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Review

The West Indies as a laboratory of biogeography and evolution

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Islands have long provided material and inspiration for the study of evolution and ecology. The West Indies are complex historically and geographically, providing a rich backdrop for the analysis of colonization, diversification and extinction of species. They are sufficiently isolated to sustain endemic forms and close enough to sources of colonists to develop a dynamic interaction with surrounding continental regions. The Greater Antilles comprise old fragments of continental crust, some very large; the Lesser Antilles are a more recent volcanic island arc, and the low-lying Bahama Islands are scattered on a shallow oceanic platform. Dating of island lineages using molecular methods indicates over-water dispersal of most inhabitants of the West Indies, although direct connections with what is now southern Mexico in the Early Tertiary, and subsequent land bridges or stepping stone islands linking to Central and South America might also have facilitated colonization. Species–area relationships within the West Indies suggest a strong role for endemic radiations and extinction in shaping patterns of diversity. Diversification is promoted by opportunities for allopatric divergence between islands, or within the large islands of the Greater Antilles, with a classic example provided by the *Anolis* lizards. The timing of colonization events using molecular clocks permits analysis of colonization–extinction dynamics by means of species accumulation curves. These indicate low rates of colonization and extinction for reptiles and amphibians in the Greater Antilles, with estimated average persistence times of lineages in the West Indies exceeding 30 Myr. Even though individual island populations of birds might persist an average of 2 Myr on larger islands in the Lesser Antilles, recolonization from within the archipelago appears to maintain avian lineages within the island chain indefinitely. Birds of the Lesser Antilles also provide evidence of a mass extinction event within the past million years, emphasizing the time-heterogeneity of historical processes. Geographical dynamics are matched by ecological changes in the distribution of species within islands over time resulting from adaptive radiation and shifts in habitat, often following repeatable patterns. Although extinction is relatively infrequent under natural conditions, changes in island environments as a result of human activities have exterminated many populations and others—especially old, endemic species—remain vulnerable. Conservation efforts are strengthened by recognition of aesthetic, cultural and scientific values of the unique flora and fauna of the West Indies.

Keywords: island biogeography; colonization; extinction; speciation; adaptive radiation; diversification

1. INTRODUCTION

Islands have inspired biologists since the beginning of scientific exploration more than two centuries ago. Darwin's (1859) insight about descent with modification developed in part from the close affinities of island inhabitants to forms on nearby continents (Darwin 1909). Wallace (1869) drew similar insights from his studies on East Indian islands, which also provided a foundation for his syntheses of biogeography (Wallace 1876) and island biology (Wallace 1880). Since Darwin's and Wallace's time, research on island biotas has contributed substantially to our understanding of species formation, adaptive radiation, community assembly and extinction (MacArthur & Wilson 1967; MacArthur 1972; Carlquist 1974; Carson & Kaneshiro 1976; Williamson 1981; Grant 1986, 1998; Woods 1989*a*; Carson & Clague 1995; Caley & Schluter 1997; Whittaker 1998; Schluter 2000; Ricklefs & Bermingham 2001, 2004*b*; Woods & Sergile 2001; Whittaker & Fernández-Palacios 2007). Islands hold special advantages for such studies owing to their discrete nature. Archipelagoes, in particular, promote diversification and provide a setting within which evolutionary processes can unfold repeatedly on multiple islands (Wagner & Funk 1995; Losos 1996; Losos *et al*. 1998; Givnish 1999; Grant & Grant 2002; Gillespie 2004).

Archipelagoes, such as the Hawaiian Islands (Wagner & Funk 1995), Galápagos Archipelago (Grant 1986) and the Canary Islands (Juan *et al*. 2000)

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have the strongest hold on our imaginations and represent idealized archetypes of island biogeography. Their isolation and opportunities for cycles of allopatric speciation have created repeated examples of endemic radiations, often resulting in unusual forms of plants and animals (Amadon 1950; Pratt 1979, 2005; Givnish & Sytsma 1997; Givnish 1999). However, the extreme isolation of the Galápagos and Hawaiian archipelagoes distils the relationship between continental and island biotas to such a degree that much of the potential complexity of interaction between the two is absent, and their tenuous connection is reduced primarily to one-way, haphazard, long-distance dispersal. At the other extreme, close islands such as those off the coast of Baja California, many of which were recently connected to the mainland (Case *et al.* 2002), and the Bismark and Solomon Islands to the north and west of New Guinea (Mayr & Diamond 2001) receive so many immigrants that endemism rarely develops. Opportunities for radiations within such archipelagoes are swamped by the steady supply of new taxa evolving in the larger source areas (Ricklefs & Bermingham 2007).

Between these extremes, the West Indies are sufficiently isolated that distinct endemic forms have accumulated in many groups of organisms, but sufficiently close to produce a dynamic interaction between continent and island for others. Colonization occurs frequently enough for its character to emerge above the veil of haphazard events. Diversity is high enough that species formation, ecological shifts and extinction take on statistical distributions. The islands are old and many elements of the endemic biota have accumulated over much of the Tertiary. Like other archipelagoes, the West Indies harbour several spectacular adaptive radiations. The most famous of these comprise not only the *Anolis* lizards of the Greater Antilles (Williams 1972; Williams 1983; Roughgarden 1995; Losos 1996; Losos & Schluter 2000) but also such diverse endemic groups as *Eleutherodactylus* frogs (Hedges 1989), the extinct sloths (White & MacPhee 2001) and mostly extinct rodents (Woods 1989*b*). Regardless, island biogeography within the region has been dominated by debates related to colonization routes, particularly by non-flying vertebrates in the Greater Antilles, and their bearing on the existence of earlier land connections to the continents (Rosen 1976; Guyer & Savage 1985; Rosen 1985; Iturralde-Vinent & MacPhee 1999), the alternative being over-water dispersal (Hedges 1996*a*,*b*, 2001). In this context, biogeographic distributions have been scrutinized for inferences concerning relationships between West Indian and continental landmasses before the Miocene, when the present-day geographical configuration of the islands was established. Beyond these dominating issues, however, the West Indies have also contributed importantly to our understanding of island biogeography, and of evolution and ecology more generally. Indeed, the West Indies provide an outstanding natural laboratory for studying processes that establish patterns in the diversity of life. Here, we focus on those processes—colonization, speciation and extinction—that are responsible for the development of island biotas. The diverse setting of the West Indies, harbouring islands of different size and age, as well as replicated ecological and evolutionary opportunities across islands, combined with different propensities of organisms for dispersal over open stretches of ocean, establishes an array of natural experiments that expose the processes underlying contemporary patterns of diversity. We focus primarily on vertebrates because these are the best known and understood.

2. GEOGRAPHY, CLIMATE AND HISTORY

The West Indies are often considered as a distinct biogeographic region adjacent to North, Central and South America within the Caribbean Basin (Olson & Dinerstein 1998, 2002; Myers *et al.* 2000), but this obscures the historic and geographical heterogeneity of the islands. The West Indies consist of three groups of islands: (i) the Greater Antilles, which are primarily old fragments of continental crust originally formed as islands to the west of the present-day Central American Isthmus and carried to their present position by plate movements, (ii) the Bahamas Islands, which are low-lying islands scattered about the shallow Bahamas platform, and (iii) the Lesser Antilles, which form a volcanic arc over the eastern edge of the eastward moving, overriding Caribbean plate (figure 1).

The Greater Antilles are old islands (Draper *et al.* 1994), with parts of present-day Cuba, Hispaniola and Puerto Rico possibly having remained above water throughout the Tertiary but certainly since the Middle Eocene (Donnelly 1988, 1989; Iturralde-Vinent & MacPhee 1999). Nonetheless, extensive inundation, particularly during the Middle Eocene and Late Oligocene created smaller, isolated landmasses, while stretching driven by the eastward moving Caribbean plate broke land connections and created deep-water channels between the contemporary Greater Antilles (Iturralde-Vinent & MacPhee 1999; Mann *et al.* 2002). Sedimentary marine formations on Jamaica suggest that the island was greatly reduced in area, or perhaps entirely submerged, during the Mid-Tertiary, until *ca* 12 Myr ago. The proto-Greater Antilles moved through the gap between North and South America at the end of the Cretaceous (over 60 Myr ago) and may have temporarily abutted what is now southern Mexico. Jamaica represents a fragment of Central American continental crust (the Chortis Block) later dragged into the Caribbean basin by plate movement. However, ancient terrestrial lineages on Jamaica with connections to North America, revealed by Early Tertiary fossil mammals (Domning *et al.* 1997; Portell *et al.* 2001), were largely or entirely obliterated by Mid-Tertiary inundation.

Throughout their evolution as islands, the Greater Antilles fragmented and rejoined in various combinations such that the present-day islands have complex geographical histories. The geologic relationships between eastern Cuba and northwestern Hispaniola are particularly close, whereas the Tiburón Peninsula of southwestern Hispaniola is a more recent acquisition (Iturralde-Vinent & MacPhee 1999). Although the historical geography of the Greater Antilles is understood in broad outline, geologists remain uncertain about many details.

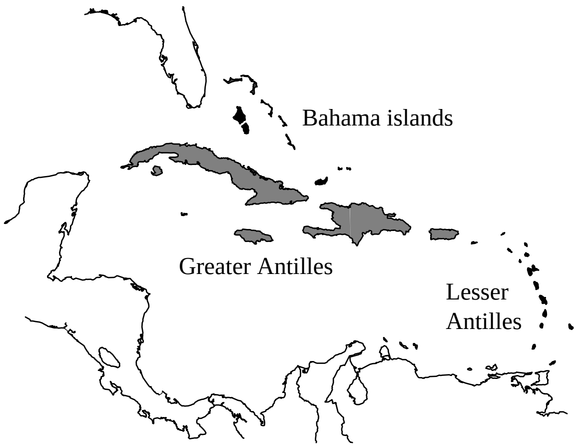

Figure 1. Map of the West Indies indicating the three major regions with different geological histories.

The Bahamas platform, which has held its geographical position relative to North America throughout the Tertiary, is an old and stable geologic feature, unrelated to, and geologically quite different from the rest of the West Indies (Meyerhoff & Hatten 1974; Mullins & Lynts 1977). The platform formed as carbonate marine sediments accumulated in warm seas. Reduced sea levels during Pleistocene glacial periods exposed the banks, and the present day islands were probably formed as wind-blown deposits that now remain above sea level during interglacial times. For the most part, the flora and fauna are recently derived from North America and the Greater Antilles and exhibit little endemism.

Although fragments of Greater Antillean basement rock occur in the northern Lesser Antilles and some volcanic deposits have been dated to the Early Tertiary, the islands of the contemporary Lesser Antilles volcanic arc probably originated less than 20 Myr ago and have been actively forming ever since. Major volcanic eruptions have occurred on Montserrat, Martinique and St Vincent during the past century. Outside the main volcanic arc to the east are several young, low-lying islands consisting of marine sediments uplifted in front of the advancing Caribbean plate capped by recent reef deposits. These islands include the eastern half of Guadeloupe, Antigua, Barbuda and smaller islands to the north, and Barbados to the south. To the west of the Lesser Antilles arc lies the submerged Aves Ridge, which was partly or wholly above water in the Middle Tertiary (Late Eocene–Oligocene), when the eastern edge of the Caribbean plate lay further to the west than at present (Iturralde-Vinent & MacPhee 1999). The Lesser Antilles have never had continental connections and, except for Antigua–Barbuda, St Kitts–Nevis–St Barts and Grenada–Grenadines, which are joined by shallow banks, the islands have not been connected to each other.

The climate of the West Indies is primarily tropical, although the Bahamas and northern parts of the Greater Antilles are affected by frontal weather systems from the north during winter. The higher elevations of mountains in the Greater Antilles (a maximum of 3175 m on Hispaniola) have cooler climates that support in part a relict temperate fauna and flora. Precipitation is moderate throughout much of the West Indies, but heavy at mid elevations on the windward sides of the higher islands and sparse on the leeward sides (e.g. Gleason & Cook 1926; Asprey & Robbins 1953; Kimber 1988; Borhidi 1991). The most prominent feature of the climate of the West Indies is the hurricane season (June through November), during which the islands may be ravaged by violent storms (Tannehill 1969; Caviedes 1991; Wiley & Wunderle 1993). Historically, the climate of the West Indies probably has paralleled that of the lowland neotropics more generally (Graham 2003), with pronounced cooling and dryness associated with glacial periods during the Pleistocene (Curtis *et al.* 2001).

Humans have lived in the West Indies for the past 6000 years (Rouse 1989, 1992; Wilson 1997, 2001), influencing the flora and fauna of the islands through habitat change, hunting and introduction of plant and animal species, often for food (Wing 1989, 2001; Wilkins 2001). The arrival of Europeans in the West Indies at the end of the fifteenth century brought widespread logging, conversion of natural vegetation to agriculture, increased hunting pressure and continuing introduction of exotic plants and animals. Kimber (1988) provides a detailed view of such anthropogenic changes on Martinique. These changes and pressures brought on widespread extinction of many of the larger animals of the West Indian fauna, including all the endemic sloths, most of the endemic rodents, and many parrots and bats (e.g. Olson 1982; Olson & Pregill 1982; Pregill *et al.* 1988, 1991, 1994; Steadman *et al.* 1997; Pregill & Crother 1999; Morgan 2001). The biogeography of the living fauna and flora of the region must therefore be interpreted with caution. Recognizing the high level of endemism in the West Indian biota and the unique value of West Indian native habitats, conservation initiatives have taken a strong hold on many of the islands (e.g. several chapters in Woods 1989*a*; Sergile & Woods 2001).

3. VICARIANCE VERSUS DISPERSAL BIOGEOGRAPHY

A fundamental issue in West Indian biogeography concerns the origins of the fauna and flora of the Greater Antilles. As in the case of oceanic archipelagoes, biologists accept that the Lesser Antilles have been colonized entirely by over-water dispersal. However, the proximity of the proto-Greater Antilles to North and Central America raises the possibility of overland dispersal to the islands and subsequent isolation of a relict fauna and flora due to plate movements. Prior to the general acceptance of continental drift in the 1970s, overland dispersal to islands required land bridges, now submerged, in the distant past (Wallace 1876; Darlington 1957). Overland dispersal and subsequent vicariance—or separation of biotas—resulting from continental drift was first argued by Rosen (1976, 1978, 1985) for freshwater fish and other land-locked organisms (Chakrabarty 2006; Echelle *et al.* 2006). This idea was strongly defended by Guyer & Savage (1985) and Crother & Guyer (1996), among others, for such land-bound taxa as lizards and snakes and terrestrial

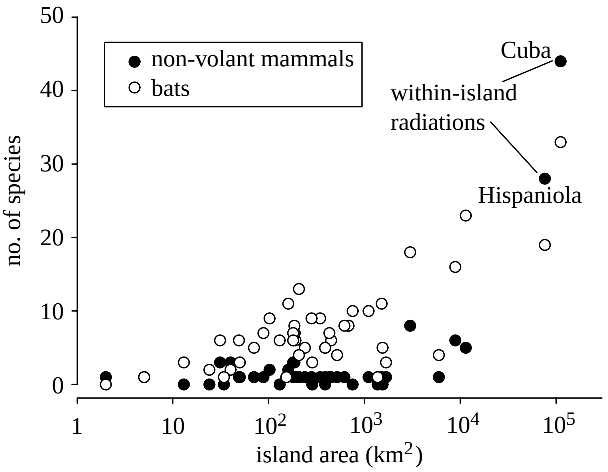

Figure 2. Species–area relationship for mammals, distinguishing between flying and non-flying mammals to show the effects of not only dispersal ability, but also adaptive radiation on the islands of Cuba and Hispaniola following colonization by individual lineages. Data are from Woods (1989*b*, table 5).

mammals (Davalos 2004). The resolution of the vicariance and dispersalist views for most Greater Antillean groups depended, in large part, on the timing of colonization. If this were close to the beginning of the Tertiary, a land route to the proto-Greater Antilles might have been possible through what is now southern Mexico. This scenario almost certainly explains the presence of a rhinoceratoid ungulate on Jamaica in the Eocene, after the island broke its continental connection (Domning *et al.* 1997). If colonization occurred later, the biota would have had to cross a widening water gap. Unfortunately, fossils of terrestrial organisms in the West Indies are rare and mostly limited to more recent formations, including the famous Miocene ambers of Hispaniola (Wilson 1985; Iturralde-Vinent & MacPhee 1996; MacPhee & Grimaldi 1996; but see MacPhee 2005).

In an early attempt to assess the timing of dispersal events, Hedges *et al.* (1992) used calibrated immunological distances between island forms and their mainland relatives to estimate the ages of island taxa (Hedges 1996*a–c*, 2001). Immunological distance between two taxa is based on the cross-reaction between antibodies formed in response to antigens from one taxon and the other (Maxson & Maxson 1986). The more similar the protein sequences, presumably reflecting the relationship between the taxa, the stronger the reaction. Immunological distance can be calibrated using taxa with divergence times known from fossil evidence (van Tuinen *et al.* 2000; van Tuinen & Hedges 2001).

Hedges' results suggested that most colonization times of reptile and amphibian lineages in the Greater Antilles were too recent to allow for overland dispersal from what is now southern Mexico, followed by vicariant isolation. The islands clearly are older than most of their inhabitants. However, Iturralde-Vinent & MacPhee (1999) postulated a more recent continuous land connection (GAARlandia, (GAAR from Greater Antilles–Aves Ridge)), dating to *ca* 33–35 Myr, between northern South America and the Greater Antilles, by the way of the Aves Ridge. This feature, which now lies deeply submerged, was at least partly exposed during the Early Oligocene (Holcombe & Edgar 1990); whether it provided a suitable avenue for dispersal for non-flying vertebrates to the Greater Antilles cannot be ascertained. If the Aves Ridge did open the door to colonization, no resulting concentration of colonization times *ca* 34 Myr ago is evident in the immunological distances for endemic lineages of reptiles and amphibians in the West Indies (Hedges 2001), although some animals and plants might have taken advantage of the connection. The absence of many types of terrestrial mammals, including ungulates and carnivores (Davalos 2004), in the West Indies also argues against a significant land bridge connection.

For non-flying animals, the primary alternative to overland dispersal is to raft on floating debris discharged by the outflow of continental rivers. Before the Mid-Oligocene, *ca* 25 Myr, the Amazon Basin drained to the north into the Caribbean Sea in what is now western Venezuela (Vonhof *et al.* 1998, 2003), still ahead (to the east) of the advancing Caribbean plate. At present, the Orinoco River flows into the Atlantic Ocean east of the Lesser Antilles and rafts of material can be carried westward by ocean currents. Rafting is a haphazard means of colonization and, as one would expect, non-flying mammals exhibit far fewer colonization events than bats (figure 2). Most islands, including Jamaica and Puerto Rico, have fewer than five lineages of non-volant mammals. The large numbers of mammal species on Cuba and Hispaniola (most of which are now extinct) represent radiations of a small number of rodent and insectivore lineages (Woods 1989*b*).

Over-water dispersal to the West Indies is a substantial barrier even for many groups of flying animals and wind-dispersed plants. The depauperate avifauna of the West Indies compared to surrounding tropical continental localities undoubtedly reflects dispersal limitation (Ricklefs & Bermingham 2001), although the role of extinction is poorly known (see below). Regardless, over-water dispersal also acts as a selective filter, preventing the colonization of groups of birds with weak flight or little inclination to venture beyond forest borders, as in the case of most tropical suboscine passerines and woodpeckers, which are underrepresented in the Greater and Lesser Antilles (Ricklefs & Cox 1972; Terborgh 1973; Lack 1976; Terborgh *et al.* 1978).

Details of colonization and spread through an archipelago are not well understood, but several inferences can be made from observations on contemporary distributions. Several species of land birds, including the shiny cowbird (*Molothrus bonairiensis*) and the bare-eyed thrush (*Turdus nudigenis*), have colonized the Lesser Antilles from South America during the past century, and their progress suggests rapid stepping-stone dispersal at intervals of a few decades following population build-up on each island (Bond 1956). Recent colonists among birds, identified by the absence of genetic differentiation between island populations, also tend to be widely distributed, without gaps between island populations (Ricklefs & Bermingham 1999, 2004*b*). However, the penetration

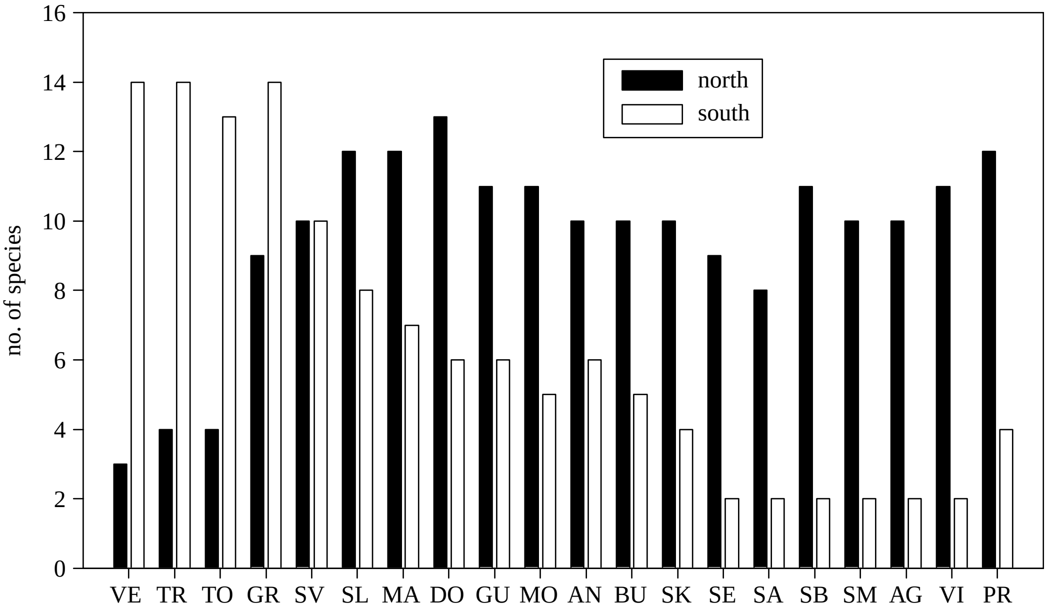

Figure 3. Number of recent colonists (judged by lack of genetic differentiation among island populations) among non-raptorial land birds on islands in the Lesser Antilles (Grenada [GR] in the south to Anguilla [AG] in the north). Colonists are distinguished by origin from the Greater Antilles (Puerto Rico [PR]) in the north and northern South America (Venezuela [VE], Trinidad [TR], Tobago [TO]) in the south (Ricklefs & Bermingham submitted).

of colonists through the Lesser Antilles depends on whether their source was to the north, from the Greater Antilles, or to the south from northern South America, although all the three regions harbour a similar range of habitats (Cox & Ricklefs 1977). Colonists from the Greater Antilles tend to spread through the entire archipelago, although few cross into continental South America; colonists from the south tend to stop short within the island chain (figure 3). Why colonists from the north and south exhibit different success in spreading through the islands is not understood. This difference might be related to prior selection for colonizing ability among species that have reached the Greater Antilles, or to selection of species with strong dispersal abilities that must cross the broad Anegada Gap separating the Greater and Lesser Antilles against prevailing winds.

One case of an apparently undifferentiated species with a broad disjunction involves the red-legged thrush, which is widely distributed in the Greater Antilles, but present only on Dominica, 600 km away in the Lesser Antilles, and absent from many intervening islands with suitable habitat. Mitochondrial gene sequences reveal that whereas island populations in the Greater Antilles are clearly differentiated, the Dominican birds have haplotypes identical to the population on Puerto Rico (Ricklefs & Bermingham submitted). This suggests that West Indian natives or early Europeans might have brought the thrush, which is an attractive songbird, to the island. Humans have played a major role in distributing species around the globe (Long 1981; Duncan 1997) and the West Indies have not escaped this activity (Raffaele *et al.* 1998). For most native species with strong dispersal powers, however, colonization appears to be relatively deterministic in that islands are not passed by in haphazard fashion. As a result, gaps in the distribution of such species indicate extirpation of island populations, providing a window on the elusive process of extinction, as we shall show below. In the case of species that depend on passive dispersal, we expect colonization to be more haphazard and patterns of distribution to be less consistent. Nevertheless, such animals as anoles are found on virtually every island in the West Indies, regardless of size or isolation (Schwartz & Henderson 1991; Roughgarden 1995), and so opportunities for rafting between islands must be relatively frequent (Glor *et al.* 2005).

4. SPECIES–AREA RELATIONSHIPS WITHIN ISLAND GROUPS

One of the primary empirical patterns of island biogeography is the species–area relationship (Lomolino 2000). In their classic treatise on island biogeography, MacArthur & Wilson (1967, fig. 2; p. 8) used the number of species of reptiles and amphibians on islands in the West Indies as an example of the relationship, which they characterized as representing a dynamic balance between colonization and extinction. The slope (z) of the relationship between the logarithm of species richness and that of area has been given particular significance in many analyses (e.g. May 1975; Connor & McCoy 1979), but in fact provides relatively little information about the processes responsible for diversity patterns. MacArthur & Wilson (1967) emphasized the relationship between extinction rate and island area, arguing that larger populations were less vulnerable to extinction from random factors. In contrast, from his ecological studies of the avifauna of Jamaica and other West Indian islands, David Lack (1976) argued that smaller islands had less ecological diversity and therefore could support fewer species. Lack believed that extinction had little to do with the species–area relationship, islands being ecologically saturated with species. MacArthur & Wilson (1967) held that the diversity of an island of any given size was

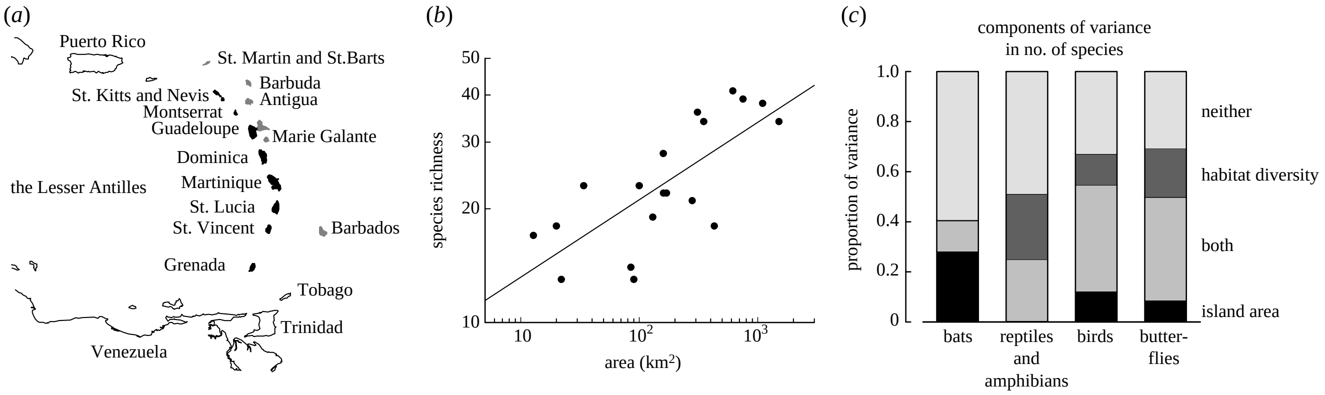

Figure 4. Species–area relationships in the Lesser Antilles. (*a*) High (black) and low (grey) islands, which have high and low habitat diversity, are distinguished in the map. (*b*) Species richness of birds as a function of island area shows a species–area (log–log) relationship with a slope of 0.21 ± 0.05 ($r^2 = 0.55$). (*c*) The bar diagram shows the proportion of the total variance in species richness among islands that is statistically associated with island area, habitat diversity, correlated variation in both variables and unexplained by either. Factors in addition to area and habitat diversity, including distance to sources of colonization (Ricklefs & Bermingham 2004*b*) clearly influence the diversity on islands. From Ricklefs & Lovette (1999).

colonization limited and that the number of species at the steady state depended on the replacement of extinct species by new ones from continental sources of colonization. Because this debate concerns historical processes that cannot be observed directly, the controversy remains largely unresolved (Ricklefs & Bermingham 2004*b*).

Lack's idea predicts that diversity should be directly related to the diversity of ecological opportunities on islands. Ricklefs & Lovette (1999) addressed this prediction statistically by comparing species richness of several groups of organisms in the Lesser Antilles to island area and habitat diversity simultaneously. Variation in area and habitat diversity is sufficiently uncoupled that the effects of each can be identified statistically. As shown in figure 4, the species richness of bats, which exhibit little habitat specialization, was sensitive primarily to island area, whereas that of reptiles and amphibians, which partition habitats more finely, was influenced uniquely only by habitat diversity. Birds and butterflies were sensitive to both. These analyses provide support for both Lack and for MacArthur & Wilson (1967), but they also emphasize the importance of ecological distributions of species among habitats within islands to larger-scale patterns of species richness.

Island area is directly related to changes in the species richness and the proportion of endemic species (e.g. figure 5). These patterns are the outcome of processes that vary with island size: colonization; extinction (influencing turnover and age of populations; Cadena *et al.* 2005); rates of morphological change (diversification); and species formation. Diversification contributes to endemism because new forms traditionally have been recognized and named according to their morphological distinctiveness (e.g. Filardi & Moyle 2005). Diversification also underlies the evolution of new species on islands because it generates the traits that individuals use to recognize members of their own populations and avoid breeding with others (Grant & Grant 1998, 2002; Coyne & Orr 2004). Thus, while the number of species on an island is influenced by colonization and extinction, it can also increase by the production of new species, giving diversity an additional historical and evolutionary dimension.

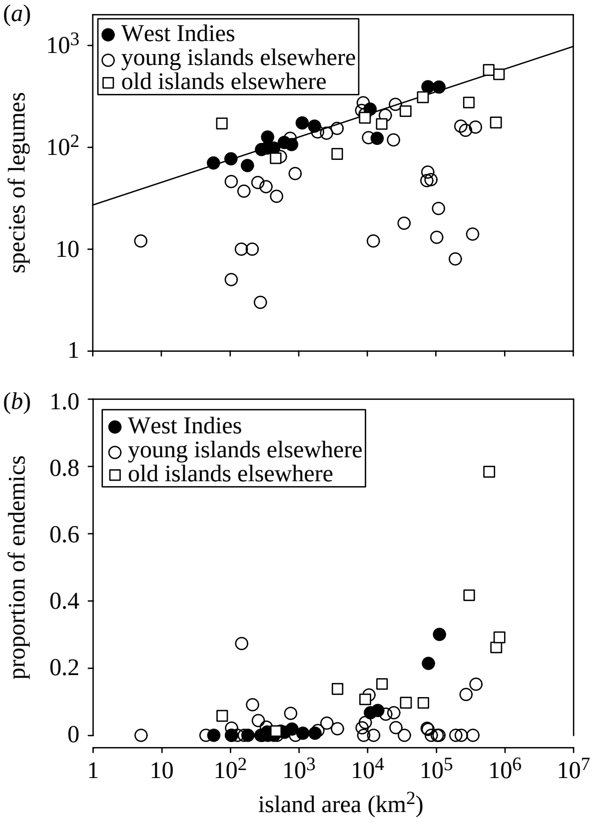

Figure 5. (*a*) Species–area relationships of legumes (Fabaceae) on islands throughout the world. Diversity is the highest in older islands that have had time to accumulate lineages through colonization and to add species through within-island or within-archipelago diversification. (*b*) Larger and older islands also have higher proportions of endemics partly because evolutionary lineages are older. Data from Lavin *et al.* (2001).

For *Anolis* lizards in the West Indies, the Greater Antillean islands of Cuba, Hispaniola, Puerto Rico and Jamaica are large enough to have supported repeated cycles of species formation, whereas islands smaller than 3000 km^2 are not. Although the mechanisms of speciation are not understood in this group, phylogenetic analysis of *Anolis* within the Greater Antilles shows that most species are more closely related to other species on the same island than they are to species on other islands (Losos *et al.* 1998), implicating local species production as the key process. Based on a phylogenetic reconstruction of West Indian species, Losos & Schluter (2000) showed that extinction on the larger islands is negligible and that speciation rate increases with island area, with the estimated exponential rate of diversification increasing with a slope of 0.76 ± 0.09 relative to the logarithm of island area.

On large islands, populations of organisms like *Anolis* lizards might become isolated by local topography, being separated by mountains, valleys, areas of unsuitable habitat, and so on. In this case, the absence of gene flow between populations would allow them to evolve independently and perhaps diverge enough that they failed to interbreed when coming into secondary contact. This is the conventional mechanism of allopatric speciation. Recently, evolutionary biologists have become interested in a variety of mechanisms that can result in the formation of new species without the separation of populations (Howard & Berlocher 1998; Dieckmann & Doebeli 1999; Doebeli & Dieckmann 2000). Sympatric or parapatric speciation can occur when individuals adapt to local variation in the environment—e.g. different host plants or habitat characteristics—and develop preferences to mate with individuals sharing these adaptations (Gray & Cade 2000; Pfenninger *et al.* 2003). Adaptation followed by mate choice sets up a regime of disruptive selection that can partition populations into independently evolving units, which eventually might develop species-level distinction (Schneider *et al.* 1999; Gavrilets *et al.* 2000; Gavrilets & Waxman 2002; Gavrilets 2006).

Studies of the anoles of the Lesser Antilles, which harbour only one or two species per island in spite of a broad range of habitats, provide a closer look at the process of adaptive or ecological speciation. Islands as small as 1 km^2 in the Greater Antilles support as many as four species of anole, and so ecological opportunity within the Lesser Antilles is not limiting. Populations of *Anolis oculatus* on Dominica and Martinique exhibit considerable ecotypic differentiation on small spatial scales combined with strong mating preferences and reduced gene flow across ecotype boundaries (Malhotra & Thorpe 1997, 2000; Thorpe & Stenson 2003), although the extent of morphological differentiation within *A. oculatus* does not approach the variation among species in the Greater Antilles (Knox *et al.* 2001). Locations of ecotypic boundaries also do not coincide with genetic boundaries associated with older lineages of the species within Dominica across which the gene flow occurs relatively freely (Thorpe & Malhotra 1996). Thus, strong selection following spatial variation in the environment clearly is a powerful force for differentiation in the face of gene flow (Thorpe *et al.* 2005) and is associated with strong mating preferences and disruption of gene flow in the case of *A. oculatus*. These are the initial steps for ecological speciation, yet on none of the islands of the Lesser Antilles has this process led to a build-up of species through within-island species formation.

The failure of small islands to sustain species diversification in *Anolis* lizards (Losos & Schluter 2000) might be a function of island size itself. Specifically, ecological gradients across which ecotypes differentiate must be persistent enough to allow time for species-level differences to accumulate between different portions of a population. Islands in the Lesser Antilles are undoubtedly dynamic, the distribution of habitats shifting with patterns of climate change through the Pleistocene or localized areas of ecotypic differentiation being obliterated by volcanic eruptions and lava flows. Larger islands are, to a greater degree, buffered against such changes owing to their greater area of particular habitats. Additional insight into the role of island area in promoting ecological speciation is provided by a recent simulation study by Gavrilets & Vose (2005). These authors recreated the ecological speciation process in computer landscapes of different size, habitat complexity and with different levels of genetic variation for ecological adaptation and mating preferences. One of the striking results of these simulations was the influence of area on the formation of new species. Gavrilets & Vose (2005) argued that larger area creates isolation of individual habitat patches by distance, reducing the immigration of individuals with genes adapted to alternative habitats, thereby allowing local adaptation—the initial stage of ecological speciation—to proceed more rapidly. It makes sense that larger islands have larger and temporally more stable patches of each type of habitat. Even on continental scales, the area of a region appears to have a major influence on the rate of species formation (Ricklefs 2006).

Ecological and phylogenetic studies of island biotas are beginning to reveal the processes that influence the diversity of island faunas and floras. The assemblage of biotas by colonization and local speciation manifests itself in ecological and evolutionary changes, including ecological compression (specialization) and release, that is, changes in habitat breadth and niche space use within habitats, as well as ecological shifts and morphological diversification. These processes are apparent in the major adaptive radiations that have taken place within the West Indies.

5. ADAPTIVE RADIATION (*ANOLIS* AND OTHER GROUPS)

Adaptive radiation refers to the process by which a lineage rapidly diversifies upon entering a new area or ‘adaptive zone’ to fill ecological space (Givnish & Sytsma 1997; Schluter 2000). It is most prominent on islands that initially present underused habitats with potentially exploitable resources (Chiba 2004; Davison & Chiba 2006). The first colonists face no competition from residents and can spread through a wide variety of habitats and exploit many different kinds of food. This favours ecotypic differentiation and may lead to sympatric or parapatric speciation on large islands or allopatric speciation on large islands and within archipelagoes (Shaw 1996, 2002;

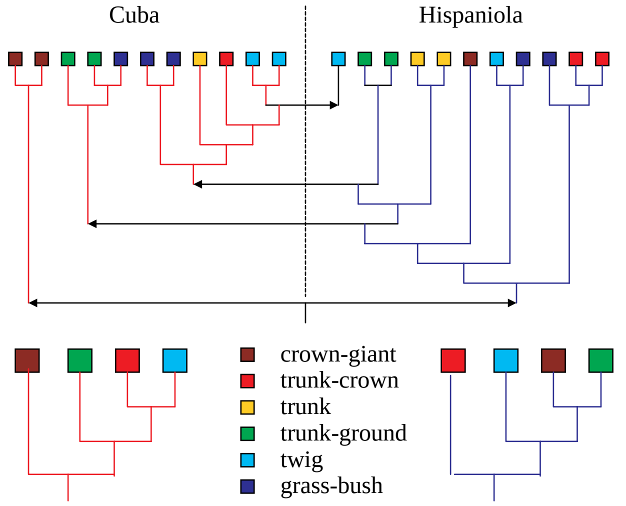

Figure 6. Simplified phylogenetic trees for several Cuban and Hispaniolan radiations of *Anolis* lizards with repeated production of same ecological and morphological types. The black arrows indicate inferred colonization events. The partial diagrams extracted at below left (Cuba) and right (Hispaniola) show that although each island now has the same array of ecological types, the sequence of their evolutionary origins differs. Adapted from Losos *et al.* (1998). Note that this figure is extracted from a larger phylogenetic tree and that the Cuban and Hispaniolan anoles are not monophyletic with respect to the other islands in the Greater Antilles.

Mendelson *et al.* 2004; Gillespie 2005; Parent & Crespi 2006). Adaptive radiation is an important cause of diversification in some groups of organisms in most archipelagoes, and the West Indies are no exception. Cuba and Hispaniola are sufficiently large and topographically heterogeneous to support species formation within islands, as has happened in the case of *Anolis* (Williams 1976; Hass *et al.* 1993; Losos & Schluter 2000; Glor *et al.* 2003, 2004) and *Leiocephalus* (Hedges *et al.* 1992; Pregill 1992; Hass *et al.* 2001) iguanid lizards, *Sphaerodactylus* geckos (Hass 1991), *Eleutherodactylus* frogs (Hass & Hedges 1991), capromyid rodents (Woods 1989*b*) and *Lyonia* (Ericaceae) trees and shrubs (Judd 2001). The anole radiations have been analysed in detail and reveal repeated and independent diversification of ancestral lineages into a series of parallel ecological types (Rand & Williams 1969; Williams 1972) on each of the major Greater Antillean islands (Losos *et al.* 1998; Glor *et al.* 2003; figure 6). Thus, the adaptive radiation appears to be ecologically deterministic when conditions promote the differentiation of geographically or ecologically isolated lineages to the level of species.

Although the Lesser Antilles have a similar geographical configuration to the Hawaiian and Galapagos archipelagoes, they have not produced spectacular adaptive radiations of birds, such as the Darwin's finches or Hawaiian honeycreepers (Pratt 1979; Grant 1986; Grant & Grant 2002; Lovette *et al.* 2002). It is possible that the relatively high colonization rates to these close islands fill the available ecological space rapidly and impede diversification of any one endemic lineage. It may be relevant that the one small radiation of four endemic thrashers (Mimidae) in the Lesser Antilles originated from one of the first lineages to colonize the Lesser Antilles. Thus, this radiation might have occurred before many other birds had colonized the islands (Hunt *et al.* 2001). In general, it would appear that the necessary ingredients for adaptive radiation are unoccupied ecological space to facilitate divergence, sufficient distance between islands or isolated areas within islands to allow genetic divergence in allopatry, and sufficient movement of individuals between areas to recolonize ancestral areas and build diversity in sympatry (Saenger *et al.* 1983; Givnish & Sytsma 1997; Givnish 1999; Schluter 2000; Grant & Grant 2002). Thus, the dispersal abilities of organisms must be 'tuned' to distances within an island or archipelago to provide the right conditions for adaptive radiation.

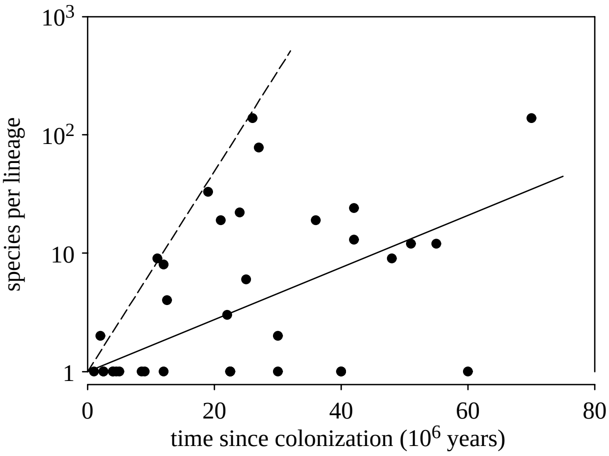

Figure 7. Relationship between species richness (S) within the West Indies and age of taxon for endemic reptiles and amphibians. The slope of the regression of ln S with respect to time, passing through the origin (time = 0, species = 1), is the average exponential rate of diversification of the lineages. This has a value of 0.051 (±0.007) per million years ($F_{1,36}=41.7$, $P<0.0001$, $R^2=0.537$) or a lineage splitting event (assuming no extinction) every 20 Myr. The dashed line, representing the upper limit for the data, represents a diversification rate of 0.17 per million years, or a splitting event every 6 Myr. Data from Hedges (1996*b*).

Adaptive radiation takes time and one would expect that diversity within lineages in an island group would increase as a function of time since colonization, at least until a radiation has filled the available ecological space. This can be tested for reptiles and amphibians within the West Indies (figure 7), among which number of species increases significantly with age of lineage. The relationship has considerable scatter, which is to be expected of an essentially random, haphazard process such as the splitting of lineages within an archipelago (Nee *et al.* 1992, 1994; Harvey *et al.* 1994; Ricklefs 2003). For a completely random process with each lineage having an equal probability of splitting per time-interval, the logarithm of species richness increases linearly with time. Furthermore, the number of species at any given time should be geometrically distributed with the standard deviation in the number of species approximately equal to the mean (S). However, when we normalized lineage diversity (S) in figure 7 by the predicted value from the log species–time regression,

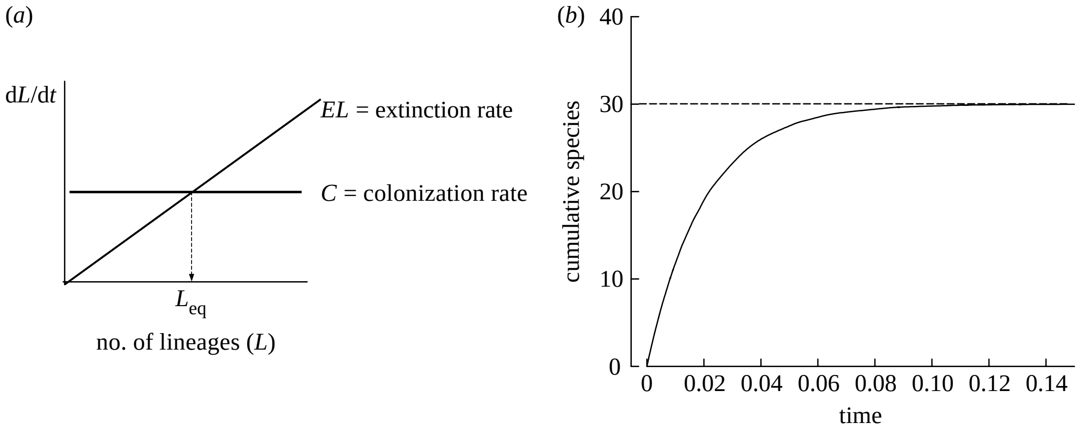

Figure 8. (*a*) A simple model of diversity dynamics within the West Indies with uniform colonization, which is independent of the number of species within the archipelago, and a constant probability of extinction per species. (*b*) Over time, looking either forward or backward from the present, the cumulative number of species approaches an equilibrium value exponentially ($C=1500$, $E=50$; $C/E=30$). After Ricklefs & Bermingham (2001).

the standard deviation of the normalized values was 6.9 times the mean rather than the value of 1.0 expected of a homogeneous stochastic process. Clearly, endemic lineages have not experienced similar rates of diversification in the Greater Antilles; the difference between the most and the least diverse lineages evidently reflects particular characteristics of the lineages that have reached the islands related to their ability to diversify within the larger islands and, to a lesser extent, allopatrically within the archipelago.

6. COLONIZATION–EXTINCTION DYNAMICS

From the ages of colonization events, one can describe the dynamics of colonization and extinction for an island within the framework of the MacArthur & Wilson (1967) equilibrium model. According to this model, once equilibrium is established, rates of colonization and extinction are equal and the distribution of colonization times assumes an exponential form with the exponential decay rate equal to the rate of extinction. Thus, the cumulative distribution of colonization times exponentially approaches the equilibrium number of lineages on an island, not including subsequent endemic diversification (figure 8). We define C as the rate of colonization in lineages per million years and E as the rate of extinction whose units are the proportion of island lineages (L) per million years. Thus, the number of lineages going extinct each million years is $E\times L$. When C and E remain constant for long periods, the cumulative distribution of lineages with respect to island age (x) is $L(x)=(C/E)(1-\exp[-Ex])$, and the equilibrium number of lineages $L(\infty)$ is equal to C/E. This equation also applies retrospectively to the ages of extant lineages on an island. That is, the cumulative number of lineages with progressively older ages of colonization (t) increases as $L(t)=(C/E)(1-\exp[-Et])$ (Ricklefs & Bermingham 2001).

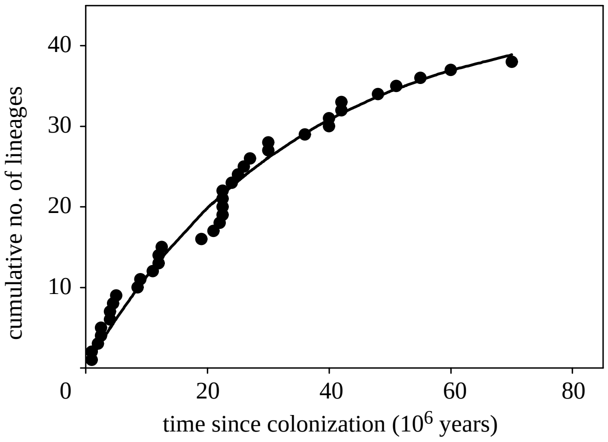

Figure 9. The colonization–extinction model fitted to Hedges' (1996*b*) data for the colonization times of reptiles and amphibians in the West Indies, revealing very low rates of both colonization and extinction. The fitted values are $C=1.31\pm0.05$ per million year, $E=0.029\pm0.002$ per million year and $C/E=45.2$ lineages.

We fitted this curve to immunological distances determined by Hedges (1996*b*) for endemic reptiles and amphibians in figure 9. In this analysis, the entire West Indian archipelago—primarily the Greater Antilles—is considered as a single island and only colonizations from the continent are considered. The fitted coefficients are $C=1.31\pm0.05$ events per million years, and $E=0.029\pm0.002$ per species per million years. Non-endemic species were not included in Hedges' table, but these presumably are relatively young and they would increase the apparent rate of colonization. The equilibrium number of endemic lineages in the Greater Antilles is $C/E=45.2$, which is somewhat greater than the observed number of endemic lineages whose colonization times were estimated. This analysis shows, first, that colonization and extinction appear to have been approximately homogeneous over the long stretch of the Tertiary period, with possible surges of colonization at *ca* 25 Myr ago and between 0 and 5 Myr ago. Overall, an exponential approach to an equilibrium faunal size fits the data well. Second, rates of colonization are extremely low—approximately one lineage each 750 000 years to the Greater Antilles as a whole—and rates of extinction are so low that the average persistence time of an individual lineage in the Greater Antilles (not necessarily an individual species or island population) is expected to be $1/0.029=34.5$ Myr! Because the number of lineages lies below the projected equilibrium, colonization and extinction evidently have not yet come into balance. Nonetheless, the data emphasize the remarkably slow dynamics of the system and bring colonization by such implausible mechanisms as rafting into the realm of possibility.

Ricklefs & Bermingham (2004*a*, figure 5) applied a similar analysis to 22 lineages of land and freshwater birds of the Hawaiian Archipelago, obtaining values of $C=388\pm29$ colonization events and an extinction rate of 15.1 ± 2.4 per unit of mtDNA sequence divergence. Assuming a 2% sequence divergence per million years (Lovette 2004), these rates are $C=7.8\pm0.6$ and $M=0.30\pm0.05$ per million years. The expected equilibrium number of lineages would be 25.7, which is only slightly higher than the current level, and the expected lifetime of a lineage in the archipelago would be 3.3 Myr. It should be noted, however, that the accumulation of lineages having a genetic distance greater than 1.0% sequence divergence showed no evidence, based on the expected curvature of the lineage–time relationship, of lineage extinction (quadratic term, $F_{1,15}=1.9$, $p=0.19$; linear slope 162 ± 7 per unit mtDNA sequence divergence, or 3.2 per million years).

Ricklefs & Bermingham (2001) applied the same analytical approach to colonization times of lineages of birds in the Lesser Antilles. They used the divergence of sequences of the mitochondrial ATPase 6 and 8 genes between island and continental source populations to estimate colonization times. Their sample of 39 colonization events included two-thirds of the small land birds of the Lesser Antilles, and most of the species in the order Passeriformes (song birds). The analysis yielded several surprising results. First, the lineage accumulation curve exhibited a distinct kink that was statistically incompatible with an exponential approach to an equilibrium number of lineages (figure 10). Thus, conditions affecting colonization, extinction, or both, apparently have not been homogeneous over the approximately 10 Myr history of the contemporary small land bird fauna of the Lesser Antilles. The kink in the lineage accumulation curve occurred at a genetic distance of approximately 1–2% nucleotide substitutions, which standard calibrations put at *ca* 0.5–1.5 Myr ago, that is, within the Pleistocene epoch.

Second, the linear relation between lineage accumulation and time over most of the curve suggests little or no extinction of lineages within the Lesser Antillean archipelago as a whole, as in the case with Hawaiian birds. Thus, although individual island populations might vanish, each lineage appears to persist by recolonizing islands from which it has gone extinct. Colonization within an archipelago appears to be an ongoing aspect of the dynamics of lineages. This is further emphasized by genetic relationships between island populations showing more recent derivation than the original colonization event from the continental or Greater Antillean source area (Ricklefs & Bermingham 2001). Because lineage extinction appears to be rare, the maximum colonization times of *ca* 7–10 Myr ago may represent the first colonists of the Lesser Antilles and indicate the time that these islands first became suitable for avian populations. Unfortunately, birds have no significant fossil record in the West Indies older than the Holocene and so we are unlikely to uncover direct evidence bearing on the history of this group.

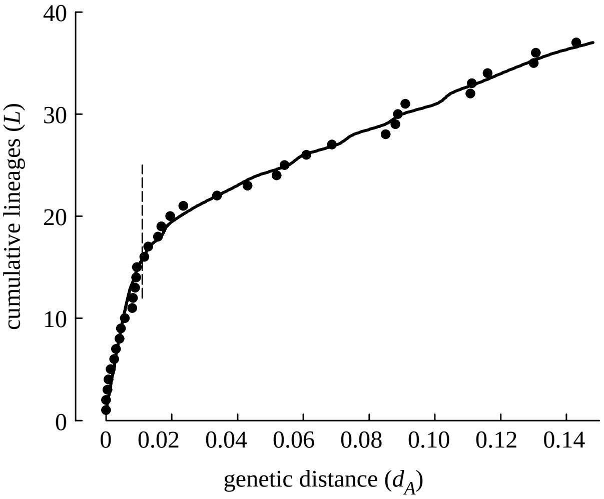

Figure 10. The cumulative number of lineages as a function of increasing genetic distance (d_A) in the terrestrial avifauna of the Lesser Antilles (Ricklefs & Bermingham 2001). Genetic distances are based on divergence in the mitochondrial ATPase 6 and 8 gene regions between lineages in the Lesser Antilles and their closest relatives in northern South America or the Greater Antilles. Assuming a molecular clock, genetic distance parallels time. The straight-line relationship between cumulative lineages and genetic distance for $d_A>0.02$ indicates that the archipelago-wide rate of extinction is close to zero, assuming a constant rate of colonization. The solid line represents a stochastic nucleotide substitution model with 13-fold increase in colonization rate or 92.3% mass extinction at $d_A=0.011$ (dashed line); no background extinction.

Although the mass extinction model is compelling, Cherry *et al.* (2002) pointed out that the data also could be fitted by a speciation-threshold model (Johnson *et al.* 2000) in which continuing migration between the continental source and the island population would prevent genetic divergence regardless of the 'age' of the species in the islands. Once a speciation threshold of genetic difference had been achieved, the gene pools of the source and the immigrant populations would evolve independently and diverge at a more rapid rate. This would result in the observed heterogeneous lineage accumulation curve. The speciation-threshold and mass extinction models are difficult to distinguish because the unique predictions of each regarding the intra-genomic distribution of genetic divergence cannot easily be tested with the genetic markers currently available. Moreover, parameter estimates for migration rates and the genetic speciation threshold for Lesser Antillean birds are reasonable, given what we know about these processes (Ricklefs & Bermingham 2004*a*).

When migration is continuous over long periods, and the number of migrants per generation is small when compared with the population size on each island, then new alleles coming from the colonization source are fixed in the island populations at random with low probability. Thus at a particular gene locus—e.g. the mitochondrial haplotype—one would expect to see alleles having varied divergence times

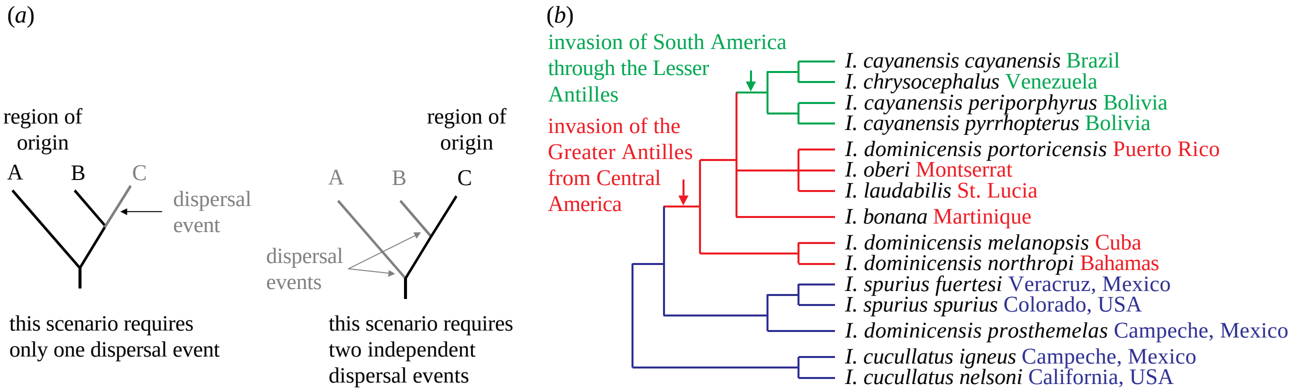

Figure 11. (*a*) The phylogenetic nestedness of island and continental lineages indicate the most parsimonious reconstruction of the direction of colonization. (*b*) The relationships among continental and West Indian orioles of the genus *Icterus* suggest that the *I. cayanensis*–*I. chrysocephalus* clade of South America originated from the Lesser Antilles. Based on Omland *et al.* (1999).

when compared with the source population, with divergence times tending to increase geographically away from the source area. What one finds frequently among Lesser Antillean birds, however, is genetic homogeneity among some or all islands, but unordered with respect to the mainland source population (Ricklefs & Bermingham 2001). This molecular phylogenetic evidence of brief phases of dispersal among islands in the past suggests that migration between islands is episodic rather than continuous and that the speciation-threshold model is not generally applicable.

Another alternative explanation is that recent colonists to islands tend to be poorly adapted to local conditions and that young populations have high extinction rates leading to rapid turnover of species, what Gavrilets & Vose (2005) distinguish as short-term establishment and long-term establishment. In this model, the essential threshold is the adaptation to the local environment, and once this threshold is crossed, a population would have a low probability of extinction. If this were true, however, recent colonists should exhibit lower population sizes and narrower habitat distributions than species with long tenure on an island. In fact, the reverse is the case. Low genetic differentiation from the source population is often associated with high population size and broad habitat distribution (Ricklefs & Cox 1978; Ricklefs & Bermingham 1999).

7. MUSEUM OR CRADLE OF DIVERSITY?

Regardless of the amount of diversification of species within islands or archipelagoes, islands are generally regarded as biological museums from which endemics do not escape (Carlquist 1974). While this has almost certainly been the case for remote archipelagoes such as the Galápagos and Hawaiian islands, some groups or organisms within the West Indies exhibit a more balanced interaction between continental and island faunas, with colonization events going in both directions. Many taxa have dispersed across remote stretches of Micronesia in the Pacific Ocean (Garb & Gillespie 2006), showing remarkable dispersal ability from small islands, and a clade of Australasian monarch flycatchers might have been derived from islands in Polynesia (Filardi & Moyle 2005).

The evidence for historical colonization of one region from another, which cannot be observed directly, lies in the logic of nestedness in phylogenetic reconstructions. When a population that occurs in one region is nested within lineages that occur in another, the most parsimonious explanation for the direction of colonization is from the region having the ancestral branches (figure 11). For example, the *Icterus cayanensis* and *I. chrysocephalus* lineages of orioles in northern South America are nested within a clade of West Indian orioles, which themselves are derived from North and Central American lineages (Omland *et al.* 1999; figure 11). One can imagine the Central American *Icterus dominicensis* spreading through the Greater Antilles and Lesser Antilles into South America almost 4 Myr ago, where the colonists spread and diversified. Most island populations of orioles in the Lesser Antilles have since disappeared, leaving disjunct species on Montserrat, Martinique and St Lucia (Lovette *et al.* 1999).

Similar evidence of colonization from the West Indies to the mainland of South America has surfaced for the *Norops* clade of *Anolis* (Nicholson *et al.* 2005), bananaquits *Coereba flaveola* (Seutin *et al.* 1994; Burns *et al.* 2002) and *Amazona* parrots (Russello & Amato 2004*a*) among others. The fact that several of these 'reverse' colonization events have been identified by phylogeographic reconstruction within the relatively depauperate Lesser Antillean avifauna, together with the long persistence times of lineages within archipelagoes, suggests that island groups such as the West Indies might be significant sources of diversity for continental regions among groups, such as birds, that have relatively high colonization rates. The West Indies also might have been a dispersal route for some groups between North/Central America and South America before the completion of the Panamanian Isthmus some 3–3.5 Myr ago (Coates 1996).

8. ECOLOGICAL CHANGES IN SPECIES OVER TIME

The dynamics of species within the West Indies include changes in ecological distribution as well as geographical range. Colonization is often followed by habitat expansion or shifts into ecological space occupied on continents by species that are poor colonists. As Wilson (1959, 1961) pointed out for ants in Melanesia, most colonists disperse through lowland marginal habitats and then extend their distributions into forested and montane habitats on progressively more remote islands. Most birds that have entered the West Indies through such marginal habitats, as well as inner forest and montane species, tend to be poor colonists. Ricklefs & Bermingham (1999) showed, however, that older taxa in the West Indies have extended their ecological distributions into these habitats over time, filling niches that would otherwise have been left empty. Many of the oldest inhabitants are restricted to such habitats and their distributions and populations may continue to decrease to extinction when the pressure of competition from new colonists is strong enough. This tendency from initial colonization towards extinction was called the 'taxon cycle' by Wilson, and was described in detail for West Indian birds by Ricklefs & Cox (1972, 1978) and Cox & Ricklefs (1977; for arthropods, see Gillespie & Roderick 2002). The temporal pattern inferred from morphological (taxonomic) distinctions and gaps in the distributions of species late in the taxon cycle was later confirmed by molecular phylogenetic studies by Ricklefs & Bermingham (1999, 2002).

Proliferation of species within islands or archipelagoes from a single ancestor leads to diversification and specialization driven by interspecific competition, either with respect to habitat or ecological position within habitats. This is particularly evident in *Anolis* lizards. Detailed ecological studies have identified a half dozen basic ecological types, including ground dwelling species, trunk anoles, crown anoles of different sizes, and grass and twig anoles, each one of which has specialized morphology to match its preferred substrate for foraging (Williams 1972; Roughgarden 1995; Losos 1996; Losos *et al.* 1998). The reiterated ecological diversification of *Anolis* on several islands (Losos *et al.* 1998) and the systematic shift of birds from coastal open habitats to forested and montane habitats (Ricklefs & Cox 1978) suggest determinism in the evolution of island biotas. However, even though certain ecological rules are evident in these shifts, their occurrence has a random component. As we have seen, for example, the phylogenetic ordering of habitat shifts during the diversification of *Anolis* lineages varies from one island to another, so that the resulting ecological diversity is more similar than the route taken to get there (Losos *et al.* 1998).

Habitat shifts in birds apparently reverse themselves on occasion, leading to phases of ecological expansion associated with colonization of new islands, thus renewing the taxon cycle. The causes of these changes in ecological and geographical distribution are not known. Ricklefs & Cox (1972) dismissed cyclic environmental factors such as Pleistocene climate change as factors, because closely related species having similar ecological requirements presently occupy different stages of the taxon cycle. Furthermore, we now know that the lengths of taxon cycles (Ricklefs & Bermingham 2001) considerably exceed the most prominent time-scales of environmental fluctuation, which are on the order of tens of thousands to a few hundred thousands of years (Dynesius & Jansson 2000).

Ricklefs & Cox (1972) suggested that taxon cycles are intrinsic to ecological systems and are driven by coevolutionary responses of predators and their prey or of pathogens and their hosts. Young colonists leave predators and disease organisms behind in their source areas (Keene & Crawley 2002; Mitchell & Power 2003; Torchin *et al.* 2003), but island biotas respond to their new presence and soon (in evolutionary time) exploit them with increasing efficiency, forcing these immigrants into more specialized ecological positions. It is possible, but by no means demonstrated, that victims can escape the constraints of their diseases for a time by mutations that provide resistance to particular limiting pathogens. Selection on pathogen specialization and virulence may also be frequency dependent (Ewald 1996), so that as host populations are driven downward pathogen pressure is reduced through evolutionary feedbacks (Rosenzweig 1973). Such a shift, whether by the acquisition of genetic resistance factors by the host or reduced virulence of pathogens, might initiate a new phase of both ecological and geographical expansion as the host population increases. The lability of specialized host–pathogen interactions is shown quite clearly by statistically independent variation among islands in the prevalence of malaria parasites in different species of avian hosts, which is apparent, for example, in total malaria infections (Apanius *et al.* 2000) and in infections by individual parasite lineages (Fallon *et al.* 2003).

9. EXTINCTION

The ultimate fate of all species is extinction. Ecologists recognize three types of extinction—background, catastrophic and anthropogenic—although these do not have sharp boundaries. Background extinction represents the disappearance of populations or species through processes that are unique to their particular circumstances and might have little influence on other species. Catastrophic extinction, for example caused by bolide impacts, affects many species simultaneously and, at the extreme, can wipe out all traces of life within an area. With respect to the West Indies, it is widely thought that the impact at the end of the Cretaceous north of the present-day Yucatan Peninsula must have exterminated most organisms on the proto-Antilles. Island submergence or a rise in sea level would have the same effect locally. Catastrophes have varying extents, and it is possible that what ecologists call background extinction is continuous in scale with catastrophes of greater impact. Human activities have been a major catastrophe for life, and the biota of the West Indies has not escaped the effects of hunting, habitat conversion and introduction of predators and pathogens. Unfortunately, the disappearance of island populations and entire species removes evidence of the history of evolution and biogeographic distribution, making it more difficult to reconstruct the past and infer the processes that shape the contemporary biota.

What is remarkable about many island populations, however, is how long they persist. Estimates of

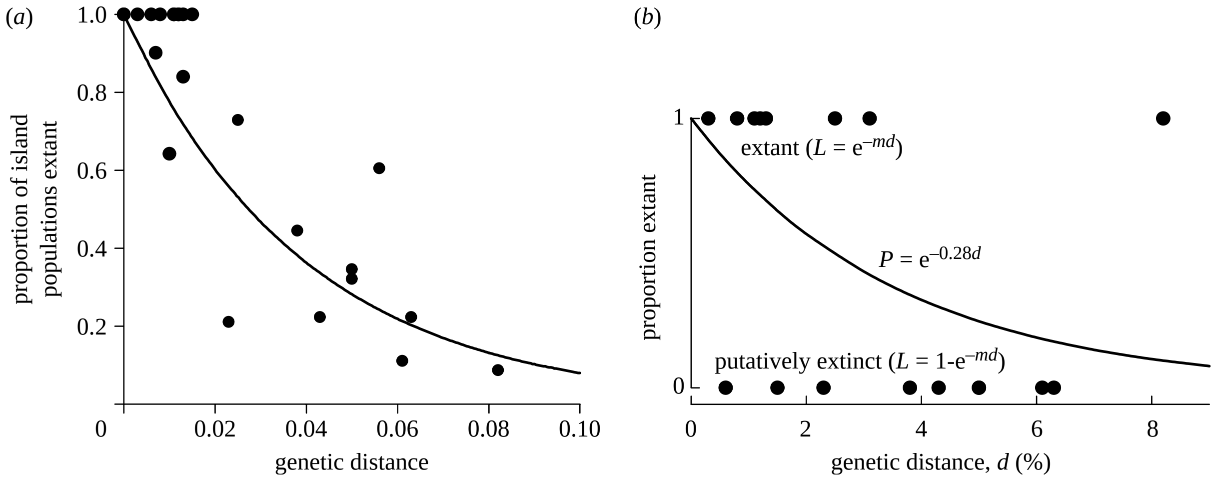

Figure 12. (*a*) Proportion of extant island populations as a function of maximum genetic divergence (x) of island populations of species of Lesser Antillean bird. Each symbol represents a single species. The exponential curve fitted to the data ($y = e^{-mx}$) has an extinction rate (m) of 0.25 (±0.02 s.e.) per percentage of genetic distance or about 50% per million years. (*b*) The relative ages (maximum genetic distance within the Lesser Antilles) of extant (top row) and putatively extinct (bottom row) West Indian endemic species on the island of St Vincent. The extant species with a genetic distance of 8.2% is the endemic whistling warbler *Catheropeza bishopi*. The exponential population survival curve (extinction rate = 0.28 per % of genetic distance) is a maximum likelihood estimate. Based on Ricklefs & Bermingham (1999).

archipelago-wide extinction rates based on colonization times are as low as 0.03 per million years for lineages of reptiles and amphibians (figure 9). Some of these have diversified within the West Indies, which must reduce the probability of extinction for an entire lineage, and others are represented by single species distributed over many islands. Persistence times of tens of millions of years through periods of major climate change emphasize the general resilience of life forms on islands, perhaps owing to their isolation from continental centres of evolution and diversification (Ricklefs 2003, 2005). Populations of birds on islands in the Lesser Antilles are many orders of magnitude smaller than those of reptiles and amphibians on the Greater Antilles (Ricklefs & Lovette 1999), but they also tend to resist extinction. Over the archipelago as a whole, Ricklefs & Bermingham (2001) could detect no significant background rate of extinction, although a few species have at present been reduced to precarious populations on single islands.

The rate of extinction of populations of small land birds on individual islands in the volcanic core of the Lesser Antilles can be estimated from gaps in the contemporary distributions of species, assuming that populations had formerly occurred on these islands. This is a reasonable assumption judging from the essentially continuous distributions of recent colonists to the islands. Ricklefs & Bermingham (1999) used two approaches to estimate the extinction rate of Antillean endemic bird taxa on islands in the Lesser Antilles. First, they fitted an exponential decay curve to the proportion of islands occupied by each species as a function of the age (genetic distance) of the species in the archipelago (figure 12*a*). Second, they estimated the extinction rate of species on each individual island from the presence or absence of species of various age (figure 12*b*). Both these approaches assume a homogeneous extinction rate over time. Accordingly, the average rate of extinction over these islands was approximately 0.25 per % sequence divergence, or about 0.50 per million years. The individual island rates of extinction varied inversely with island size, as one might expect from the species–area relationship, from more than 0.6 per % sequence divergence on the low-lying northern island of Antigua to less than 0.1 per % on St Lucia (figure 13). Thus, the average persistence time of island populations of birds in the Lesser Antilles appears to be in the order of 2 Myr, but might be as high as 5 Myr on the core volcanic islands.

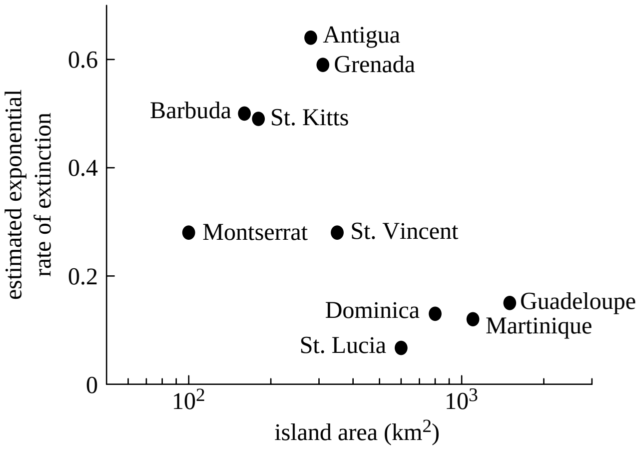

Figure 13. Maximum likelihood estimates of extinction rates of West Indian endemic non-raptorial land birds on several islands in the Lesser Antilles plotted as a function of island size (log scale). The regression of the logarithm of extinction rate on the logarithm of area has a slope of −0.61 (±0.23 s.e.). After Ricklefs & Bermingham (1999).

The longer duration of lineages in the archipelago as a whole, which exhibit apparently negligible extinction, might be attributed to recolonization of islands during expansion phases of the taxon cycle. The shorter persistence times of birds in the Lesser Antilles compared with reptiles and amphibians in the Greater Antilles reflects the smaller size of the Lesser Antillean islands, lower population densities of birds and the higher rate of colonization, hence the rate of appearance of new competitors and diseases, among birds. There are presently too few data available to evaluate these factors quantitatively.

Contrasting with the general persistence of island populations, the kink discovered by Ricklefs & Bermingham (2001) in the curve of lineage accumulation of Lesser Antillean land birds over time (figure 10) might have been caused by a mass extinction event *ca* 0.5–1 Myr ago. As one can see in figure 10, a model of island colonization without background extinction, but interrupted by the extinction of more than 90% of lineages at a time equivalent to an mtDNA genetic divergence of 0.011, fits the data well. Alternatively, the abrupt change in slope of the curve could have resulted from a 10-fold increase in colonization rate at the same time, which would imply an equally spectacular change in conditions for immigration to the islands. Such a change might have been caused by drier conditions associated with the onset of glacial climates, which would have expanded the area of open habitat at low elevation through which most colonization apparently takes place.

10. THE HUMAN IMPACT

Barring mass extinction, the long-term prospects for island populations appear to be excellent when they are left alone. However, we are now witnessing greatly accelerated extinction at the hand of man on islands. Species and island populations that survived the vicissitudes of the Ice Age, colonization of islands by new predators and competitors, natural introductions of disease organisms and a long history of recurrent hurricanes and volcanic eruptions, have disappeared at an alarming rate since human occupation of the West Indies. For example, 48 of 61 species and 15 of 18 genera of endemic West Indian rodents have disappeared (Woods 1989*b*), all but 12 of as many as 50–60 species of parrots are gone (Williams & Steadman 2001), 27 of 57 species of bats are extinct or locally extirpated (Morgan 2001), and all of at least 17 species of megalonychid sloths are extinct (White & MacPhee 2001). Pre-European extinctions, revealed only by fossil data, include primarily large terrestrial species hunted for food by native islanders. However, since European colonization, the clearing of land for agriculture and the introduction of predators, particularly the mongoose (Horst *et al.* 2001), have drastically modified the general character of most of the West Indies (Kimber 1988). Many species disappeared before scientists could properly describe them, but others have gone extinct since and many are currently threatened or gravely endangered.

The management of endangered populations should be dictated by factors directly affecting survival and reproduction, but often these are not known and are difficult to control. Removing predators such as mongooses from large islands in the West Indies probably will not be possible, despite the success of predator control programmes on smaller islands in other parts of the world (Bloomer & Bester 1991; Robertson *et al.* 1994; Courchamp *et al.* 2003). Direct intervention by providing nesting sites, predator control (Engeman *et al.* 2006) and captive propagation (Russello & Amato 2004) is being attempted for several of the parrot populations of the West Indies with mixed success. Where populations of a species occur on several islands, introductions from one island to bolster a failing population on another island is possible, but it is important to determine the genetic distinctiveness of individual island populations before mixing them (e.g. Malone *et al.* 2000). For example, although populations of the Adelaide's warbler on Barbuda and St Lucia are not endangered, their mitochondrial DNA indicates that the populations have been evolving independently for more than 1 000 000 years (Lovette *et al.* 1998). This knowledge gives greater impetus not only to local conservation efforts but also cautions against unforeseen consequences of hybridization and the loss of genetic distinctiveness resulting from movement of organisms between islands.

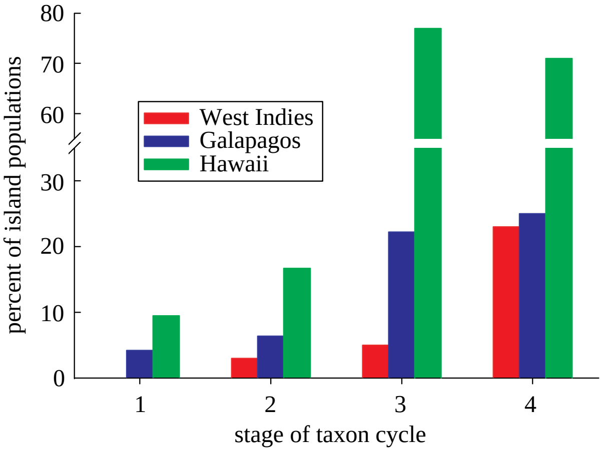

Figure 14. The probability that an island population has suffered extinction or has critical conservation status relative to its stage in the taxon cycle. From Ricklefs & Bermingham (1999); population status from Stattersfield *et al.* (1998) and Stattersfield & Capper (2000).

Although natural and human-caused extinction differ dramatically in rate, and probably in their causes and selectivity, it would be useful to determine whether general attributes of species are associated with increased risk of extinction. For species of birds in the West Indies, one pattern stands out: island populations at later stages in the taxon cycle, that is, populations that occupy few habitats and generally have low population sizes—generally old populations—more frequently have suffered extinction or presently are vulnerable to extinction (figure 14). We have found that this pattern holds, to an even greater extent, in more isolated archipelagoes such as the Galapagos and Hawaiian Islands, where species have evolved in a benign environment without frequent immigration of potential predators and disease organisms.

Our research on birds in the West Indies, combined with many studies of other groups of organisms, allow us to draw some tentative conclusions about the most invisible of island processes, extinction.

(i) Lineage accumulation plots suggest that extinction rates in most groups have been very low during most of the Tertiary period. In fact, extinction rates are so low that the oldest lineages in the West Indies may represent descendants of the original inhabitants when the islands were first available for colonization.

(ii) The heterogeneous lineage accumulation plot of birds in the Lesser Antilles suggests the possibility of a mass extinction during the Mid-Pleistocene. Such an event almost certainly occurred at the Cretaceous–Tertiary transition as the impact site off the Yucatan Peninsula would have been close to the position of the proto-Greater Antilles (Perfit & Williams 1989). The cause of widespread extinction during the Pleistocene epoch, if it indeed occurred, is unknown. Heterogeneity in lineage accumulation curves taken to infer mass extinction events can also be explained by speciation threshold models of divergence, and so this issue requires more detailed genetic analysis of island populations and their continental sources before it can be fully resolved.

(iii) It would appear that background extinction rates in the West Indies were not elevated during Pleistocene glacial cycles. Drier climates during glacial maxima may have resulted in the disappearance of mesic habitat types and their inhabitants from low islands (Pregill & Olson 1981), but probably had relatively little effect on the range of habitats available on the larger, higher islands in both the Greater and Lesser Antilles.

(iv) Natural catastrophic events, including hurricanes and volcanic eruptions, are commonplace in the West Indies, but their effect on populations, except on very small islands (Spiller *et al.* 1998; Schoener *et al.* 2001; Schoener & Spiller 2006), probably is rather low owing to the small area of such disturbances and the fact that present-day island inhabitants have been selected as survivors of such disturbances in the past (e.g. Wiley & Wunderle 1993; Arendt *et al.* 1999; Hilton *et al.* 2003).

(v) American natives, who began to colonize the West Indies as early as 3500–4000 BC (Wilson 2001), almost certainly caused the rapid extinction of large, terrestrial vertebrates (Morgan & Woods 1986). Evidence for this first wave of anthropogenic extinction comes from bones of vertebrates in cave deposits and middens (Wing 1989) that provide direct evidence for former inhabitants of islands and for the fact that they were depredated by humans for food (Wilkins 2001).

(vi) Extinction during the initial period of European colonization of the islands was due to massive habitat alteration for agriculture (primarily sugar cane production; e.g. Kimber 1988) and the introduction of alien species, especially the mongoose (Horst *et al.* 2001) and, more recently, the shiny cowbird *M. bonairiensis* (a semi-natural introduction).

The future of diversity in the West Indies depends on the efforts of conservationists, managers and researchers from both within the archipelago and outside. The task is made difficult by the presence of many independent island governments and lack of financial and educational resources. There are now several effective networks for conservation and management within the West Indies, which provide an optimistic outlook for the future of the West Indies and their natural inhabitants (e.g. Ottenwalder 1989; Woods 1989*a*; Raffaele *et al.* 1998; Sergile & Woods 2001). As long as the human inhabitants of the islands take pride in the unique plants and animals among which they live and value their preservation, the continued persistence of the native biota will be assured.

The West Indies are a valuable laboratory for studying the dynamics of biodiversity at a regional as well as local scale. The islands are more strongly dominated by colonization than are distant archipelagoes, resulting in a relatively high diversity of lineages. However, many groups also have diversified within the islands, providing an opportunity to study both intrinsic and extrinsic processes responsible for the build-up of diversity within a region. One of the most surprising findings of studies on West Indian vertebrates is the relatively long persistence times of lineages in the archipelago, many of which colonized the islands tens of millions of years ago, and some of which have existed as isolated populations on individual islands for millions of years. Islands and archipelagoes constitute a continuum of isolation from continental source populations, which depends on the physical distance of the islands and the dispersal abilities of particular taxa. These control the overall dynamics and diversity of groups of organisms on islands. The West Indies, with the variety of sizes and histories of islands, and their proximity to three major sources of colonization, provide an outstanding laboratory for studying the regional dynamics of biotas.

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