navigated by another – for sunbirds, forest patches spread over a 100 km<sup>2</sup>



**Figure 8.9** Structures of metapopulations that can arise from fragmentation.

Adapted from Hoopes & Harrison, 1998; after Harrison (1991). The four cases are those described in the text.

landscape may sustain a metapopulation but, for dispersal-limited snails, they can at best sustain isolated populations.

Metapopulation models, therefore, are not generally applicable to all organisms in fragmented systems (Fahrig & Paloheimo, 1988). Hoopes & Harrison (1998) caution against the general use of such models in conservation decision-making because of the prevalence of situations where functional metapopulation dynamics either do not occur, or where they fail to match the assumptions of the models.

The following are additional important shortcomings of the metapopulation approach:

- Several authors have noted that metapopulation models are extremely data-demanding and usually require data that are very difficult to obtain (Kindvall & Ahlén, 1992; Doak & Mills, 1994). Moreover, model results tend to be very sensitive to poorly estimated parameters, and the predictions of such models have therefore frequently been found to be inaccurate (e.g. Harrison *et al.*, 1993; Wilson *et al.*, 1994).
- Most empirical examples of metapopulations pertain to single species or a group of interacting species (Hanski & Gilpin, 1991), but not to multi-species ecological communities.
- Most metapopulation models assume no distance effects (Fahrig & Merriam, 1994) although, in practice, dispersal abilities vary from species to species. For instance, metapopulations of frogs may be influenced by the availability of suitable habitat in the surrounding  $\approx 500$  m, whereas for birds this distance may be  $\approx 3$  km, because of large differences in mobility resulting in the different abilities of frogs and birds to disperse. The issue of 'scale' has therefore been considered important in studying fragmented landscapes (e.g. Doak *et al.*, 1992) – an issue which classic metapopulation models do not address.
- It is important for conservationists to recognize that many local populations may not be at equilibrium and regional processes may be critical in sustaining metapopulations (Hanski 1999).

In conclusion, metapopulation theory offers a useful framework for thinking about isolation and fragmentation (Hanski, 1999) but, if the concept is to be useful as a theoretical framework for conservation decision-making, it must be extended from the original simplistic models to allow for the differing degrees of population connectivity in fragmented landscapes and differing forms of inter-patch relationships, as in real-world systems.

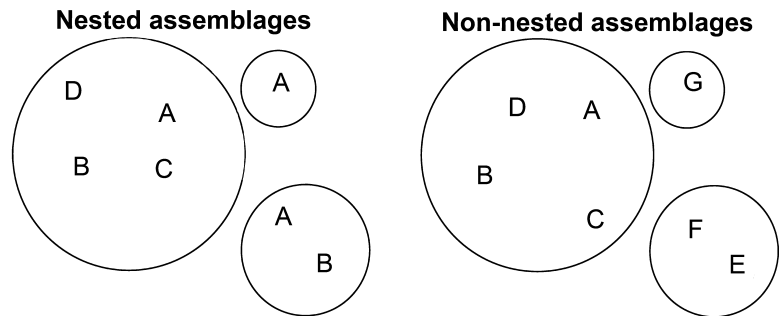
## 8.4 NESTEDNESS

The concept of nestedness was first introduced some 70 years ago (see Ulrich *et al.*, 2009) to describe patterns of species composition within continental biotas and among isolated habitats such as islands and landscape fragments. In a perfect nested pattern, when a set of habitat patches is ordered by increasing species richness, it will be found that the smallest assemblages make up a subset of the species found in the next larger assemblage, and so on, throughout the series (see Figure 8.10).

Nestedness is thus a particular form of non-randomness of assemblage composition across a set of isolates. Any such non-random pattern is potentially of interest to conservation biogeographers, as it may inform judgements about the design of protected area systems within landscapes and regions. Nestedness may, in theory, arise from differential dispersal and colonization abilities (especially for young islands); or differential rates of extinction (e.g. for land bridge islands or newly fragmented habitat islands); or from a strong nestedness of habitat types with increasing 'island' size (Whittaker & Fernández-Palacios, 2007); or possibly from other processes (Table 8.3).

Nestedness analyses became popular among ecologists and biogeographers only after Patterson and Atmar (1986) developed a statistically rigorous approach for analysing nested subsets. They were interested in nestedness patterns derived by extinction of species from land bridge islands, and their metric reflects this emphasis. They proposed that nestedness patterns for such islands most likely reflect orderly sequences of extinctions on such islands and in fragmented landscapes (see their Fig. 4). They introduced an intuitive 'matrix temperature' metric to quantify the pattern of nestedness. Hot matrices are those with more random presences of species and cool matrices are those where species presences are more nested. The matrix temperature could be calculated with a software package, *The Nestedness Temperature Calculator* (Atmar & Patterson, 1993, 1995).

The nestedness concept, as applied by Patterson and Atmar, is based on ordering the data matrix by the size of fauna or flora, i.e. it is richness-ordered nestedness. Some authors, however, have ordered the data matrix not by species richness but by island area, which has been termed area-ordered nestedness, or even by island isolation, i.e. distance-ordered nestedness (e.g. Lomolino & Davis, 1997; Whittaker &



**Figure 8.10** Nested subset relationships. Circles represent islands of different size and letters represent species. Circle size is positively correlated with species richness. The left biota is perfectly nested; all the species present in relatively species-poor assemblages are present in relatively species-rich assemblages. The right biota is perfectly non-nested because none of the species in the species-poor assemblages is present in the richer ones. Note that although the species richness of the three islands is the same in the two cases, the overall species richness of the non-nested set is greater than of the nested system.

**Table 8.3** Causes of nested subset patterns (adapted from Ulrich *et al.*, 2009).

Hypothesis	Assumption/precondition		Explanation/Example
	Site and species properties	Gradient of:	
Passive sampling	carrying capacities of sites	regional abundance	Species are drawn randomly from the pool with the constraint that the availability of propagules is itself strongly non-random (e.g. Higgins <i>et al.</i> , 2006).
Neutrality	carrying capacities of sites	dispersal ability	The availability of propagules is random and species' dispersal ability is driving the pattern (e.g. Ulrich & Zalewski, 2007).
Selective colonization	isolation	dispersal ability	There are predictable limits to species' dispersal abilities. The system consists of islands 'sampling' a series of species' isolation/incidence functions (e.g. Darlington, 1957; Patterson, 1990).
Selective extinction	carrying capacities of sites	extinction susceptibility	Selective occupancy of sites according to the area of sites, which sets their carrying capacity. Relaxation in the case of mainland/habitat islands (e.g. Patterson & Atmar, 1986).
Nested habitats	habitat heterogeneity	degrees of specialization	Absence of certain habitat types in smaller and/or resource-poor patches. Higher proportion of generalist species in smaller and/or resource-poor patches (Wright & Reeves, 1992).
Selective environmental tolerances	environmental harshness, environmental tolerances		Selective occupancy of sites according to species tolerance of environmental stress (e.g. Blake, 1991).
Habitat quality	environmental harshness		Species are distributed according to the harshness exhibited by patches of the same habitat (e.g. Bloch <i>et al.</i> , 2007).



Fernández-Palacios, 2007). Intuitively, however, ordering by species richness would appear the most appropriate approach.

Apart from sequential extinctions, a variety of different mechanisms can also produce nestedness patterns (see Table 8.3), some of which are deterministic and some of which are stochastic, requiring different metrics for quantifying nestedness (Wright *et al.*, 1998; Ulrich *et al.*, 2009). All of the explanations for nested subsets can be seen as variations of ordered colonizations or extinctions along environmental or biological gradients (area, isolation, habitat) of the target areas. Frequently, these mechanisms cannot be distinguished by just establishing the statistical pattern of nestedness. Inferences of causation ideally require independent lines of verification beyond manipulations and analyses of the original presence/absence matrix (Ulrich *et al.*, 2009).

Although nestedness can be driven by a number of processes, it appears that differential extinction plays a major role in producing nested structure in many habitat island data sets (Wright *et al.*, 1998). Knowledge of nested subset structure might therefore provide a basis for predicting the ultimate community composition of a fragmented landscape, particularly if it is possible to attribute patterns to particular causes (Fischer & Lindenmayer, 2005; Fleishman *et al.*, 2007).

Feeley's (2003) study of bird communities inhabiting recently isolated land bridge islands in Lago Guri, Venezuela, showed how nestedness calculations can provide useful insights. Lago Guri is a large hydroelectric reservoir created in 1986 in east-central Venezuela. The inundation of an area of hilly terrain expanding over 4,000 km<sup>2</sup> resulted in the fragmentation of once-continuous forest into hundreds of land bridge islands (e.g. Terborgh *et al.*, 2001). Feeley found that the resident forest-interior bird communities displayed a significantly nested distributional pattern that was hypothesized to be the result of species' differential extinction rates.

In an earlier study of forest birds, Blake (1991) also found a significant degree of nestedness, particularly among birds breeding in the forest interior and among species wintering in the tropics. By contrast, species breeding in forest-edge habitat showed more variable distribution patterns.

These findings concur with those of Patterson (1990) from São Paulo, Brazil (original data from Willis, 1979). Patterson reported significant nestedness amongst sedentary bird species but, when

transient species were also included, the system as a whole was found to be non-nested.

These results are indicative of a large number of studies of nestedness, which show the outcome of nestedness analyses to be variable across different systems and for different ecological groups of species, but which show that significant nestedness is a common pattern. Such analyses often indicate that species that are restrictive habitat specialists, including many of high conservation value, do require larger, more species-rich patches (Fleishman *et al.*, 2007; Whittaker & Fernández-Palacios, 2007).

In theory, a nestedness analysis can contribute a simple answer to the SLOSS question, as a strong degree of nestedness implies that most species could be represented by conserving the richest (largest) patch. According to Atmar & Patterson (1993), the widespread occurrence of nested subsets speaks for the value of larger protected areas. However, Boecklen (1997) and Fischer & Lindenmayer (2005) convincingly showed that this argument is only valid for perfectly nested subsets, which are very rare in nature. Even for highly significantly (but not perfectly) nested subsets, the total species numbers from subsets of many smaller sites are often higher than the respective number of species from a single larger site of the equivalent total area (Ulrich *et al.*, 2009). On the other hand, a low degree of nestedness may be considered as indicative that specific habitat patches are sampling distinct species sets, and thus an array of reserves of differing size and internal richness may be required to maximize regional diversity in such circumstances (e.g. Kellman, 1996).

Broadly speaking, a nestedness index can provide one compositional descriptor and can perhaps aid identification of risk-prone species. However, it should not be given primacy in conservation planning. Identifying a community as nested at a certain point in time, has limited predictive ability as to the probability of the community maintaining the same sets of species (or even a single species) over time (Simberloff & Martin, 1991). The isolates may be subject to turnover and/or species attrition in new ways dictated by the changing biogeographical circumstances of the landscape in which the fragments occur. As Worthen (1996, p. 419) put it, nestedness is not a 'magic bullet', '... no single index should be expected to distil the informational content of an entire community, let alone predict how it will react to habitat reduction or fragmentation'.

According to Ulrich *et al.* (2009), there are three key steps in a nestedness analysis:

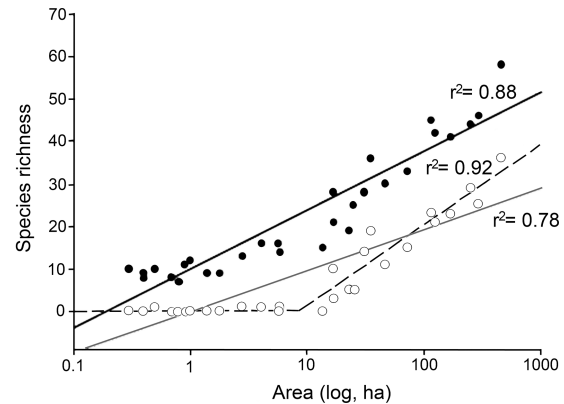
- 1 calculation of a metric to quantify the pattern of nestedness in a matrix;
- 2 comparison with an appropriate null model or randomization test to assess the statistical significance of the metric;
- 3 inference of the mechanism that generated the pattern of nestedness.

Unfortunately, on all three points, no consensus has yet been reached among scientists, which has hindered a general understanding of the frequency, causes, and consequences of nestedness (Whittaker & Fernández-Palacios, 2007; Ulrich & Gotelli, 2007; Almeida-Neto *et al.*, 2008). This lack of consensus, along with the growing number of applied and theoretical studies of nestedness, therefore calls for a critical review of the state of the art and for perspectives for future research. This review should take into account other patterns related to but distinct from nestedness patterns, such as island assembly theory (Diamond, 1975b) and species incidence (see also Section 8.3).

#### 8.4.1 Edge effects

Where two habitats abut, they often intermingle, forming a zone of species overlap (and of locally higher diversity) – a pattern termed an *ecotone*. In the case of many protected areas, habitat alteration often produces quite sharp ecotones or edges, but it is often the case that species numbers are elevated in these edge habitats (Kellman, 1996). However, many of these species are dependent on the matrix habitat rather than on the habitat within reserves. Such species are unlikely to be those that are most in need of protection.

Watson *et al.* (2004) studied birds in littoral forest habitat islands and surrounding habitats in south-eastern Madagascar. Core forest locations were found to be richer than edge or matrix habitats, with some 68 per cent of the forest dependent species found to be edge-sensitive. Frugivorous species and canopy insectivores were generally edge-sensitive, while sallying insectivores preferred edges. The vegetation structure at remnant edges contributed to edge-sensitivity. The relationship between fragment area and overall species richness conceals the fact that forest-dependent species were generally lacking from fragments of less than 10 ha (Figure 8.11).

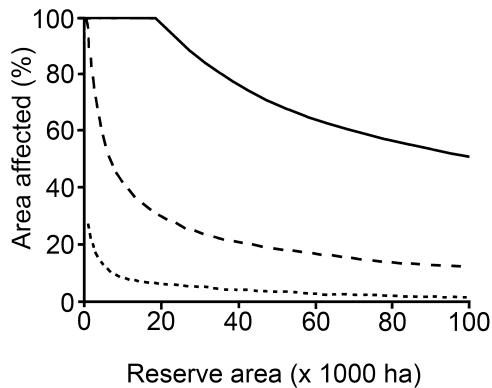


**Figure 8.11** Bird species richness–area relationships in the littoral forests of southeastern Madagascar, including regression lines and  $r^2$  values. Two classifications of species richness were considered: total species richness (closed circles) and forest-dependent species richness (open circles). Linear regressions: unbroken lines; break-point regression: dashed line. The break-point regression procedure followed Lomolino & Weiser (2001). All regressions are significant ( $P < 0.01$ ). From Watson *et al.* (2004).

Wilcove *et al.* (1986) suggest that reserves of less than 100 ha cannot support viable populations of forest songbirds due to high densities of nest predators such as blue jay (*Cyanocitta cristata*), weasel (*Mustela erminea*) and racoon (*Procyon lotor*) around forest edges. Laurance (2000) suggests that edge effects can occur on even large spatial scales. For example, Curran *et al.* (1999) found that recruitment of canopy trees in the 90,000 ha Gunung Palung National Park in western Borneo collapsed because vertebrate seed predators flooded into the park from surrounding degraded areas. A core-area model proposed by Laurance (2000) illustrates the impacts of edge effects on nature reserves ranging from 1,000 to 100,000 ha (Figure 8.12).

These examples illustrate that the relationship between a reserve and its surrounding matrix is not subject to easy generalization. There are species that share both zones and, just as there are matrix species that may impact negatively upon core reserve species, there may also be reserve species which exploit resources in the matrix. Therefore, the heterogeneous





**Figure 8.12** A core-area model illustrating the impacts of edge effects on nature reserves ranging from 1000 to 100,000 ha. The curves show the percentage of the reserve's total area that is influenced by edge effects that penetrate to distances of 100 m (dotted line), 500 m (dashed line) or 2 km (solid line) inside the reserve. For an edge effect that penetrates to 5 km (not shown), the reserve would need to be approximately 650,000 ha in size to ensure that half of its area is free from edge effects. Source: Laurance (2000).

nature of habitats within reserves needs to be taken into account when understanding patterns of species distribution and habitat suitability.

#### 8.4.2 Habitat corridors

Habitat connectivity can be achieved by 'stepping stones' or 'corridors' of suitable habitat linking larger reserves together. In addition to forest peninsulas or hedgerows, other linear landscape features such as rivers, roads, and railways may act as conduits for the movement of particular species. However, for others they may represent barriers or hazards (Reijnen *et al.*, 1996). Therefore, habitat corridors act as differential filters, enabling the movement of some species but being of little value, or presenting an impediment, to others (Table 8.4).

A useful illustration of how corridors can be beneficial comes from the study by Saunders and Hobbs (1989; from Whittaker & Fernández-Palacios, 2007)

of Carnaby's cockatoo (*Calyptorhynchus funereus latirostris*) from the Western Australian wheat belt – an area of 140,000 km<sup>2</sup> in the south-west of the state, 90 per cent of which has been cleared for agriculture. The Carnaby's cockatoo is one of Australia's largest and most striking parrots and was once the most widely distributed cockatoo in the region.

The widespread clearance of the native forest has removed extensive areas of their foraging and breeding habitat, replacing it with annual crops of no value to the species. In more recently cleared areas, however, wide verges of native vegetation have been left uncleared along the roads. These act to channel the cockatoos to other areas where food is available. Cockatoos have not persisted in areas of earlier clearances that were carried out without these connecting strips because, once they run out of a patch of acceptable habitat, it takes a long time for the flock to find another patch of native vegetation. The big reduction in suitable habitat across the region is fairly recent, and the cockatoo is not yet in equilibrium with the new regime (and indeed is considered to be an endangered species). So, it is not clear yet if the degree of connectivity and remaining area of woodland habitat are sufficient for the long-term persistence of this cockatoo.

Some scientists argue that the requirement of corridors for faunal movement may have been overstated and that corridors may not be required for many taxa (see discussion in Simberloff *et al.*, 1992). While movement along corridors is frequently assumed to occur, there have been relatively few studies which have shown that corridors are actually required for movement (Hobbs, 1992). Some studies of marked or radio-tagged animals, however, have provided clear indication that certain species use corridors for movement (e.g. Dmowski & Kozakiewicz, 1990; Merriam & Lanoue, 1990), as do observations such as those above for the Carnaby's cockatoo.

In historical biogeography, the term 'corridor' is used for very broad connecting areas between regions, which are assumed to provide relatively unfettered movement between them. However, in considering habitat corridors at finer scales, within landscapes, and given that each species has its own requirements for habitat, its own ability to move and its own behaviour, few corridors can be considered all-purpose (Dawson, 1994). Rather, like other elements of the landscape matrix, habitat corridors act as filters. Many rare and threatened species are unlikely to benefit from

**Table 8.4** Advantages and disadvantages of habitat corridors (adapted from Noss, 1987).

Potential advantages of corridors	Potential disadvantages of corridors
<ol style="list-style-type: none"> <li>1 Increase immigration rate to a reserve, which could:               <ol style="list-style-type: none"> <li>a increase or maintain species richness and diversity, as predicted by the equilibrium theory of island biogeography;</li> <li>b increase population sizes of particular species and decrease probability of extinction (rescue effect) and/or permit establishment of extinct local populations;</li> <li>c prevent inbreeding depression and maintain genetic variation within populations.</li> </ol> </li> <li>2 Provide increased foraging area for wide-ranging species.</li> <li>3 Provide predator-escape cover for movement between patches.</li> <li>4 Provide a mix of habitats for different activities or stages of their life-cycles.</li> <li>5 Provide alternative refugia from large disturbances (a 'fire escape').</li> <li>6 Provide 'green belts' to limit urban sprawl, abate pollution, provide recreational opportunities and enhance scenery and land values.</li> </ol>	<ol style="list-style-type: none"> <li>1 Increase immigration rate to a reserve, which could:               <ol style="list-style-type: none"> <li>a facilitate the spread of epidemic diseases, insect pests, exotic species, weeds, and other undesirable species into reserves and across landscapes;</li> <li>b decrease the level of genetic variation among populations or subpopulations, or disrupt local adaptation and coadapted gene complexes ('outbreeding depression').</li> </ol> </li> <li>2 Facilitate spread of fire and other abiotic disturbances ('contagious catastrophes').</li> <li>3 Increase exposure to wildlife hunters, poachers and other predators.</li> <li>4 Riparian strips, often recommended as corridor sites, might not enhance dispersal or survival of upland species.</li> <li>5 Cost and conflicts with conventional land preservation strategy to preserve endangered species' habitat (when inherent quality of corridor habitat is low).</li> </ol>

corridors, because their specialist habitats are unlikely to be found throughout the length of most corridors.

For some populations, corridors may even act as 'sinks', drawing out individuals from the main habitat area, perhaps into dangerous places with higher risks of predation, but not returning individuals to supplement the main source area. Alternatively, they may be fairly neutral in their ecological cost-benefit, but perhaps be quite expensive to purchase and set up if not already existing in a landscape. On the other hand, some corridors are essential in providing links between preferred habitats for animals that undertake regular seasonal migrations.

In the longer term, it has been argued that climate change is likely to drive substantial shifts in the distribution of species, and that the resulting species migrations will be impeded by the human sequestration of land to agriculture and other purposes. Therefore, on these grounds, it would seem prudent to plan more or less continuous habitat corridors that straddle major climatic/elevational gradients where this is feasible (e.g. Bush, 1996, 2002 – Box 7.4).

#### 8.4.3 Landscape context – matrix effects

The presence of a species within a reserve will depend not only on the suitability of habitat within the reserve, but also on the species' ability to use the intervening landscape matrix. If this matrix is hospitable, species can also move between reserves (Gustafson & Gardner, 1996). Therefore, although reserves are important, an increasing emphasis is now being placed on the role of the quality of the landscape matrix between reserves.

For example, Baum *et al.* (2004) have demonstrated that corridors and stepping stones are more effective if surrounded by a hospitable matrix. In tall-grass prairie ecosystem in the central USA, they showed that the effectiveness of corridors and stepping stones for promoting dispersal of the planthopper *Prokelisia crocea* among patches containing prairie cordgrass *Spartina pectinata* (the sole host plant for the planthopper) depended strongly on the intervening matrix habitat. In a low-resistance matrix (one that facilitates high rates of inter-patch dispersal), where both stepping stones and corridors promoted high connectivity, the

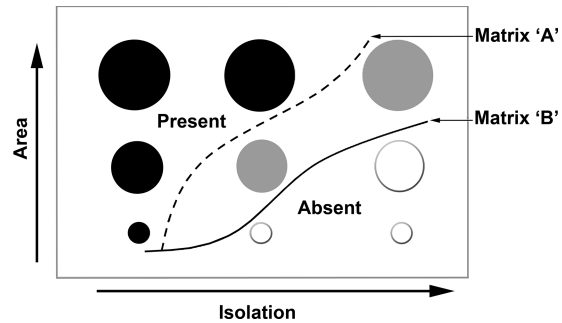
number of planthopper colonists increased by three-fold relative to patches separated by matrix habitat only. The effectiveness of stepping stones and corridors was significantly lower in a high-resistance matrix (one that provides only low rates of interpatch dispersal), with stepping stones failing to improve connectivity for the planthoppers relative to controls (Baum *et al.*, 2004).

To test whether the type of interpatch matrix can contribute significantly to patch isolation, Ricketts (2001) conducted a mark–recapture study on a butterfly community inhabiting meadows in a naturally patchy landscape. The relative resistances of the two major matrix types (willow thicket and conifer forest) to butterfly movement between meadow patches were estimated. For four of the six butterfly taxa (subfamilies or tribes) studied, conifer forest was 3–12 times more resistant than willow thicket. For the two remaining taxa (the most vagile and least vagile in the community), resistance estimates for the two differing matrix types were not significantly different, indicating that responses to matrix differ even among closely related species. These results suggest that the surrounding matrix can significantly influence the ‘effective isolation’ of habitat patches, rendering them more or less isolated than patch size and/or isolation would indicate (as Figure 8.13).

In a study conducted in grasslands in western Victoria, Australia, Williams *et al.* (2006) assessed how both the spatial attributes of remnant patches (area and isolation) and the landscape factors (extent of urbanization and maximum inter-fire interval) influence the persistence of native plant species. They found that, on average, 26 per cent of populations of native species distributed across 30 remnants became locally extinct between the 1980s and 2001. While area and isolation had little effect on the probability of local extinction, urbanization and longer maximum inter-fire intervals corresponded with increased extinction risk (Williams *et al.*, 2006).

Most nature reserves are now surrounded by human-dominated landscape matrix, which is often inhospitable to many species. For example, intensively cultivated agriculture landscape is unable to support forest-dwelling species. Modification of this agricultural matrix, therefore, may provide opportunities for reducing patch isolation and thus the extinction risk of populations in fragmented landscapes.

Tropical agro-forestry systems, where crops are grown under the shade of native tree species, often



**Figure 8.13** A modified species incidence function for a hypothetical species in a series of habitat islands. The occupancy of the species depends primarily on the area and isolation of the habitat island but also varies between Landscape A and Landscape B as a function of the quality of the matrix habitat. Black circles indicate occupied habitat islands and white cells unoccupied habitat islands. The grey remnants and solid line indicate that a species would inhabit these remnants when in a landscape with matrix composition ‘B’ (favourable) but would not in matrix composition ‘A’ (less favourable; dashed line). From Whittaker *et al.* (2005) and based on original ideas developed by Mark V. Lomolino and James E. Watson.

provide matrix habitats suitable for a substantial proportion of native species, although typically not for certain habitat-specialist forest dwellers (Bhagwat *et al.*, 2008). Therefore, it can be argued that for successful conservation within reserves, a whole-landscape approach is needed that accounts for maintaining suitable matrix habitat.

## 8.5 EMERGENT GUIDELINES FOR CONSERVATION

Theories are nets cast to catch what we call ‘the world’: to rationalize, to explain, and to master it. We endeavour to make the mesh ever finer and finer.

(Karl R. Popper, 1959, p. 59)

MacArthur & Wilson (1967) and MacArthur (1972) have described ‘habitat patches’ such as farmer’s woodlots surrounded by fields and recent fire burns, as

'islands', but they carefully differentiate them from true islands. MacArthur (1972, p. 105) pointed out that true islands are 'separated by a vacuum insofar as land birds and insects are concerned', whereas habitat islands are 'separated by other habitats filled with birds and insects', thus the spill-over of organisms from adjacent habitats is a primary factor for habitat islands.

Island biogeography theory and the subsequent theories and applications it has inspired and influenced have made an important contribution to conservation biogeography. The theory has inspired much thinking about the importance of the size and connectivity of protected areas in the maintenance of species diversity, and it has stimulated an avalanche of research on fragmented ecosystems. However, generalizations derived from this theory have given rise to models that are too simplistic (e.g. Laurance, 2008).

Recent advances in island theory demonstrate that we are moving towards a new synthesis, identifying and incorporating aspects of the island systems that were not considered in the past. For example:

**i** Within oceanic island biogeography, efforts have recently been made to adjust the MacArthur–Wilson (1967) model to accommodate the dramatic changes in the carrying capacity and environmental characteristics of islands that occur through the life history (ontogeny) of an oceanic island itself (see e.g. Whittaker *et al.*, 2008, 2010).

**ii** Application of genetic analyses are producing a more nuanced grasp of species and gene flow between insular and mainland habitats.

**iii** Scale-dependency of isolation and fragmentation effects are beginning to be quantified.

**iv** Efforts have been made to incorporate matrix effects and to consider the implications of longer term changes within habitat islands post-isolation.

**v** Assumptions of initial equilibrium in pre-fragmentation landscapes have been challenged (for discussion and exemplification of the foregoing, see Whittaker & Fernández-Palacios, 2007).

These considerations suggest that the dynamic process at the heart of the island equilibrium theory needs to be embedded in a much more dynamic model of the physical environment (a point argued more generally in Chapter 7).

We have selected four key areas that we consider important for a more successful application of island theory to conservation biogeography. These include examination of (1) the life history of habitat islands,

(2) threshold effects, (3) assembly rules, and (4) the role of the matrix for conservation in habitat islands.

**1 Life history of habitat islands:** As Whittaker *et al.* (2005) comment: 'It is disappointing that we still know so little about the power and timescale of "species relaxation".' Here we suggest that the consideration of the life history (ontogeny) of habitat islands could be particularly insightful in revealing the patterns and processes shaping species richness, species assembly and disassembly. Although a number of theoretical frameworks have been put forward to describe the sequential process of species relaxation after habitat loss and fragmentation (Section 8.2.2), the temporal scale of habitat loss and fragmentation has received the least attention. This has restricted our knowledge on how, for example, the abiotic characteristics of a fragment (e.g. net primary productivity) and rates of nutrient cycling change through time after its isolation, and how this affects the fragment's capacity in maintaining biodiversity.

Habitat conversion is almost always a non-random process (e.g. Raheem *et al.*, 2009). In forest landscapes, for example, the most accessible and productive areas tend to be deforested first. Thus, the remaining fragments show a non-random spatial distribution with respect to age, because the geographical distribution of older fragments (i.e. isolated earlier) is different from that of those isolated later. Moreover, other environmental factors, ranging from anthropogenic disturbance (e.g. hunting) to physical gradients (e.g. topography and climate) may be correlated with fragmentation and forest loss (Laurance *et al.*, 2002). We believe that the integration of research on the ontogeny of habitat islands will help us towards estimating more accurately the rates at which species extinctions are likely to occur. The time-lags and 'extinction debt' involved in such extinction processes are still poorly explored and in need of much attention (Box 8.2; Tilman *et al.*, 1994). By focusing further work on the above questions, we will be able to approach more analytically questions related to the time-lag for relaxation and extinction debt.

**2 Thresholds:** Taxon- and system-dependent thresholds, beyond which species losses accelerate (see Ewers & Didham 2006; Whittaker & Fernández-Palacios, 2007; Suding & Hobbs, 2009) have received very limited attention. Analyses of critical value ranges, where even small changes in environmental variable(s) will lead to large changes in the system, will help us towards understanding relaxation as a result

of habitat loss and fragmentation (Simberloff & Martin, 1991; Laurance 2002).

A highly relevant island phenomenon is the so-called 'small island effect' (see Lomolino & Weiser, 2001; Triantis *et al.*, 2006). The main feature of the phenomenon is the absence of the commonly found relationship of island area and species richness below a certain island size (dashed line in Figure 8.11). The particular threshold of this effect appears to vary depending on the taxon and archipelago selected, but it generally appears to occur only with islands of a very small size and diversity. In practice, within the limits of the small island effect, species richness is independent from the direct effects of area and is mainly driven by the effects of habitat diversity. Hence, it would be interesting to assess the existence of such thresholds in habitat island data sets for which the usual explanatory variables – such as area and isolation – are not important (see Prugh *et al.*, 2008) and other variables – such as island age, productivity, energy and environmental heterogeneity – are important. The consideration of such variables, although challenging, is necessary if we are to build up a more predictive science of species richness variation across true and habitat island systems.

In a fragmented landscape, species can either become extinct or go through changes in life history traits that will adapt them to the changed living conditions. Another issue related to spatial thresholds of fragmented landscapes that has received limited attention is how the evolutionary dynamics of species change in response to landscape transformation. Adaptation in a fragmented landscape may influence measurable features of the phenotype of a species, e.g. body size. In island studies, it is well established that islands favour the change of species body size, compared to their mainland counterparts; usually small species become larger (gigantism) and large species smaller (nanism) – a phenomenon termed the 'island rule' (Lomolino, 1985). These changes lead to a more effective exploitation of the available resources in the context of the limited available space on islands. The absence of the full collection of competitors and predators found on the mainland contributes towards these size changes (see Lomolino, 2005; Lomolino *et al.*, 2006; but see Meiri *et al.*, 2006).

In illustration of these effects within a habitat island context, Schmidt & Jensen (2003) studied the body size changes within the entire Danish mammalian community during the last 175 years. They found that the

rate of body length change was increased for both smaller and larger mammals, while it was lower for the medium-sized species. Following the general trend of the island rule, small mammals have generally increased, whereas large mammals have decreased in length. Schmidt & Jensen suggested that the major, but not the only, driver of these changes was habitat fragmentation.

Based on island studies, Losos & Schluter (2000) have identified that for *Anolis* lizards in the Great Antilles, below a certain island size threshold there is little or no cladogenesis. The identification of such size thresholds not only in the short term, but over evolutionary timescales, could be quite insightful for conservation biogeography (e.g. Triantis *et al.*, 2008). This corresponds to the plea of Gunderson & Folke (2003), who called upon conservation biologists to work towards the 'science of the long view' and to integrate insights from other disciplines in the search for new predictive and transcalar models in time and space (see also Lomolino, 2006).

**3 Assembly rules (phylogeny):** Island biotas are not simply random draws from regional species pools. Instead, they typically exhibit compositional structure: some species, species combinations, or species types, are found more frequently, and some less frequently, than might be expected by chance. This idea was presented in Jared Diamond's island assembly theory (Diamond, 1975b; reviewed in Whittaker & Fernández-Palacios, 2007). Related to island assembly theory is an increasing number of studies appearing to show deterministic patterns of evolution on islands, i.e. independent evolutionary diversification events, producing on different islands the same set of habitat specialists adapted to use different parts of the environment (see Losos *et al.*, 1998; Chiba, 2004; Gillespie, 2004; Losos & Ricklefs, 2010).

The incorporation of phylogenetics into community ecology will offer key insights into the assembly and structure of communities (see Webb *et al.*, 2002; Emerson & Gillespie, 2008), with insular systems having a pivotal contribution to make within this research programme. Extinction and extinction risk are often phylogenetically non-random (Purvis, 2008). Nonrandomness when species are faced with a similar threat intensity indicates that some species are more extinction resistant than others (e.g. Purvis *et al.*, 2000). Hence the use of phylogenies for identification of those traits that are associated with a high extinction risk in declining species, e.g. high trophic level,



low population density, slow life history, small geographical range, 'ecological naivety', is currently one of the great challenges of conservation biology. Studies on islands, nature's test tubes and the location of a high proportion of globally threatened species, will certainly offer significant insights in this research program.

**4 Matrix:** The number of species held in a reserve (or reserve system) is actually less important than the conservation of those species which cannot survive outside the remnants (e.g. Newmark, 1991). Some recent efforts have been made to move beyond an exclusive focus on (forest) fragments and towards understanding the role of such habitat islands within mixed-use landscapes. This switch in emphasis comes under varying headers. For example, Watson *et al.* (2005) show that the incidence functions of woodland bird species in three different landscapes in the Canberra area of Australia differ significantly, seemingly as a function of differences in properties of the landscape matrix within which the woodlands are embedded. Hence, Watson *et al.* (2005) join others (e.g. Ewers & Didham, 2006) in calling for greater attention to 'matrix effects'.

J.B. Hughes *et al.* (2002) adopted a slightly different approach within their study in southern Costa Rica, focusing on the extent to which native forest species make use of the surrounding countryside. They found that some 46 per cent of bird species foraged often kilometres away from extensive areas of native forest. Although they stress that not all species can be so readily accommodated outside large tracts of native forests, their work supports the importance of developing 'countryside' landscapes that are biodiversity-friendly and penetrable by native fauna (as Harris, 1984). Daily and colleagues (e.g. Daily *et al.*, 2001, 2003) coin the term 'countryside biogeography' for this switch in attention from remnants *per se* to the way in which remnants function within whole landscapes. This switch in emphasis is similar to that promoted by Rosenzweig (2003) under the heading 'reconciliation ecology'. But whether we label it 'matrix effects', 'countryside biogeography' or 'reconciliation ecology', the common element is a realization that effective conservation must include consideration of what happens outside reserves. The way we shape the countryside, whether we farm intensively or extensively, whether we retain hedgerows and trees within mixed landscapes, can all have profound implications for regional diver-

sity and for abundances of wildlife (e.g. see Gascon *et al.*, 1999; Gates & Donald, 2000).

Conservation requires pragmatic decision-making. As we continue to fragment landscapes, island effects may inform such decision-making, but should not be oversimplified. There is no single message, and no single island effect; indeed, insularity may sometimes bring positive as well as negative effects (Lockwood & Moulton, 1994). Island effects may be weak or strong. The implications of insularity vary, depending on such factors as the type(s) of organism involved, the type(s) of landscapes involved, the nature of the environmental dynamics, the biogeographical setting and the nature of human use and involvement in the system being fragmented.

In closing this chapter, we return to the basic question posed in the introduction: is it realistic to expect habitat islands to behave according to the same principles as real islands? Our answer is *yes*, but caution is needed in the island theories and models we are using. Island systems of generally restricted spatial extent and most importantly similar age and intrinsic rates of change in time to habitat islands (e.g. Terborgh *et al.*, 2001, 2006; Cody, 2006) will probably continue to offer more relevant principles for the understanding of processes such as relaxation in habitat islands and their more effective preservation.

As island biogeography moves towards new syntheses and theories, we anticipate that this body of work will become increasingly helpful for understanding and conserving our natural world.

## FOR DISCUSSION

- 1 In what circumstances are scattered protected areas of modest size better than a few large ones?
- 2 What is the relationship between the SLOSS debate and nestedness?
- 3 How important is it to take account of underlying biogeographical structure within a region when applying island models to projecting species extinctions?
- 4 Is there any optimal slope ( $z$ ) value for models projecting species losses based on species-area relationships, and what is the relevance of such models if no account is taken of efforts made to mitigate these losses?
- 5 How important is connectivity between patches for maintaining species diversity in a landscape?

**6** In what ways can the landscape outside protected areas be managed to support biological diversity?

**7** How far do you agree that the problem for oceanic islands is the loss of their isolation, while within continents the reverse is the case?

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