Journal of Biogeography, **29**, 823–834

# A conceptual framework for studying species composition in fragments, islands and other patchy ecosystems

David M. Watson *Applied Ornithology Group, The Johnstone Centre, Charles Sturt University, Thurgoona, NSW, Australia*

## Abstract

**Aim** I propose and develop a new classification system to explain diversity patterns in habitat fragments, equally applicable to islands and other inherently patchy ecosystems. My primary goal is to provide an inclusive model to improve the comparability of studies and enhance future efforts to synthesize their findings, yielding a generalized basis for understanding species composition in patchy ecosystems.

**Results** Differentiating islands from fragments and incorporating patch age and patch: matrix contrast, eight classes of patch are distinguished, spanning a range of geographical features. To compare studies of diversity patterns among and between patch types, patch biota are divided into three categories based on their origin—relict species (present before fragmentation), matrix-derived species and interpatch dispersers. Applying this novel scheme to existing data, the effects of insularization are synthesized. Direct comparisons among fragments revealed broad similarity in the long-term effects of habitat fragmentation compared with highly divergent patterns in younger landscapes (< 200 years). Holding patch: matrix contrast and age constant, fragments and islands were compared. Despite initial differences in community assembly, the biota of islands and fragments converge in several properties over time, as diversities stabilize and patch biotas become distinct from the surrounding matrix.

**Main conclusions** Although necessarily broad, this framework provides an explicit context within which to test forty-four specific predictions regarding the distribution of diversity in patchy landscapes and thereby gain a clearer understanding of the long-term biological consequences of insularization. I propose that the fragments-as-islands analogy be revisited, potentially yielding valuable insight into the long-term future awaiting anthropogenically altered ecosystems.

**Keywords**
Diversity, habitat fragments, Islands, patch, species composition.

## INTRODUCTION

Factors affecting species composition on islands have been the subject of considerable research, resulting in a broad understanding of the variation exhibited by insular communities (Simberloff, 1974; Bramwell, 1979; Williamson, 1983; Lomolino, 1986; Whittaker, 1998) and an appreciation of the fundamental structuring influences (Abbott, 1978; Brown, 1986; Pignatti, 1995; Ricklefs & Lovette, 1999; Brown & Lomolino, 2000). Although the original, defining paradigm (MacArthur & Wilson, 1963, 1967) has now been overturned (Gilbert, 1980; Williamson, 1989; Brown & Lomolino, 2000; Heaney, 2000), there is an acknowledged need for a new one (Lomolino, 2000) and an explicit recognition of the challenges awaiting future research on island biogeography (Lomolino, 2000; Whittaker, 2000).

Conversely, our understanding of the consequences of habitat fragmentation is, ironically, fragmented. Early research into fragmented landscapes invoked island biogeographical models to study distribution patterns

Correspondence: David M. Watson, Applied Ornithology Group, The Johnstone Centre, Charles Sturt University, Thurgoona, NSW 2640, Australia. E-mail: dwatson@csu.edu.au

(Forman *et al.*, 1976; Kitchener *et al.*, 1982; Harris, 1984; Freemark & Merriam, 1986), treating fragments as 'islands in a sea of habitats modified by man' (Wilson & Willis, 1975). As more studies found conflicting results and identified key differences between these landscapes and islands (e.g. Lynch & Whigham, 1984; Wiens, 1995), the consensus was reached that islands and fragments were fundamentally different systems, affected by different processes and subject to different pressures and constraints (Simberloff & Abele, 1982; Wiens, 1989, p. 227). There have since been many empirical studies examining diversity patterns in fragmented landscapes, but translating these disparate findings into a general understanding of the processes affecting diversity is difficult. Most studies use novel combinations of sampling protocols and statistical tools, resulting in little uniformity in the literature and considerable redundancy. While there have been several reviews of the ecological consequences of habitat fragmentation, many have been too generalized (Collinge, 1996; Bierregaard *et al.*, 1997; Laurance *et al.*, 1997) or too specific (Hobbs & Hopkins, 1990; Paton, 1994; Simberloff, 1995; Debinski & Holt, 2000) to be widely applicable (Crome, 1997). There is no over-arching paradigm guiding research, but rather a prevailing view that most systems differ and any commonalities in the responses of communities to fragmentation are too generic to be of any real utility.

In this contribution, I present a novel way to classify fragmented landscapes and their associated biota, equally applicable to islands and other inherently patchy systems. My primary goal is to provide a generalized model for researchers to adopt, improving the comparability of studies and enhancing subsequent efforts to synthesize their results. Having developed the model I apply this novel classification-based approach to existing data, yielding a suite of between-system comparisons.

## FRAMEWORK DEVELOPMENT

At the most general level, two broad classes of patchy habitats have been studied with respect to species composition—islands and fragments. The key difference between these systems is their origin: fragments are remnants of a previously widespread habitat, whereas islands have always been restricted and isolated in their spatial extent. Islands are defined here as disjunct, isolated patches that were never contiguous with other patches and have developed their biota exclusively from colonists (similar to the 'ecological' islands of Whittaker, 1998; Fig. 1). In addition to oceanic islands, this functional definition encompasses many other insular systems including alpine grasslands, caves, salt-lakes, certain kinds of wetlands (e.g. desert oases, bogs, mound-springs) and outlying rock massifs or inselbergs. This list is not exhaustive and the number of habitat features that qualify as islands is much greater (MacArthur & Wilson, 1967; Culver, 1969; Mabberly, 1979; Coleman *et al.*, 1982; Pignatti, 1995; Bruhl, 1997). Fragments are defined here as remnants of previously more continuous features, isolated by the imposition of a contrasting matrix (Fig. 1). In addition to the typical fragment of native vegetation surrounded by anthropogenically altered habitat, this definition includes a

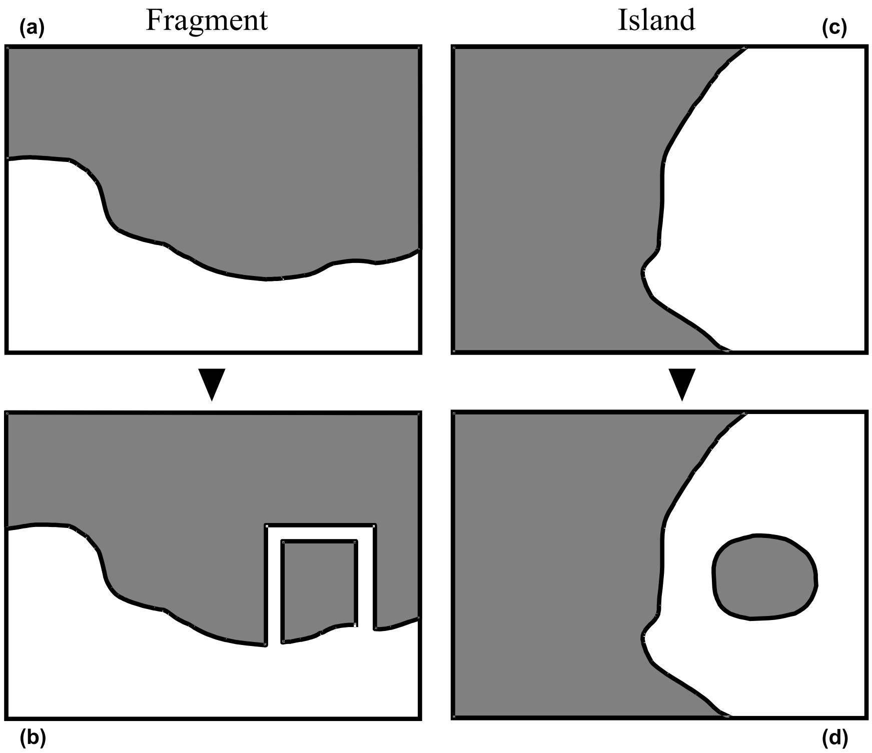

**Figure 1** Schematic diagram of the origin of a fragment and an island. (a) and (b) depict the creation of a fragment by a change in the extent of the matrix; (c) and (d) depict the formation of an island, separated from similar pre-existing habitat by a dissimilar matrix. Note that this classification scheme does not distinguish which habitat is the patch or the matrix, but is concerned solely with the contrast between them. Thus, the round patch in (d) could represent a pond beside a lake or a volcanic island next to the mainland—both would be classified as islands.

range of geographical features including icebergs, land-bridge islands, oxbow lakes, tidal pools and even continents (Quinn & Harrison, 1988; Watson, 1999). Unlike islands in which the recently formed feature is the patch, fragments are defined by a change in the matrix often with little change to the patch itself (Fig. 1).

The first factor in my approach is determining whether the patch is an island or a fragment. While seemingly straightforward, this distinction can often be unclear, and frequently requires historical information (Diamond & Gilpin, 1983). Thus, in the Solomon Islands northeast of Australia, some islands were joined to New Guinea during Pleistocene glacial minima while others are volcanic in origin and have never been connected to other landmasses (Mayr & Diamond, 1976 and references therein). Hence, in a single archipelago there can be a combination of islands and fragments, having an important bearing on distribution patterns of native organisms (Diamond, 1973, 1974; Diamond & Mayr, 1976).

The second factor hinges upon the contrast between the physical structure of the patch and the surrounding matrix. Here I consider two classes of patch: matrix contrast—high contrast, typically involving phase-differences (i.e. aquatic vs. terrestrial) but also above-ground: below-ground in the case of caves and mine-shafts; and low-contrast, typically in the same phase (i.e. both aquatic or both terrestrial). Hence, a remnant of heathland bounded by cultivated pasture and a patch of seagrass surrounded by sandy seafloor both represent low contrast patches, whereas an iceberg in the ocean and a land-locked salt-lake are both high contrast patches.

The final factor in the model is time. Many patchy features are temporary or ephemeral, lasting hours or days, but here I restrict the scope of discussion to patches that persist over longer time-scales. Specifically, I distinguish between those systems in which patches are between 1 and *c.* 200 years old, and systems in which patches are older. While this division corresponds to many natural thresholds (Magnuson, 1990; Schneider, 1994), other temporal divisions may be equally appropriate, especially those scaled to generation times of organisms.

Therefore, in order to classify any inherently patchy ecosystem, three questions have to be addressed: (1) Is it a fragment or an island? (2) Is there a high or low contrast between the patch and the surrounding matrix? (3) Was the patch formed more or less than 200 years ago? (Table 1). Using this approach, a broad range of ecosystems can be classified (after Rabinowitz *et al.*, 1985) permitting a range of within- and between-group comparisons.

Having classified the ecosystem, associated biota can then be categorized according to their origin. Organisms inhabiting islands are derived exclusively from colonists (Whittaker, 1998), either from another patch (interpatch dispersers), or from the matrix surrounding the patch (matrix-derived species; Fig. 2). For the biota of fragments, these colonists are complemented by a third category – those organisms that inhabited the patch prior to fragmentation (relict species; after Patterson & Atmar, 2000; Fig. 2). Depending on the temporal scale of enquiry, these three categories can be applied to individuals, species and, in older systems, entire lineages of organisms. By scoring the relative numbers of these three categories of organism, results of studies in many different systems can be compared directly.

## EIGHT FORMS OF PATCH

Using the three-factor classification, studies of diversity patterns in patchy ecosystems can be consolidated into a single eight-cell table (Table 2). These studies were drawn from a thorough search of ecology-related journals and are used here as exemplars, not necessarily representative of the cell generally. The first thing to note is the disproportionate amount of research conducted in two classes of patch – young low-contrast fragments (i.e. typical habitat fragments)

**Table 1** Examples of the eight forms of patch distinguished here, based on three traits. Low- and high-contrast refers to the structural difference between patch and matrix, with low-contrast typically denoting both habitats are in the same phase, while high-contrast patches represent a different phase to the surrounding matrix

| | Fragments | | Islands | |
|---|---|---|---|---|
| | Low contrast | High contrast | Low contrast | High contrast |
| Young<br>1–200 years | Forest fragment<br>Internal fragment<br>Refugium from fire<br>Seagrass fragment | Floating raft, mat<br>Flooded tree<br>Hydroelectric island<br>Oxbow lake<br>Pack-ice, iceberg<br>Tidal pool | Boulder<br>City, town<br>Lava flow<br>Plantation, orchard<br>Tree-fall gaps<br>Vacant lot | Artificial dam, pond<br>Artificial island<br>Mine shaft<br>Sand shoal<br>Volcanic island |
| Old<br>> 200 years | Cliff-face fragment<br>Lava flow refugium<br>Mesa, tepui<br>Montane remnant<br>Riparian fragment | Continent<br>Inter-river valley<br>Land-bridge island<br>Riverine island<br>Lacustrine island | Alpine grassland<br>Bog, fen, pothole<br>Canyon, gorge<br>Inselberg, kopje<br>Landslide<br>Morraine field<br>Mound-reef | Cave, cavern<br>Desert oasis<br>Geothermal vent<br>Hot spring<br>Mound spring<br>Oceanic island<br>Salt lake |

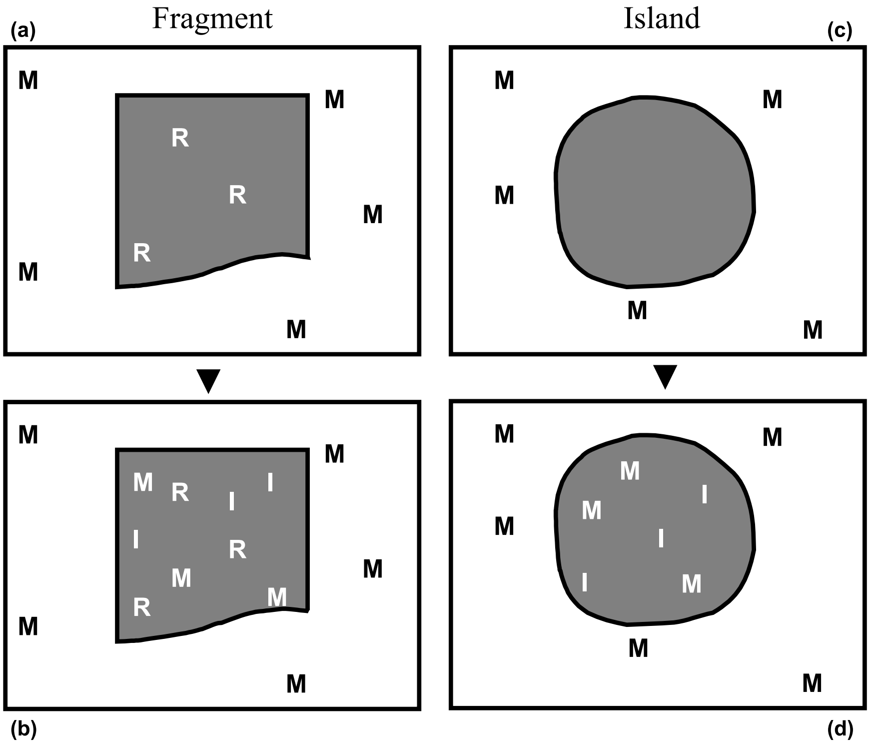

**Figure 2** Schematic diagram of biotic development on islands and fragments. (a) depicts a recently created fragment, containing a biota composed entirely of relict species (R; present prior to fragmentation). With time some matrix-derived species (M) and inter-patch dispersers (I) occupy the fragment (b); (c) depicts a recently formed island, with no associated biota. Over time (d), the biota develops exclusively from colonists, derived from other patches and the matrix.

**Table 2** Exemplar studies of species composition and distribution of diversity in patchy habitats. Numbers in the first line of cells indicate the approximate number of relevant empirical studies, followed by the number of papers presented at the Ecology of Insular Biotas Conference out of sixty-nine spoken papers and posters (six theoretical presentations were not classified)

| | Fragments | | Islands | |
|---|---|---|---|---|
| | Low-contrast | Low-contrast | Low-contrast | High-contrast |
| Young | 1000's 13 | 10's 0 | 10's 2 | 10's 2 |
| 1–200 years | Freemark & Merriam (1986) | Coleman *et al.* (1982) | Crowe (1979) | Drake (1991) |
| | Kitchener *et al.* (1982) | Kadmon & Pulliam (1993) | Duffy & Meier (1992) | Hubbard (1973) |
| | Loman & von Shantz (1989) | Karr (1982) | Eggleton *et al.* (1999) | March & Bass (1995) |
| | Lovejoy *et al.* (1986) | Lynam & Billick (1999) | Gemmel (1982) | Schoener *et al.* (1978) |
| | Lynch & Whigham (1984) | Rydin & Borgegård (1988) | Martell (1983) | Simberloff & Wilson (1970) |
| | Robinson *et al.* (1992) | Sieving & Karr (1998) | Thébaud & Strasberg (1997) | Thornton (1996) |
| | Watson *et al.* (2000) | Terborgh *et al.* (1997a, b) | Walker *et al.* (1996) | Wilbur & Travis (1984) |
| Old | 10's 0 | 10's 0 | 10's 5 | 100's 41 |
| > 200 years | Haig *et al.* (2000) | De Sante & Ainley (1980) | Bruhl (1997) | Barbour & Brown (1974) |
| | Johnson (1975) | Diamond (1969, 1972, 1974) | Burke *et al.* (1998) | Culver (1969) |
| | Kratter (1992) | Faaborg (1979) | Dobkin & Wilcox (1986) | Diamond (1974, 1975) |
| | Lawlor (1998) | Hope (1973) | Riebesell (1982) | Martin & Lepart (1989) |
| | Simpson (1974) | Lomolino (1986, 1994) | Porembski *et al.* (2000) | Paulay (1994) |
| | Watson & Peterson (1999) | Millien-Parra & Jaeger (1999) | Sarthou & Villiers (1998) | Ricklefs & Cox (1972) |
| | Wilcox *et al.* (1986) | Woinarski *et al.* (1999) | Tsuyuzaki (1991) | Ricklefs & Lovette (1999) |

and old high-contrast islands (i.e. oceanic islands) – relative to the remaining six classes. This is manifested in both the primary literature and the programme of the Ecology of Insular Biotas conference (Table 2), highlighting important gaps in our knowledge.

Hence, there are two classes for which there is extensive literature, but relatively few community-level studies of diversity patterns in the remaining classes of patch. Best represented of these six classes are the old low-contrast fragments with at least thirty-two studies of diversity patterns in Pleistocene-age montane fragments (reviewed by Watson, 1999) and old high-contrast fragments with many studies of land-bridge islands (reviewed by Lawlor, 1986; Quinn & Harrison, 1988). Young high-contrast fragments are poorly understood, known primarily from studies of biota inhabiting hill-top remnants in artificial dams (Coleman *et al.*, 1982; Karr, 1982; Sieving & Karr, 1997; Terborgh *et al.*, 1997, 1998; Lynam & Billick, 1999). Young islands have been studied with a range of approaches, including several famous experiments in high-contrast systems (Simberloff & Wilson, 1970; Hubbard, 1973; Schoener *et al.*, 1978) and work on forest clearings (Martell, 1983; Duffy & Meier, 1992; Walker *et al.*, 1996), industrial and urban habitats in low-contrast landscapes (Crowe, 1979; Gemmel, 1982). Finally, old low-contrast islands are represented by studies of inselbergs and some alpine grasslands (Riebesell, 1982; Hadley, 1987; Bruhl, 1997; Burke *et al.*, 1998; Porembski & Barthlott, 2000).

## GENERAL EFFECTS OF INSULARIZATION

Drawing on empirical studies examining diversity patterns in patchy ecosystems, generalized qualitative results can be derived. Only broad statements can be made and for those cells represented by hundreds to thousands of studies, these statements will not be wholly supported. Nonetheless, I have distilled the findings down to six key points in terms of composition of patch biota: stability of species richness, number of the three categories of organism (relict, matrix-derived, interpatch disperser), number of endemics and comparison with the matrix biota (Table 3). In addition to providing a generalized summary of the effects of insularization, these statements comprise a set of forty-four explicit, testable hypotheses to stimulate future research.

### Young low-contrast fragments

For low-contrast fragments soon after fragmentation, the biota of a patch is similar to pre-fragmentation conditions, composed primarily of relict species with some local extinctions because of the net loss of habitat caused by fragmentation (Robinson *et al.*, 1992; Bierregaard & Stouffer, 1997; Debinski & Holt, 2000). There are few matrix-derived species (primarily habitat generalists) and a variable component of interpatch dispersers (Lovejoy *et al.*, 1986; Saunders *et al.*, 1991; Robinson *et al.*, 1992). Subsequently, more matrix species enter (Forman *et al.*, 1976; Lynch & Whigham, 1984; Watson *et al.*, 2000) and additional relict species become locally extinct through both demographic and stochastic processes (Harris, 1984; Freemark & Merriam, 1986; Wiens, 1995). These generalized patterns are exemplified by results of the Biological Dynamics of Forest Fragments Project (Lovejoy *et al.*, 1986)—a cross-taxon series of studies based on a set of experimentally produced forest fragments in central Brazil. After fragmentation, butterfly diversity increased, as losses of forest-dependent relict species were more than compensated by an influx of matrix-derived gap-specialists (Brown & Hutchings, 1997). Diversities of understory hummingbirds and terrestrial frogs increased because of the combination of relict species being unaffected by fragmentation and an influx of matrix-derived edge-dependent species (Stouffer & Bierregaard, 1995; Tocher *et al.*, 1997). Small mammal diversity increased (Malcolm, 1997) through an influx of matrix-derived species, while diversity of primates and several forest-dependent bird groups (large-bodied frugivores, members of mixed-species flocks and ant-following groups) decreased as relict species became locally extinct (Lovejoy *et al.*, 1986; Bierregaard & Stouffer, 1997). Examining these results in terms of taxonomic affiliation yields a confusing set of seemingly contradictory results, but by partitioning the biota into the three functional categories, striking congruence is revealed.

### Old low-contrast fragments

With time, extinctions of relict species decrease and patch diversities stabilize. These older landscapes include Pleistocene-age montane fragments (Watson, 1999), and while still susceptible to stochastic disturbance, demographic repercus-

**Table 3** Characteristics of biota inhabiting the eight forms of patch. In addition to summarizing the consequences of insularization, these forty-four statements represent explicit hypotheses to promote future research

| | | Fragments | | Islands | |
|---|---|---|---|---|---|
| | Patch attributes | Low-contrast | High-contrast | Low-contrast | High-contrast |
| Young 1–200 years | Species richness | Decreasing slowly | Decreasing rapidly | Increasing rapidly | Increasing slowly |
| | No. relict species | High | High | N/A | N/A |
| | No. matrix-derived species | Medium | Low | High | Low |
| | No. interpatch dispersers | Low | Low | Low | High |
| | No. endemics | None | None | None | None |
| | Patch vs. matrix biota | Broad overlap | Slight overlap | Subset | Distinct |
| Old >200 years | Species richness | Stable | Stable | Stable | Stable |
| | No. relict species | High | High | N/A | N/A |
| | No. matrix-derived species | Low | Low | High | Medium |
| | No. interpatch dispersers | Low | Medium | Medium | High |
| | No. endemics | Low | High | Low | High, species & genera |
| | Patch vs. matrix biota | Distinct | Distinct | Similar, distinct forms (morphotypes) | Distinct |

sions following fragmentation have largely subsided. Biotas remain dominated by relict taxa, some of which may have speciated since insularization, generating range-restricted neo-endemics (*sensu* Fjeldså & Rahbeck, 1997). Species derived from other patches remain uncommon and despite some colonizing matrix species, the patch biota becomes distinct (Lomolino *et al*., 1989; Nores, 1995). Assemblages of organisms in these patches typically display highly nested patterns (less diverse assemblages are predictable subsets of more diverse assemblages), reflecting a combination of deterministic autecological and patch-level effects (Watson, 1999; Patterson & Atmar, 2000). Work in montane forests of Mesoamerica reveals how these broad trends vary between groups, with low vagility groups like salamanders and tree frogs exhibiting high levels of endemism (Duellman, 1970; Wake & Lynch, 1976), compared with more mobile organisms like mammals and birds (Watson & Peterson, 1999; Watson, 1999).

### Young high-contrast fragments

For high-contrast fragments (represented mostly by hill-top remnants in hydroelectric dams and other artificial water bodies), the role of matrix-derived species is greatly diminished. Immediately following insularization, the biota has changed little, but an increasing number of relict species becomes locally extinct through time (Lynam & Billick, 1999) leading to lower diversities than remaining continuous habitat (or 'mainland'). Relict species may also be absent from patches through incomplete sampling of the original habitat (Terborgh *et al*., 1997). Interpatch dispersers are rare, and there is little overlap with the surrounding matrix. Research on these patches has been primarily descriptive, focusing on which species have gone extinct and the time taken for the biota to stabilize after insularization (Coleman *et al*., 1982; Rydin & Borgegård, 1988; Kadmon & Pulliam, 1993; Sieving & Karr, 1998). One of the most complete data sets comes from Barro Colorado Island, a fragment of humid rainforest isolated during the building of the Panama Canal (Karr, 1982; Sieving & Karr, 1997). The extinction of more than fifty resident species of birds has been documented since isolation in 1914, representing more than one quarter of the resident bird species historically recorded from the patch (Karr, 1982). Several interpatch dispersers have since colonized the forest fragment, in addition to several matrix-derived species (waterbirds) but the resident avifauna of adjacent continuous forest exceeds the diversity on the patch by more than 100 species (Karr, 1982). Such 'faunal collapse' is known from other high-contrast fragmented systems (Coleman *et al*., 1982; Quinn & Harrison, 1988; Terborgh *et al*., 1998), and has been considered a general repercussion of fragmentation (Mikkelson, 1993; Burkey, 1995).

### Old high-contrast fragments

After sufficient time, these high-contrast patches typically develop endemic species, both because of speciation since fragmentation and extinction of species in the remainder of their former range (Diamond, 1972, 1973; Hope, 1973). The component of interpatch dispersers increases with time, often with regular movement between patches for more vagile taxa. Few matrix-derived species occur, resulting in almost complete complementarity between matrix and patch biotas. Research on species composition in these patches has concentrated on describing distributional patterns and relating them to extinction, competition and associated patch-scale characteristics (Hope, 1973; Diamond & Mayr, 1976; Abbott, 1978; Humphrey & Péfour, 1979). Studies of resident birds inhabiting land-bridge islands near New Guinea have documented the dynamic nature of species composition (Diamond, 1969, 1972), with the extinction of relict species offset by colonists from other patches. These colonists are primarily highly dispersive species characteristic of second-growth habitats, with colonization frequency decreasing with distance from the mainland (Diamond, 1972). Thus, in island arcs like the Madang and Bismark archipelagos, there are progressively more interpatch dispersers on islands closer to the mainland (Diamond, 1972), and fewer relict species on smaller islands (Diamond & Mayr, 1976).

### Young high-contrast islands

Moving to true islands, there is no relict component of the biota. For young high-contrast islands, diversities are low and the biota dominated by recent colonists from other patches, typically highly vagile taxa (Simberloff & Wilson, 1970; Thornton, 1996). There are few matrix-derived species and no endemics. Consequently, the biota differentiates rapidly from the matrix and biota of different islands reflect unique colonization histories, leading to dynamic 'checkerboard' distributional patterns (*sensu* Diamond, 1975). Studies in these systems have revealed highly non-nested biotas with little influence of area or other patch-level effects, distributions explained better by species-specific attributes. Small-scale pond experiments have revealed patterns of community development in detail, with the biota of adjacent ponds often differing dramatically (Wilbur & Travis, 1984; see also Robinson & Dickerson, 1987; Drake, 1991; and references therein), highlighting the influence of short-term historical effects on community assembly.

### Old high-contrast islands

These systems, represented mostly by oceanic islands and several intracontinental features (e.g. caves, salt-lakes), exhibit a high degree of biotic complementarity between patch and matrix. Interpatch dispersers are abundant (although not necessarily diverse) and may require resources from both habitats—using patches for roosting or nesting (e.g. bats in caves, seabirds on islands) but foraging in the intervening matrix. Over time, some matrix inhabitants may diverge into patch inhabitants (terrestrial crabs on oceanic islands, blind cave-dwelling arthropods), yielding range-restricted endemic species (Peterson & Watson, 1998).

Older islands would thus be expected to have higher relative proportions of matrix-derived narrow endemics. Interpatch dispersers may diversify over time if colonization events are sufficiently rare (e.g. giant herbaceous plants and flightless rails on isolated oceanic islands; Mabberly, 1979; Steadman, 1995), but this category of organisms is typically more vagile, with frequent colonizations precluding evolutionary divergence (Ricklefs & Cox, 1972; Culver *et al*., 1973; Diamond, 1974). Relative proportions of matrix-derived species and interpatch dispersers vary with the nature of the intervening matrix, island size, degree of isolation and an array of other parameters (MacArthur & Wilson, 1967; Simberloff, 1974). Studies of island biota typically focus on these factors, and how they affect rates of extinction and colonization from the overall species pool (Culver, 1969; Diamond, 1972; Brown & Kodric-Brown, 1977; Brown, 1986; Paulay, 1994; Ricklefs & Lovette, 1999).

### Young low-contrast islands

Many islands, however, are comprised of habitat similar to the surrounding matrix. Soon after formation, low-contrast island biotas are founded by matrix-derived species, with relatively few colonists from other patches. Coupled with an absence of endemics, these islands develop biotas that are subsets of the interstitial matrix, typically composed of early successional, highly vagile species (Gemmell, 1982; Walker *et al*., 1996; Thébaud & Strasberg, 1997). While there may be some between-patch variation, the biota of these young islands converge over time, with little evidence of area and other patch-scale effects constraining diversity (Martell, 1983; Thébaud & Strasberg, 1997). Research on these systems has focused not only on succession and assembly rules, but also factors affecting diversity. A pertinent example involves diversity patterns of plants in vacant lots in Chicago (Crowe, 1979)—successional islands surrounded by buildings and roads. Communities were dominated by highly dispersive, early successional species with broad habitat tolerances (i.e. weeds). Species composition was influenced primarily by patch age, with area and degree of isolation playing a lesser role. Studies from industrial habitats yield similar results, with highly vagile groups (e.g. orchids) and those species able to tolerate mineral-rich soils especially well-represented (Gemmell, 1982 and references therein).

### Old low-contrast islands

Matrix-derived species remain a prominent component of low-contrast islands over time, because they are typically capable of surviving in either habitat. These systems typically have few endemics and are dominated by highly dispersive species, often at the edge of their distributional range (Burke *et al*., 1998). Nonetheless, slight differences in edaphic, hydrologic or microclimatic factors can lead to divergence over evolutionary time and thus some of these systems are characterized by high levels of endemism, both in terms of species (Porembski *et al*., 2000), but more commonly, locally adapted races and morphotypes (Hadley, 1987; Burke *et al*., 1998). Interpatch dispersers are a minor biotic component, with most specialist forms derived from matrix species. Research on these systems has been primarily descriptive—enumerating the assemblage of species and often focusing on those organisms that display ecomorphological specializations (e.g. Porembski & Barthlott, 2000). A noteworthy example comes from the growing literature on inselberg biotas which has included the description of the only known protozoan-trapping plant (Barthlott *et al*., 1998) among numerous other aberrant forms. As these islands can be millions of years old, proportions of endemic species are high, with number of endemics often related to diversities in the surrounding matrix (Porembski & Barthlott, 2000).

## IMPLICATIONS AND PRIORITIES FOR FURTHER WORK

Following fragmentation of previously continuous habitat a variable component of relict species becomes locally extinct, because of the initial loss of habitat but subsequently due to a cascading series of demographic and stochastic processes operating at patch- and species-scales. Many studies have focused on these organisms, identifying common ecological traits and evaluating different suites of patch attributes that may minimize these extinctions (Abbott, 1978; Faaborg, 1979; DeSante & Ainley, 1980; Karr, 1982; Rydin & Borgegård, 1988; Bierregaard & Stouffer, 1997; Sieving & Karr, 1997). In some cases, this loss of diversity is offset by an influx of matrix-derived species, occasionally resulting in fragmentation having a positive effect on diversity (Brown & Hutchings, 1997; Malcolm, 1997). Despite commencing immediately after fragmentation, these changes in community composition often take several generations to occur—time-scales that usually extend well beyond the scope of enquiry (Magnuson, 1990; Saunders *et al*., 1991; Schneider, 1994). As such, the net effects of fragmentation on diversity patterns can rarely be measured with confidence, and some theoretical estimates suggest that hundreds to thousands of years are required before this becomes possible (Mikkelson, 1993; Burkey, 1995; Andren, 1996). These concerns notwithstanding, most research carried out in anthropogenically fragmented systems does not focus on long-term effects. Rather, most studies are motivated by site-specific application-orientated goals, generating valuable data on the short-term responses of communities to fragmentation.

In contrast to the highly divergent consequences of fragmentation in the short-term, studies of older systems have revealed broad similarity in the long-term effects of fragmentation. Biotas remain composed primarily of relict taxa, with diversity patterns explained primarily by area, age and other patch-scale variables (landscape-scale factors like isolation have consistently low explanatory power; Watson, 1999). If these isolated populations of relict taxa are of sufficient size, they can diverge over evolutionary time generating narrow endemics, a pattern seen repeatedly in studies of montane fragments (Duellman, 1970; Wake & Lynch, 1976; Fjeldså, 1992; Fjeldså & Rahbek, 1997).

In previous comparative reviews, the confounding effects of patch: matrix contrast and age were not explicitly accounted for (Kitchener *et al.*, 1982; Harris, 1984; Pignatti, 1995; Patterson & Atmar, 2000). Thus, habitat fragments were typically compared with land-bridge islands or, using my approach, old high-contrast fragments to young low-contrast fragments – the two classes of fragments least likely to show commonalities. To enable more meaningful comparisons, age and contrast should be held constant, allowing direct comparison among fragments, and between fragments and islands.

Among young patches, many differences are apparent. Fragments are initially species rich – diversity decreasing rapidly as relictual species are lost with little compensation from interpatch dispersers – whereas islands are species poor, gaining species rapidly from both the matrix and other patches (differences noted explicitly by MacArthur & Wilson, 1967, p. 114). For older landscapes however, there are several noteworthy similarities between fragments and islands. For those patches in low contrast matrices (e.g. montane remnants and inselbergs) diversity has stabilized and the biota has become distinct from the matrix. Islands have become dominated by matrix-derived taxa, corresponding to the predominance of relict taxa in fragments, and both have since speciated to yield narrow endemics. Hence, despite different origins and initial differences following insularization, older island and fragment biotas exhibit broad similarities and are frequently studied together (Bruhl, 1997; Larson *et al.*, 2000). Similarly, old high-contrast islands and fragments (e.g. oceanic islands, land-bridge islands) are so similar that there is considerable confusion in the literature as to which is which (DeSante & Ainley, 1980; Diamond & Gilpin, 1983; Quinn & Harrison, 1988). Both have stable diversities and high levels of endemism, with island forms derived from interpatch dispersers and matrix species, and fragment forms from relict taxa. Biotas of both systems show similar differentiation from the matrix and diversities of particular patches are similarly constrained by a combination of patch-level and regional-scale effects.

Despite initial differences in origin, assembly and species composition, island and fragment biotas converge over thousands of years. This suggests that much of the variance seen in the effects of insularization may be essentially short-term phenomena, overwhelmed over the long-term by stochastic and demographic processes known to structure insular assemblages. This finding has far-reaching consequences for the theoretical and applied study of habitat fragments, especially regarding the management of fragmented landscapes. Despite initial reservations, findings from island systems may indeed have relevance to the study of habitat fragmentation, and may provide valuable insight into the long-term future awaiting anthropogenically altered landscapes.

To enhance further our understanding of factors affecting diversity in fragmented systems, more empirical studies are required especially from the three most under-represented cells in Table 2. To guide future studies of diversity patterns in fragmented landscapes and maximize their utility for future synthetic and comparative reviews, the following suggestions are made: (1) include the matrix in patch-scale projects; (2) consider fragment age explicitly; (3) compare diversities and abundances of interpatch dispersers vs. relict species; (4) contrast findings with islands at the species-scale.

In addition to generating more data, further synthetic assessments are required. In developing this framework, I have used groups of patches defined by simplified divisions of patch: matrix contrast and patch age—two continuous variables. Modelling-based approaches would be an ideal means to explore the full range of patchy systems, and derive more finely resolved predictions regarding species composition. Regardless of whether this classification-based approach is adopted, I hope that this contribution will help to initiate a redefinition of the discipline of fragmentation biology—a process which island biogeography has recently undergone. An entire journal issue was devoted to inclusive, far-reaching discussions on how island biogeography should proceed (Brown & Lomolino, 2000; Lomolino, 2000), what the main research goals should be and how best to address them (Whittaker, 2000). This constructive process has already commenced among fragmentation biologists, with several thoughtful essays providing a solid philosophical foundation (Bierregaard *et al.*, 1997; Crome, 1997). The key challenge now is to gather more empirical data, continue synthesizing existing knowledge about these dynamic systems and incorporate temporal scaling explicitly to work towards a discipline with the predictive capacities of island biogeography.

## ACKNOWLEDGMENTS

I am grateful to Bob Holt for early discussions, and indebted to David Roshier and Maggie Watson for insightful comments on the manuscript. Christa Mulda and an anonymous referee contributed useful suggestions, improving the clarity of this paper. Thanks also to Don Drake, Christa Mulder and Charles Daugherty for organizing the excellent Ecology of Insular Biotas conference, which helped crystallize the concepts presented here.

## REFERENCES

Abbott, I. (1978) Factors determining the number of land bird species on islands around south-western Australia. *Oecologia*, **33**, 221–233.

Andren, H. (1996) Population responses to habitat fragmentation: statistical power and the random sample hypothesis. *Oikos*, **76**, 235–242.

Barbour, C.D. & Brown, J.H. (1974) Fish species diversity in lakes. *American Naturalist*, **108**, 473–489.

Barthlott, W., Porembski, S., Fischer, E. & Gemmel, B. (1998) First protozoa-trapping plant found. *Nature*, **392**, 447.

Bierregaard, R.O. Jr, Laurance, W.F., Sites, J.W. Jr, Lynam, A.J., Didham, R.K., Anderson, M., Gascon, C., Tocher, M.D., Smith, A.P., Viana, V.M., Lovejoy, T.E., Sieving, K.E., Kramer, E.A., Restrepo, C. & Moritz, C. (1997) Key priorities for the study of fragmented tropical ecosystems. *Tropical forest remnants: ecology, management and conservation of fragmented communities* (eds W.R. Laurance and R.O. Bierregaard, Jr), pp. 515–525. University of Chicago Press, Chicago.

Bierregaard, R.O. Jr & Stouffer, P.C. (1997) Understory birds and dynamic habitat mosaics in Amazonian rainforests. *Tropical forest remnants: ecology, management and conservation of fragmented communities* (eds W.R. Laurance and R.O. Bierregaard, Jr ), pp. 138–155. University of Chicago Press, Chicago.

Bramwell, D. (ed.) (1979) *Plants and islands*. Academic Press, London.

Brown, J.H. (1986) Two decades of interaction between the MacArthur–Wilson model and the complexities of mammalian distribution. *Biological Journal of the Linnean Society*, **28**, 231–251.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effects of immigration on extinction. *Ecology*, **58**, 445–449.

Brown, J.H. & Lomolino, M.V. (2000) Concluding remarks: historical perspective and the future of island biogeography theory. *Global Ecology and Biogeography*, **9**, 87–92.

Brown, K.S. Jr & Hutchings, R.W. (1997) Disturbance, fragmentation, and the dynamics of diversity in Amazonian forest butterflies. *Tropical forest remnants: ecology, management and conservation of fragmented communities* (eds W.R. Laurance and R.O. Bierregaard, Jr), pp. 91–110. University of Chicago Press, Chicago.

Bruhl, C.A. (1997) Flightless insects: a test case for historical relationships of African mountains. *Journal of Biogeography*, **24**, 233–250.

Burke, A., Jürgens, N. & Seely, M.K. (1998) Floristic affinities of an inselberg archipelago in the southern Namib desert—relic of the past, center of endemism or nothing special? *Journal of Biogeography*, **25**, 311–317.

Burkey, T.V. (1995) Extinction rates in archepelagoes: implications for populations in fragmented habitats. *Conservation Biology*, **9**, 527–541.

Coleman, B.D., Mares, M.A., Willig, M.R. & Hsieh, Y.H. (1982) Randomness, area, and species richness. *Ecology*, **63**, 1121–1133.

Collinge, S.K. (1996) Ecological consequences of habitat fragmentation: implications for landscape architecture and planning. *Landscape and Urban Planning*, **36**, 59–77.

Crome, F.H.J. (1997) Researching tropical forest fragmentation: shall we keep on doing what we're doing? *Tropical forest remnants: ecology, management and conservation of fragmented communities* (eds W.R. Laurance and R.O. Bierregaard, Jr), pp. 485–501. University of Chicago Press, Chicago.

Crowe, T.M. (1979) Lots of weeds: insular phytogeography of vacant urban lots. *Journal of Biogeography*, **6**, 169–181.

Culver, D.C. (1969) Analysis of simple cave communities I. Caves as islands. *Evolution*, **24**, 463–474.

Culver, D., Holsinger, J.R. & Baroody, R. (1973) Toward a predictive cave biogeography: the Greenbrier valley as a case study. *Evolution*, **27**, 689–695.

Debinski, D.M. & Holt, R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology*, **14**, 342–355.

DeSante, D.F. & Ainley, D.G. (1980) The avifauna of the South Farallon Islands, California. *Studies in Avian Biology*, **4**, 1–104.

Diamond (1969) Avifaunal equilibria and species turnover rates on the Channel Islands of California. *Proceedings of the National Academy of Sciences USA*, **64**, 57–63.

Diamond, J.M. (1972) Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. *Proceedings of the National Academy of Sciences USA*, **69**, 3199–3203.

Diamond, J.M. (1973) Distributional ecology of birds. *Science*, **179**, 759–769.

Diamond, J.M. (1974) Colonization of exploded volcanic islands by birds: the supertramp strategy. *Science*, **184**, 803–806.

Diamond, J.M. (1975) Assembly of species communities. *Ecology and evolution of communities* (eds M.L. Cody and J.M. Diamond), pp. 342–444. Harvard University Press, Cambridge.

Diamond, J.M. & Gilpin, M.E. (1983) Biogeographical umbilici and the origin of the Phillipine avifauna. *Oikos*, **41**, 307–321.

Diamond, J.M. & Mayr, E. (1976) Species-area relation for birds of the Solomon Archipelago. *Proceedings of the National Academy of Sciences USA*, **73**, 262–266.

Dobkin, D.S. & Wilcox, B.A. (1986) Analysis of natural forest fragments: riparian birds in the Toiyabe Mountains, Nevada. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates* (eds J. Verner, M.L. Morrison and C.J. Ralph), pp. 293–299. University of Wisconsin Press, Madison.

Drake, J.A. (1991) Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist*, **137**, 1–26.

Duellman, W.E. (1970) The hylid frogs of Middle America. *Monographs of the Museum of Natural History, The University of Kansas*, **1**, 1–173.

Duffy, D.C. & Meier, A.J. (1992) Do Appalachian herbaceous understories ever recover from clearcutting? *Conservation Biology*, **6**, 196–201.

Eggleton, D.B., Elis, W.E. & Posey, M.H. (1999) Organism responses to habitat fragmentation and diversity: habitat colonization by estuarine macrofauna. *Journal of Experimental Marine Biology and Ecology*, **236**, 107–132.

Faaborg, J. (1979) Qualitative patterns of avian extinction on neotropical land-bridge islands: lessons for conservation. *Journal of Applied Ecology*, **16**, 99–107.

Fjeldså, J. (1992) Biogeographic patterns and evolution of the avifauna of relict high-altitude woodlands of the Andes. *Steenstrupia*, **18**, 9–62.

Fjeldså, J. & Rahbeck, C. (1997) Species richness and endemism in South American birds: implications for the design of networks and nature reserves. *Tropical forest remnants: ecology, management and conservation of fragmented communities* (eds W.R. Laurance and R.O. Bierregaard, Jr), pp. 467–482. University of Chicago Press, Chicago.

Forman, R.T.T., Galli, A.E. & Leck, C.F. (1976) Forest size and avian diversity in New Jersy woodlots with some land use implications. *Oecologia*, **26**, 1–8.

Freemark, K.E. & Merriam, H.G. (1986) Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biology Conservation*, **36**, 115–141.

Gemmell, R.P. (1982) The origin and botanical importance of industrial habitats. *Urban ecology* (eds R. Bornkamm, J.A. Lee and M.R.D. Seaward), pp. 33–39. Blackwell, Oxford.

Gilbert, F.S. (1980) The equilibrium theory of island biogeography, fact or fiction? *Journal of Biogeography*, 7, 209–235.

Hadley, K.S. (1987) Vascular plant distributions within the central and southern rocky mountains, U.S.A. *Arctic and Alpine Research*, **19**, 242–251.

Haig, A.R., Matthes, U. & Larson, D.W. (2000) Effects of natural habitat fragmentation on the species richness, diversity, and composition of cliff vegetation. *Canadian Journal of Botany*, **78**, 787–797.

Harris, L.D. (1984) *The fragmented forest: island biogeography and the preservation of biotic diversity*. University of Chicago Press, Chicago.

Heaney, L.R. (2000) Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography*, **9**, 59–74.

Hobbs, R.J. & Hopkins, J.M. (1990) From frontiers to fragments: European impact on Australia's vegetation. *Proceedings of the Ecological Society of Australia*, **16**, 93–114.

Hope, J.H. (1973) Mammals of Bass Strait islands. *Proceedings of the Royal Society of Victoria*, **85**, 163–195.

Hubbard, M.D. (1973) Experimental insular biogeography: ponds as islands. *Florida Scientist*, **36**, 132–141.

Humphrey, P.S. & Péfour, J.E. (1979) Glaciation and species richness of birds on austral South American islands. *Occasional Papers of the Natural History Museum, The University of Kansas*, **80**, 1–9.

Johnson, N.K. (1975) Controls on the number of bird species on montane islands in the Great Basin. *Evolution*, **29**, 545–567.

Kadmon, R. & Pulliam, H.R. (1993) Island biogeography: effect of geographical isolation on species composition. *Ecology*, **74**, 977–981.

Karr, J.R. (1982) Avian extinction on Barro Colorado Island, Panama: a reassessment. *American Naturalist*, **119**, 220–239.

Kitchener, D.J., Dell, J., Muir, B.G. & Palmer, M. (1982) Birds in Western Australian wheatbelt reserves—implications for conservation. *Biological Conservation*, **22**, 127–163.

Kratter, A.W. (1992) Montane avian biogeography in southern California and Baja California. *Journal of Biogeography*, **19**, 269–283.

Larson, D.W., Matthes, U. & Kelly, P.E. (2000) *Cliff ecology*. Cambridge University Press, U.K.

Laurance, W.F., Bierregaard, R.O. Jr, Gascon, C., Didham, R.K., Smith, A.P., Lynam, A.J., Viana, V.M., Lovejoy, T.E., Sieving, K.E., Sites, J.W. Jr, Anderson, M., Tocher, M.D., Kramer, E.A., Restrepo, C. & Moritz, C. (1997) Tropical forest fragmentation: synthesis of a diverse and dynamic disipline. *Tropical forest remnants: ecology, management and conservation of fragmented communities* (eds W.R. Laurance and R.O. Bierregaard, Jr), pp. 502–514. University of Chicago Press, Chicago.

Lawlor, T.E. (1986) Comparative biogeography of mammals on islands. *Biological Journal of the Linnean Society*, **28**, 99–125.

Lawlor, T.E. (1998) Biogeography of Great Basin mammals: paradigm lost? *Journal of Mammalogy*, **79**, 1111–1130.

Loman, J. & von Shantz, T. (1991) Birds in a farmland: more species in small than in large habitat islands. *Conservation Biology*, **5**, 176–186.

Lomolino, M.V. (1986) Mammalian community structure on islands: the importance of immigration, extinction and interactive effects. *Biological Journal of the Linnean Society*, **28**, 1–21.

Lomolino, M.V. (1994) Species richness of mammals inhabiting nearshore archipelagoes: area, isolation, and immigration filters. *Journal of Mammalogy*, **75**, 39–49.

Lomolino, M.V. (2000) A call for a new paradigm of island biogeography. *Global Ecology and Biogeography*, **9**, 1–6.

Lomolino, M.V., Brown, J.H. & Davis, R. (1989) Island biogeography of montane forest mammals in the American southwest. *Ecology*, **70**, 180–194.

Lovejoy, T.E., Bierregaard, R.O. Jr, Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown, K.S. Jr, Powell, A.H., Powell, G.V.N., Schubart, H.O.R. & Hays, M.B. (1986) Edge and other effects of isolation on Amazon forest fragments. *Conservation biology: the science of scarcity and diversity* (ed. M.E. Soulé), pp. 257–285. Sinauer, Sunderland.

Lynam, A.J. & Billick, I. (1999) Differential responses of small mammals to fragmentation in a Thailand tropical forest. *Biological Conservation*, **91**, 191–200.

Lynch, J.F. & Whigham, D.F. (1984) Effects of forest fragmentation on breeding bird communities in Maryland USA. *Biological Conservation*, **28**, 287–324.

Mabberly, D.J. (1979) Pachycaul plants and islands. *Plants and islands* (ed. D. Bramwell), pp. 259–277. Academic Press, London.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton.

Magnuson, J.J. (1990) The invisible present. *Bioscience*, **40**, 495–501.

Malcolm, J.R. (1997) Biomass and diversity of small mammals in Amazonian forest fragments. *Tropical forest remnants: ecology, management and conservation of fragmented communities* (eds W.R. Laurance and R.O. Bierregaard, Jr), pp. 207–221. University of Chicago Press, Chicago.

March, F. & Bass, D. (1995) Application of island biogeography theory to temporary pools. *Journal of Freshwater Ecology*, **10**, 83–85.

Martell, A.M. (1983) Changes in small mammal communities after logging in north-central Ontario. *Canadian Journal of Zoology*, **61**, 970–980.

Martin, J.L. & Lepart, J. (1989) Impoverishment in the bird community of a Finnish archipelago: the role of island size, isolation and vegetation structure. *Journal of Biogeography*, **16**, 159–172.

Mayr, E. & Diamond, J.M. (1976) Birds on islands in the sky: origin of the montane avifauna of northern Melanesia. *Proceedings of the National Academy of Sciences USA*, **73**, 1765–1769.

Mikkelson, G.A. (1993) How do food webs fall apart? A study of the changes in trophic structure during relaxation of habitat fragments. *Oikos*, **67**, 539–547.

Millien-Parra, V. & Jaeger, J.J. (1999) Island biogeography of the Japanese terrestrial mammal assemblages: an example of a relict fauna. *Journal of Biogeography*, **26**, 959–972.

Nores, M. (1995) Insular biogeography of birds on mountaintops in north western Argentina. *Journal of Biogeography*, **22**, 61–70.

Paton, P.W.C. (1994) The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology*, **8**, 17–26.

Patterson, B.D. & Atmar, W. (2000) Analyzing species composition in fragments. *Isolated vertebrate communities in the tropics* (ed. G. Rheinwald), pp. 93–108. Proceedings of the 4th International Symposium, Bonn. *Bonner Zoologische Monographen*, **46**, 93–108.

Paulay, G. (1994) Biodiversity on oceanic islands: its origin and extinction. *American Zoologist*, **34**, 134–144.

Peterson, A.T. & Watson, D.M. (1998) Problems with areal definitions of endemism: the effects of spatial scaling. *Diversity and Distribution*, **4**, 189–194.

Pignatti, S. (1995) Insular ecosystems and insularity. *Bollettino Della Societa Sarda Di Scienze Naturali*, **30** (suppl.), 383–401.

Porembski, S. & Barthlott, W. (eds) (2000) *Inselbergs: biotic diversity of isolated rock outcrops in tropical and temperate regions*. Ecological Studies 146, Springer-Verlag, Berlin.

Porembski, S., Seine, R. & Barthlott, W. (2000) Factors controlling species richness of inselbergs. *Inselbergs: biotic diversity of isolated rock outcrops in tropical and temperate regions* (eds S. Porembski and W. Barthlott), pp. 451–478. Ecological Studies, Vol. 146. Springer-Verlag, Berlin.

Quinn, J.F. & Harrison, S.P. (1988) Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. *Oecologia*, **75**, 132–140.

Rabinowitz, D., Cairns, S. & Dillon, T. (1985) Seven forms of rarity and their frequency in the flora of the British Isles. *Conservation biology: the science of scarcity and diversity* (ed. M.E. Soulé), pp. 182–204. Sinauer, Sunderland.

Ricklefs, R.E. & Cox, G.C. (1972) Taxon cycles in the West Indian avifauna. *American Naturalist*, **106**, 195–219.

Ricklefs, R.E. & Lovette, I.J. (1999) The roles of island area *per se* and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology*, **68**, 1142–1160.

Riebesell, J.F. (1982) Arctic-alpine plants on mountaintops: agreement with island biogeographic theory. *American Naturalist*, **119**, 657–674.

Robinson, G.R., Holt, R.D., Gaines, M.S., Hamburg, S.P., Johnson, M.L., Fitch, H.S. & Martinko, E.A. (1992) Diverse and contrasting effects of habitat fragmentation. *Science*, **257**, 524–526.

Robinson, J.V. & Dickerson, J.E. Jr (1987) Does invasion sequence affect community structure? *Ecology*, **68**, 587–595.

Rydin, H. & Borgegård, S. (1988) Plant species richness on islands over a century of primary succession: Lake Hjalmaren. *Ecology*, **69**, 916–927.

Sarthou, C. & Villiers, J.F. (1998) Epilithic plant communities on French Guiana inselbergs. *Journal of Vegetation Science*, **9**, 847–859.

Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, **5**, 18–32.

Schneider, D.C. (1994) *Quantitative ecology: spatial and temporal scaling*. Academic Press, San Diego.

Schoener, A., Long, E.R. & DePalma, J.R. (1978) Geographic variation in artificial island colonization curves. *Ecology*, **59**, 367–382.

Sieving, K.E. & Karr, J.R. (1997) Avian extinction and persistence mechanisms in lowland Panama. *Tropical forest remnants: ecology, management and conservation of fragmented communities* (eds W.R. Laurance and R.O. Bierregaard, Jr), pp. 156–170. University of Chicago Press, Chicago.

Simberloff, D.S. (1974) Equilibrium theory of island biogeography. *Annual Review of Ecology and Systematics*, **5**, 161–182.

Simberloff, D. (1995) Habitat fragmentation and the population extinction of birds. *Ibis*, **137** (Suppl.), 105–111.

Simberloff, D. & Abele, L.G. (1982) Refuge design and island biogeographic theory: effects of fragmentation. *American Naturalist*, **120**, 41–50.

Simberloff, D.S. & Wilson, E.O. (1970) Experimental zoogeography of islands. A two-year record of colonization. *Ecology*, **51**, 934–937.

Simpson, B.B. (1974) Glacial migrations of plants: island biogeographical evidence. *Science*, **185**, 698–700.

Steadman, D.W. (1995) Prehistoric extinctions of Pacific Island birds: biodiversity meets zooarchaeology. *Science*, **267**, 1123–1131.

Stouffer, P.C. & Bierregaard, R.O. Jr (1995) Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. *Conservation Biology*, **9**, 1085–1094.

Terborgh, J., Lopez, L. & Tello, J. (1997) Bird communities in transition: the Lago Guri islands. *Ecology*, **78**, 1494–1501.

Terborgh, J., Lopez, L., Tello, J., Yu, D. & Bruni, A.R. (1998) Transitory states in relaxing ecosystems of land bridge islands. *Tropical forest remnants: ecology, management and conservation of fragmented communities* (eds W.R. Laurance and R.O. Bierregaard, Jr), pp. 256–274. University of Chicago Press, Chicago.

Thébaud, C. & Strasberg, D. (1997) Plant dispersal in fragmented landscapes: a field study of woody colonization in rainforest remnants of the Mascarene archipelago. *Tropical forest remnants: ecology, management and conservation of fragmented communities* (eds W.R. Laurance and R.O. Bierregaard, Jr), pp. 321–332. University of Chicago Press, Chicago.

Thornton, I.W.B. (1996) *Krakatau: the destruction and reassembly of an island ecosystem*. Harvard University Press, Cambridge.

Tocher, M.D., Gascon, C. & Zimmerman, B.L. (1997) Fragmentation effects on a central Amazonian frog community: a ten-year study. *Tropical forest remnants: ecology, management and conservation of fragmented communities* (eds W.R. Laurance and R.O. Bierregaard, Jr), pp. 124–137. University of Chicago Press, Chicago.

Tsuyuzaki, S. (1991) Species turnover and diversity during early stages of vegetation recovery on the volcano Usu, northern Japan. *Journal of Vegetation Science*, **2**, 301–306.

Wake, D.B. & Lynch, J.F. (1976) The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. *Natural History Museum of LA County Science Bulletin*, **25**, 1–65.

Walker, L.R., Zarin, D.J., Fetcher, N., Myster, R.W. & Johnson, A.H. (1996) Ecosystem development and plant succession on landslides in the Caribbean. *Biotropica*, **28**, 566–576.

Watson, D.M. (1999) *Temporal scale and the consequences of habitat fragmentation: case studies of Mesoamerican highland birds*. PhD Dissertation. The University of Kansas, Lawrence.

Watson, D.M., Mac Nally, R. & Bennett, A.F. (2000) The avifauna of severely fragmented Buloke *Allocasuarina luehmanni* woodland in western Victoria, Australia. *Pacific Conservation Biology*, **6**, 46–60.

Watson, D.M. & Peterson, A.T. (1999) Determinants of diversity in a naturally fragmented landscape: humid montane avifaunas of Mesoamerica. *Ecography*, **22**, 582–589.

Whittaker, R.J. (1998) *Island biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford.

Whittaker, R.J. (2000) Scale, succession and complexity in island biogeography: are we asking the right questions? *Global Ecology and Biogeography*, **9**, 75–85.

Wiens, J.A. (1989) *The ecology of bird communities, Vol. 2 Processes and variations*. Cambridge University Press, Cambridge.

Wiens, J.A. (1995) Habitat fragmentation: island vs. landscape perspectives on bird conservation. *Ibis*, **137** (Suppl.), 97–104.

Wilbur, H.M. & Travis, J. (1984) An experimental approach to understanding pattern in natural communities. *Ecological communities: conceptual issues and the evidence* (eds D.R. Strong, Jr, D. Simberloff, L.G. Abele and A.B. Thistle), pp. 113–122. Princeton University Press, Princeton.

Wilcox, B.A., Murphy, D.D., Ehrlich, P.R. & Austin, G.T. (1986) Insular biogeography of the montane butterfly faunas of the Great Basin: a comparison with birds and mammals. *Oecologia*, **69**, 188–194.

Williamson, M. (1983) *Island populations*. Oxford University Press, Oxford.

Williamson, M. (1989) The MacArthur and Wilson theory today: true but trivial. *Journal of Biogeography*, **16**, 3–4.

Wilson, E.O. & Willis, E.O. (1975) Applied biogeography. *Ecology and evolution of communities* (eds M.L. Cody and J.M. Diamond), pp. 522–534. Belknap Press, Cambridge.

Woinarski, J.C.Z., Horner, P., Fisher, A., Brennan, K., Lindner, D., Gambold, N., Chatto, R. & Morris, I. (1999) Distributional patterning of terrestrial herpetofauna on the Wessel and English Company Island groups, northeastern Arnhem Land, Northern Territory, Australia. *Austral Ecology*, **24**, 60–79.

## BIOSKETCH

**David Michael Watson** is a lecturer in Ecology and Ornithology at Charles Sturt University, Thurgoona, Australia. His primary research interests centre on the determinants of diversity in fragmented landscapes and the interplay between resource availability and species distribution. He has conducted empirical studies in eastern Australia and Mesoamerica, incorporating both species-specific and community-level approaches. He recently published a major review of mistletoe–animal interactions in Annual Review of Ecology and Systematics, (**32**: 219–49, 2001) proposing that mistletoes act as a keystone resource in forested habitats throughout the world. In addition to ongoing theoretical work on the ecological consequences of insularization, current research projects include a landscape-scale manipulative experiment to test the keystone resource hypothesis and exploring the relationship between clutch volume and body mass across birds.