introductions, as well as a blind snake and an agamid. Lemurs were also introduced from Madagascar. Various bird species have been introduced, including chickens, pigeons, and sparrows. Some freshwater fish, such as the very common guppies on Mayotte, are known to be introduced, whereas the status of others remains unclear. The status of many invertebrate species is similarly unknown.

HUMAN HISTORY, GEOGRAPHY, AND INFLUENCE

The first-known human inhabitants of the Comoro islands were Polynesians and Melanesians, around the sixth century BC, although settlement may have occurred earlier. Since then, diverse groups have arrived, from the coast of Africa, the Persian Gulf, and Madagascar. Portuguese explorers visited in 1505, and France established colonial rule in 1841. In 1975 the Comororan parliament declared independence. In the following referendum, the population of Mayotte voted against independence, and currently Mayotte remains under French political control, whereas the other islands form the Union of the Comoros. The current population (2005 estimate: 798,000) means an average human density of over 275/km², although values are higher on Anjouan and lower on Moheli. Agriculture, including fishing and forestry, is the leading sector of the economy, and this way of life, combined with high population density, means that the Comoros are facing an environmental crisis. Between 1973 and 1983, forests declined by 73% on Anjouan, and across the islands approximately half the forest was lost. The forest has been predominantly replaced with fields and plantations of banana, coconuts, and ylang-ylang. Extensive felling of forest to develop fields has led to much greater levels of soil erosion on the steep volcanic landscape. Freshwater supplies have also been seriously influenced by this, with the number of perennial rivers being greatly reduced. Opening of roads into forested regions intensifies this process. The effect of this on endemic plants and invertebrates is unknown, but it is probably catastrophic. Few endemic birds survive in the non-forest areas, although the sunbirds (Nectarina) are better adapted to deal with the changes, flourishing on the introduced exotic flowers. Similarly, many of the reptiles appear relatively capable of surviving in secondary forest areas. For most of these, introduced species, such as rats, mice, and civets, pose a possibly more serious threat.

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FURTHER READINGS


CONTINENTAL ISLANDS

DAVID M. WATSON
Charles Sturt University, Albury, Australia

As evidenced by the breadth of systems covered in this volume, the term “island” can be applied to a range of ecosystems extending well beyond conventional notions of land masses surrounded by water. Be they caves, rock outcrops, mountaintops, or oases, these systems share many biotic and abiotic features with their oceanic counterparts. One of the primary distinctions between different island systems is whether they were formed de novo, or instead formed by fragmentation. In the former case, the islands have never been in contact with the source of colonists and have abundant “empty” ecological niche space. Fragments are fundamentally different. In these patches, the ecological space will initially be filled as a consequence of connection to the source of colonists and have abundant “empty” ecological niche space. Fragments are formed by the process of fragmentation, and the resulting characteristics of such islands (and how they differ from islands formed de novo) are discussed.

FRAGMENTS VERSUS DE NOVO ISLANDS

Rather than being a trivial technicality or a question of semantics, establishing the historic origin of an island is crucial to formulating expectations of the ecological patterns represented. Many features referred to as islands are actually fragments of previously more widespread ecosystems. Islands formed de novo (such as oceanic islands) are habitat patches that were formed more recently than their surrounding habitat—they are relatively new features that are initially unoccupied, becoming colonized in a variably predictable fashion by a sequence of organisms (Fig. 1A). In contrast, continental islands are patches defined by continental rifting (e.g., causing a fragment to break away from a continent) or by the imposition of a new or modified matrix (e.g., isolating a habitat island
and diminishing movement rates of organisms into and out of the habitat patch) (Fig. 1B).

Three features of this distinction are important. First, note the complete lack of reference to water—-islands may occur on land, in water: anywhere. Thus, a salt lake can be considered analogous to an oceanic island (formed de novo), whereas an oxbow lake qualifies as a fragment; most caves are formed de novo, whereas icebergs are fragments. Second, there is no reference to temporal or spatial scale: Tasmania can be considered a fragment of the Australian continent isolated by rising sea levels around 14,000 years ago, just as a tidepool is a fragment lasting for less than a day. Finally, this functional distinction demonstrates that the key difference between islands formed de novo and fragments lies in the sequence of events that defines them. For islands formed de novo, the patch itself is the new feature, whereas for fragments the habitat comprising the patch is preexisting, and patch boundaries are determined by the imposition of a new or modified matrix habitat. Spanning a wide range of ecosystems ranging in extent from centimeters to thousands of kilometers, and time periods from hours to millions of years, this distinction provides a useful framework to arrange our current understanding of how inherently patchy ecosystems function and to identify which factors best explain patterns of diversity and distribution within them.

A FUNCTIONAL CLASSIFICATION OF ISLANDS

Islands that have been formed de novo as well as those formed through fragmentation can be further divided into old systems (older than 1000 years) and young landscapes (younger than 100 years), allowing for a surprising number of generalities. These four classes can be further subdivided using a convenient third factor relating to the contrast between the patch (de novo island or fragment) and the surrounding habitat or matrix. Phase differences (i.e., land-locked water bodies, patches of land surrounded by water [Fig. 2]) are deemed high contrast, whereas within-phase differences (e.g., a forest patch surrounded by grassland, rock outcrops within heathland) are low contrast. Using this three-factor approach and some objective thresholds, most patchy landscapes can be readily assigned to one of eight classes (Table 1).

The first step in applying this classification is to establish whether or not a particular patch is a de novo island or a fragment. Although usually simple, it is not always straightforward, and historic information may be equivocal or simply unavailable. Once the origin of the patch is established, patch age and matrix contrast determine which of eight classes it represents. As summarized in Table 1, this classification groups together a wide range of ecosystems, often studied using divergent methods and typically not regarded as islands or fragments.

FIGURE 1 Schematic representation of the formation of a generic island de novo and by fragmentation. (A) In this example, lowering sea or lake levels expose a new habitat patch—a small island without any preexisting terrestrial biota. As with all islands, the biota gradually develops from two classes of organism: inter-patch dispersers coming from similar habitat elsewhere and matrix-derived species coming from the surrounding habitat. (B) Here, the fragment becomes isolated by subsidence, with the matrix habitat (in this case, water) surrounding the habitat patch. The fragment biota is initially dominated by relictual organisms (represented by trees in this example), with matrix-derived and inter-patch disperser taxa adding to the fragment biota. Illustrations by Margaret J. Watson.

FIGURE 2 A small patch of lowland rain forest in Gatun Lake, Panama, created by erosion from wave action associated with passing ships. Although referred to informally as an island, this patch is actually a habitat fragment, isolated from similar habitat by a high-contrast matrix. This photograph also illustrates the species-area relationship: Of the 250 plus species of birds recorded from the adjacent Barro Colorado Island (a 1500-ha fragment isolated in 1914), this tiny fragment supports a single species—the black vulture Coragyps atratus.
Using this approach, physically similar systems are revealed to be functionally divergent. Thus, inselbergs and caves—two ecosystems that have received considerable attention from researchers—are de novo islands, whereas tepuis, mesas, and most other montane patches are functionally fragments. One implication of this historic difference is manifested in the origin of organisms occurring within these patches, with an additional class of organism being associated with habitat fragments. Known as relictual taxa, these are organisms that were living in the habitat prior to fragmentation and became isolated as the matrix surrounded the patch. A pertinent example comes from the cloud forests of Mesoamerica, which are home to many groups of moisture-dependent bolitoglossine salamanders (Fig. 3). These animals were originally more widespread, but, just like fish in an oxbow lake, these habitat specialists became trapped by the surrounding inhospitable habitat. Although they need not be restricted to the fragment and may occasionally or regularly move to other patches, relictual taxa are typically lower-vagility organisms that either persist or become locally extinct after fragmentation.

Two other classes of organism occur on both de novo islands and fragments, albeit in differing proportions. Matrix-derived taxa are those organisms originally associated with the matrix habitat, secondarily occupying the habitat patches. Although this may be short term or opportunistic (e.g., grassland birds nesting in forest fragments, migrating raptors using inselbergs as staging areas), it becomes most evident over evolutionary time, as the organisms adapt to the new habitat. Examples of matrix-derived species include many cave-dwelling arthropods, which exhibit a suite of adaptations that confer advantages in the new habitat. The final class of organism—inter-patch dispersers—consists of medium- to high-vagility taxa that are associated primarily with the patchy habitat, but which can readily move between patches. Thus, swiftlets and rock wallabies are inter-patch dispersers, being dependent on specific habitat patches (caves and rocky massifs, respectively) but being variously able to move between nearby patches across the intervening matrix.

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**TABLE 1**

Functional Classification of Patchy Landscapes

<table>
<thead>
<tr>
<th>Fragments</th>
<th>Islands</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low-Contrast</td>
<td>High-Contrast</td>
</tr>
<tr>
<td><strong>Young (&lt; ∼100 years)</strong></td>
<td></td>
</tr>
<tr>
<td>Forest fragment</td>
<td>Floating raft/mat</td>
</tr>
<tr>
<td>Internal fragment/clearing</td>
<td>Flooded tree</td>
</tr>
<tr>
<td>Refugium from fire</td>
<td>Hydroelectric island</td>
</tr>
<tr>
<td>Seagrass fragment</td>
<td>Oxbow lake</td>
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<tr>
<td></td>
<td>Pack-ice/iceberg</td>
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<tr>
<td></td>
<td>Tidal pool</td>
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<tr>
<td><strong>Old (&gt; ∼1000 years)</strong></td>
<td></td>
</tr>
<tr>
<td>Cliff-face fragment</td>
<td>Continent</td>
</tr>
<tr>
<td>Lava-flow refugium</td>
<td>Inter-river valley</td>
</tr>
<tr>
<td>Mesa/tepui</td>
<td>Land-bridge island</td>
</tr>
<tr>
<td>Montane remnant</td>
<td>Riverine/lacustrine island</td>
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<tr>
<td>Riparian fragment</td>
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<td></td>
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</tbody>
</table>

*note: By using age, origin, and matrix contrast to define eight forms of patch, this approach holds across a wide range of spatial and temporal scales, from continents to ephemeral ponds.*

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**FIGURE 3** A minute bolitoglossine salamander in the genus Thorius from a humid pine–oak forest fragment in southern Mexico. These poorly known species illustrate how habitat fragmentation can promote diversification, with populations having become separated as the cold-adapted forests retreated upslope when the region became warmer and drier after the last glacial period ended approximately 40,000 years ago. The evolutionary consequences of vicariance, which affect many groups in this region, are most obvious with low-vagility species like salamanders, with the two mountain ranges separated by the Oaxaca Valley supporting completely complementary assemblages.
CONTINENTAL ISLANDS: FRAGMENTS SURROUNDED BY WATER

A special class of fragment that illustrates some of the key differences between de novo islands and fragments consists of what is known as continental “islands”: large areas of continental shelf surrounded by water that were isolated from adjacent continents, either by rising sea levels (e.g., Sicily, Great Britain, Tasmania) or by rifting over millions of years (New Caledonia, Madagascar, New Zealand). Unlike the biota of oceanic islands that formed de novo, where species numbers reflect a dynamic balance between immigration, speciation, and local extinction, continental islands did not start with vacant ecological space. Rather, they carry with them the descendants of those organisms initially present on the land mass prior to fragmentation, with diversity patterns subsequently changing through the process of relaxation. Thus, they start with a “full” complement of organisms and gradually lose taxa over time, unlike oceanic islands, which start out empty and progressively gain taxa. During this period, taxa may become extinct in the remainder of their range but persist in isolation. Over time, this process yields an increasing proportion of species, genera, families, and even orders that are restricted to continental islands—taxa known as paleoendemics (as compared with neoendemics—that is, the comparatively recently formed species that diverged after colonizing oceanic islands).

Continental islands, and the differences between paleoendemics and neoendemics, are exemplified by New Zealand, which became isolated from Gondwanaland around 80 million years ago. New Zealand contains a large number of relictual forms found nowhere else: Considering birds alone, there are the Zealand wrens (Acanthisittidae [Fig. 4A]), widely considered to represent the sister taxon to the diverse passerine order; kakas; keas (Fig. 4B); and kakapos (Nestoridae), which are con-

FIGURE 4 Two examples of relictual species from families wholly restricted to a continental island: New Zealand. (A) A rockwren Xenicus gilviventris on the South Island of New Zealand, one of two surviving representatives of the New Zealand wren family (Acanthisittidae). Numerous phylogenetic studies have suggested that these small, almost tail-less birds are sister taxa to the entire Passerine order. (B) A kea Nestor notabilis in the alpine grasslands of New Zealand. These intelligent birds and their close relatives in the family Nestoridae are sister to all other parrots.
sidered to be the basal clade in the parrot order; there are also two other endemic families, which include the wattled birds (Calleatidae) and kiwis (Apterygidae). Even more striking are the two species of tuatara (Fig. 5), the sole living representatives of the order Rhynchocephalia, which became extinct elsewhere in the Jurassic. This diverse assemblage of paleoendemics is complemented by neoendemics, many of which are derived from colonists from nearby Australia. This second source of endemics is exemplified by the takahe (Fig. 6), a large flightless gallinule, which eats a restricted diet of tussock grasses and herbs. In the absence of any terrestrial mammals, a variety of novel morphotypes evolved within birds, including a radiation of gregarious browsers and grazers (moas), a role occupied by mammals elsewhere. Rather than being exceptional, these examples are representative of patterns seen repeatedly on continental islands: aberrant forms evolving in isolation, and relictual taxa surviving long after becoming extinct elsewhere. Despite being frequently labeled islands, these systems and the patterns of diversity associated with them show many parallels with other fragmented landscapes, allowing insight into the long-term consequences of habitat fragmentation.

**MONTANE REMNANTS AS CONTINENTAL ISLANDS**

One class of patchy ecosystem that has received disproportionate attention is montane remnants, and they serve as instructive examples to evaluate in more depth. Mountain-tops often contain vegetation types and specific habitats that are altitudinally restricted—found only under specific climatic conditions associated with high elevations; such habitats include cloud forests, alpine grasslands, herbfields, and paramo. Despite being poetically referred to as “sky islands” by some researchers, these vegetation types are often relictual fragments of previously more widespread habitats, which have been isolated by changing climate (Fig. 7).

These habitat fragments are similar in many ways to the woodland and forest fragments isolated by agricultural development, but they differ dramatically in age. Most anthropogenically created fragmented landscapes were formed by broad-scale clearing 150 to 80 years ago, as the regions of North America, Australasia, Latin America, and Southeast Asia were developed. Montane remnants worldwide were defined much earlier, as regional climates became warmer and drier—coinciding in most cases with...
the last interglacial period in the late Pleistocene. Hence, the fragments in many of these landscapes are 10,000 to 30,000 years old; although subject to further and ongoing disturbance, including additional clearing, these landscapes still retain the imprint of this initial shift.

Although most habitat change associated with anthropogenic activities (i.e., clearing, agricultural intensification, development) occurs over periods of years, vegetation change mediated by regional climatic shifts is often considered to take tens of thousands of years. Recent information, however, is dispelling this assumption. A growing body of research has examined changes in plant distributions associated with recent climate change, demonstrating that even subtle changes in mean temperature and rainfall can effect dramatic shifts in plant occurrence. These data are reinforced by studies of fluctuations in the northern extent of boreal forest during the Pleistocene, as forest boundaries changed rapidly in response to drought associated with postglacial warming. Hence, the creation of elevational remnants may have occurred far more rapidly than is frequently assumed, and many regions may have been transformed from continuous habitat into mosaics of fragments within several thousand years or less.

Compared with anthropogenically fragmented landscapes that have been the focus of several thousand separate ecological investigations, these montane remnants are less thoroughly understood: Determinants of diversity have been studied in less than 50 landscapes. Many studies of montane assemblages were conducted in response to MacArthur and Wilson’s equilibrium theory of island biogeography, to find out whether similar processes operated in these continental ecosystems. Having established presence/absence data for selected organism groups, the researchers then related these richness estimates to fragment area, distance to nearest continuous habitat patch (or “mainland”), and a range of other biogeographic metrics.

Unlike anthropogenically created fragments, which are typically embedded within a developed matrix to which access is straightforward, many montane remnants occur in remote and inaccessible regions. These logistical issues are compounded by a pronounced taxonomic impediment. Fewer researchers have visited many of these areas, and, given the pronounced environmental heterogeneity in these mountainous landscapes, species often exhibit highly restricted distributions, with small-scale neoendemics being well represented. Thus, there are many undescribed or poorly known species, and working out the identities of the species present can pose very real challenges. Moreover, the repeated visits and thorough sampling required to generate accurate richness estimates are often not possible, thus reducing the accuracy of analyses and limiting a researcher’s ability to explain recorded patterns of occurrence.

**CASE STUDY 1: MAMMALS IN GREAT BASIN BOREAL FOREST FRAGMENTS**

The implications of these logistical and procedural issues are exemplified by studies of mammals living in boreal forest fragments in the Great Basin of western North America, isolated around 8000 years ago when this forest type retreated northward, leaving relictual stands on high mountain ranges throughout the region. This landscape is the best studied of all montane remnants, with multiple studies having been conducted of resident birds, mammals, butterflies, and plants. Noted ecologist James H. Brown studied 15 cold-adapted subalpine mammal species (excluding large carnivores, ungulates, and bats) in these forests from 1968 to 1970, complementing published records from the 1930s, 1940s, and 1950s with his own observations to build faunal lists for 17 forest fragments. His analysis demonstrated that species richness did not reflect a balance between colonization and extinction expected under an equilibrium model. Rather, the mammalian fauna of these forest fragments was extinction driven, with larger patches retaining greater numbers of species and greater proportions of larger species with more strict habitat and dietary needs. This study was instrumental in developing the nonequilibrium or relaxation biogeographic model, which eventually became a widely accepted paradigm.

Some 25 years later, mammalogist Tim Lawlor returned to these forests, spending at least three days in each forest fragment and confirming species identities with voucher specimens (essential for morphologically conservative groups such as chipmunks and shrews). He added 25 new records to Brown’s dataset, involving 13 of the original 15 subalpine species. Given the distance between mountains and the arid intervening habitat, it is unlikely that these additional records represent recent colonists. Although Brown acknowledged that his data matrix was likely incomplete, he suggested that additional data would have little qualitative effect on the findings. Surprisingly, Lawlor’s reanalysis revealed a much weaker association between fragment area and species richness, with similar weak effects for individual species. Isolation from various “mainlands” continued to have little effect on species richness, with patch-restricted relictual taxa occurring in lower proportions than inter-patch dispersers.

Rather than being exceptional, this example is likely to be representative of many other landscapes, most of which have
not been studied more than once. In addition to issues of inventory completeness, many historic studies await reanalysis. As described earlier, most studies of elevational fragments were conducted in the 1970s and 1980s, using the analytical tools available to ecologists at the time. Many of these techniques now seem rudimentary, especially when compared with the nestedness analyses and spatially explicit multivariate approaches routinely used to infer determinants of diversity in anthropogenically fragmented landscapes today.

**CASE STUDY 2: BIRDS IN HUMID PINE–OAK FORESTS IN SOUTHERN MEXICO**

One of the few studies to have applied these modern analytical tools to studying ecological patterns of diversity in montane remnants was a study of resident birds in humid pine–oak forests in southern Mexico conducted by the author. Dominated by various species of pine and oak with associated alder, fir, and other palearctic plants, these temperate forests are restricted to elevations of 2500 m or higher. Originally widespread throughout Mesoamerica (from Texas to Colombia), these cold-adapted forests retreated upslope during the last interglacial period beginning approximately 30,000 years ago, attaining their present configuration approximately 12,000 years ago. The Oaxaca Valley occurs between the two dominant ranges of the region (the Sierra Madre Oriental and Occidental) and has been the focus of comprehensive archaeological research including detailed paleoclimate and vegetation reconstructions for the past 40,000 years.

Exhaustive bird surveys were conducted in 17 patches of humid pine–oak forest, ranging in size from 2 to 160,000 ha. To minimize the issues associated with incomplete inventories, particular attention was paid to the methodology used to survey resident bird assemblages. Because no other study had attempted to conduct inventories for patches spanning five orders of magnitude, a new sampling approach was devised, which applied results-based stopping rules to sample forests at the patch scale to the same degree of completeness (known as the “standardized search”). These field data were complemented with historic data from unpublished records and with specimen data, yielding comparable inventories of consistently high completeness. These data were analyzed using a range of methods and compared qualitatively with findings from comparable studies of other montane remnants.

The most striking finding from this work was the consistent importance of patch-scale factors in determining species richness. Whereas isolation (measured as distance from the nearest forest larger than 100,000 ha) and other landscape-scale factors had little effect (either on overall richness or occurrence patterns of 60 resident species), fragment area, vegetation complexity, and elevational range all emerged as key drivers of diversity. All three predictors were closely interrelated, however, such that larger forests typically contained a higher number of habitats and spanned greater elevational ranges. Patterns of richness among the 17 fragments were found to be highly nested, with the arrangement of subsets being closely related to patch area. These findings echo previous results from other montane remnants elsewhere, with patch-scale factors consistently overwhelming landscape-scale factors. This suggests that much of the isolation effect described in younger systems or patches surrounded by high-contrast matrices is transitory, with fragment size and other patch-scale factors being more crucial to retaining species over thousands of generations. Examining occurrence patterns of individual species, 27 of the 30 habitat specialists were found only in forests larger than 3000 ha, with eight especially sensitive species being found only in montane remnants larger than 30,000 ha (Fig. 8).

**THE ROLE OF TEMPORAL SCALE**

Comparing findings from these old fragmented systems with those from other classes of patchy landscape, time since formation emerges as critical. Indeed, after thousands of years, continental islands converge in many community-scale properties. For those patches in low-contrast matrices (including montane remnants and inselbergs),
diversity stabilizes over time, and the biota becomes distinct from the interstitial matrix. De novo islands become dominated by matrix-derived taxa, whereas relictral taxa continue to dominate fragments, with inter-patch dispersers showing indistinguishable patterns of occurrence. Hence, despite different origins and initial differences, the biotas of older islands, whether formed de novo or by fragmentation, exhibit broad similarity, explaining why they are so frequently studied together.

Over evolutionary time, the process of habitat fragmentation can lead to vicariant speciation—that is, isolated populations of organisms diverging and acquiring novel traits. At the global scale, tectonic movement driving the breakup of Gondwana and Laurasia exemplifies this process, but, so long as patch size and quality are sufficient to allow populations to persist, allospecies can result from fragmentation at much smaller scales. The proportion of these endemics is generally greater in high-contrast systems, but populations isolated by changing courses of rivers, intrusion of lava flows, or shifting dune fields in terrestrial systems can also go on to form distinct species.

Because fragmentation necessarily leads to smaller populations in the short term, it can initiate a sequence of demographic processes culminating in local or complete extinction. Aside from smaller population sizes, fragments have higher proportions of edge habitat, attracting early successional species that can eventually replace the relictual taxa. This explains why patch size consistently emerges as so important in explaining distribution patterns in these older landscapes, and, as revealed by the findings from Oaxaca, why these thresholds can be surprisingly high.

LESSONS FROM THE PAST: IMPLICATIONS FOR RECENT FRAGMENTS

Despite the concerted efforts of ecologists to derive generalized principles that explain the short- to medium-term effects of habitat fragmentation on biodiversity, overall trends are obscured by site- and taxon-specific factors. Following fragmentation of any previously continuous habitat, a variable proportion of relic species becomes locally extinct, initially because of loss of habitat but subsequently because of demographic and stochastic processes. Many studies have focused on these processes, identifying ecological traits of those species especially prone to extinction and patch attributes that may minimize these extinctions. Initial diversity losses can be offset by an influx of matrix-derived species, occasionally resulting in fragmentation having a positive effect on diversity.

These adjustments in community composition can take many generations to occur. Most studies, however, focus on habitats dominated by woody plants (i.e., forests and woodlands), ecosystems defined by organisms with lifespans that generally exceed the time since initial disturbance. Accordingly, net effects of recent fragmentation on diversity patterns can rarely be measured with confidence, and some theoretical estimates suggest that hundreds to thousands of years are required before communities adjust. 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-oriented goals, generating valuable data on the short-term responses of communities to fragmentation.

In contrast to the highly divergent consequences of habitat fragmentation in the short term, studies of older systems reveal broad similarities in the long-term effects of fragmentation. Biotas remain composed primarily of relict taxa, with diversity patterns being best explained by area, age, and other patch-scale variables, and landscape-scale factors such as isolation consistently have little influence. Hence, despite comprising less than 50 studies, inferences generated from studying these older, high-elevation fragments yield valuable insight into the future awaiting anthropogenically altered landscapes. Moreover, the close interrelationships between the patch-scale variables in studies of older landscapes suggest that much of the debate between the influence of habitat versus area is needless, with these and other patch-scale factors interacting and combining in their influence on biodiversity occurrence over the long term.

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