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## The West Indies as a Laboratory of Biogeography and Evolution

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Islands have provided inspiration for biologists since the beginning of scientific exploration more than two centuries ago. Charles Darwin's (1859) insight about descent with modification was formed in part from the close affinities of island inhabitants to forms on nearby continents (Darwin 1909). Alfred Russel Wallace drew similar insights from his studies on East Indian islands (Wallace 1869), which also provided a foundation for his synthesis 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 and Wilson 1967; MacArthur 1972; Carson and Kaneshiro 1976; Grant 1986; Woods 1989a; Carson and Clague 1995; Caley and Schluter 1997; Grant 1998; Whittaker 1998; Schluter 2000). Islands hold special advantages for such studies because of their discrete nature. Archipelagoes, in particular, consist of multiple islands that promote diversification and over which evolutionary processes can unfold repeatedly (Wagner and Funk 1995; Losos 1996; Losos et al. 1998; Givnish 1999; Grant and Grant 2002; Gillespie 2004).

Isolated archipelagoes, such as the Hawaiian Islands (Wagner and Funk 1995), Galápagos Archipelago (Grant 1986), and the Canary Islands (Juan et al. 2000) have the strongest hold on our imaginations and are idealized as 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, the likes of which occur nowhere else on earth (Amadon 1950; Pratt 1979; Givnish and Sytsma 1997; Givnish 1999). However, the extreme isolation of these archipelagoes distills 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 consists only of one-way, haphazard, long-distance dispersal. At the other extreme, close islands such as the islands off the coast of Baja California (Case et al. 2002) and the Bismark and Solomon Islands to the north of New Guinea (Mayr and Diamond 2001), receive so many immigrants that endemism is rare and phylogenetically shallow in many groups and opportunities for radiations within archipelagoes are swamped by the steady supply of new taxa evolving in the larger source areas (Ricklefs and Bermingham, in review).

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 is frequent enough that its character emerges 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 enough to leave traces of the tectonic history of the region in their inhabitants. To be sure, the West Indies harbor several spectacular adaptive radiations, the most famous of which are the *Anolis* lizards of the Greater Antilles (Roughgarden 1995; Losos 1996; Losos and Schluter 2000). However, island biogeography within the region has been dominated by several highly charged debates related to colonization, particularly whether the presence of non-flying vertebrates in the Greater Antilles resulted from earlier land connections to the continents (Rosen 1976; Guyer and Savage 1985; Rosen 1985; Iturralde-Vinent and MacPhee 1999) or by over-water dispersal (Hedges 1996a; Hedges 1996b; Hedges 2001). This dominating issue should not mask the important role that the West Indies have played in our understanding of island biogeography, and of evolution and ecology more generally. Here we examine processes responsible for the development of island biotas as they have been revealed by studies of the West Indian flora and fauna.

### 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 (Myers et al. 2000), but this obscures the heterogeneity of the islands, which provides unique opportunities for the study of island biogeography. The West Indies consist of three groups of islands: (1) the Greater Antilles, which are 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; (2) the Bahamas Islands, which are low-lying islands scattered about the shallow Bahamas platform; and (3) the Lesser Antilles, which form a volcanic arc over the eastern edge of the eastward moving, overriding Caribbean plate (Figure 1).

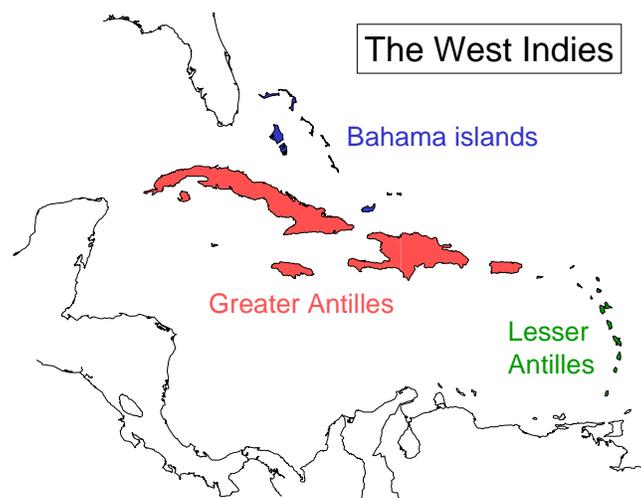


Figure 1: Map of the West Indies indicating the three major regions with different geological histories.

The Greater Antilles are old islands (Draper et al. 1994), with parts of present-day Cuba, Hispaniola, and Puerto Rico having remained above water throughout the entire Tertiary (Donnelly 1988; Donnelly 1989). Sedimentary marine formations on Jamaica suggest that the island was greatly reduced in area, or perhaps even entirely submerged, during the mid-Tertiary. The proto Greater Antilles moved through the gap between North and South America at the end of the Cretaceous (over 60 million years ago) and may have temporarily abutted what is now southern Mexico. Throughout their evolution as islands, the Greater Antilles fragmented and rejoined in various combinations such that the present-day islands have complex geographic histories. The geologic relationships between eastern Cuba and northern Hispaniola are particularly close, whereas the Grand'Anse peninsula of southern Hispaniola is a more recent acquisition (Iturralde-Vinent and MacPhee 1999). The Bahamas platform is an old and stable geologic feature that has held its geographic position relative to North America throughout the Tertiary (Meyerhoff and Hatten 1974; Mullins and 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 windblown 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 occur in the northern Lesser Antilles and some volcanic deposits have been dated to the early Tertiary, the islands of the Lesser Antilles—as they appear now—probably originated less than 20 million years 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 are several low-lying islands consisting of uplifted marine sediments, notably the eastern half of Guadeloupe, Antigua, Barbuda, and smaller islands to the north, and Barbados to the south. The Lesser Antilles never had continental connections and, except for Antigua-Barbuda and St. Kitts-Nevis-St. Barts, which are joined by shallow banks, the islands have never 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 3,175 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 and Cook 1926; e.g., Asprey and 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 time the islands may be ravaged by storms so violent as to completely strip vegetation over paths that might encompass an entire island in the Lesser Antilles (Tannehill 1969; Caviedes 1991; Wiley and 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 6,000 years (Rouse 1989; Rouse 1992; Wilson 1997; Wilson 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; Wilkins 2001;

Wing 2001). The arrival of Europeans in the West Indies at the end of the 15<sup>th</sup> 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 anthropogenic changes on Martinique. These changes and pressures brought on widespread extinction of many of the larger, flightless components of the West Indian fauna (e.g., Olson 1982; Olson and Pregill 1982; Pregill et al. 1988; Pregill et al. 1991; Pregill et al. 1994; Steadman et al. 1997; Pregill and 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 (see, for example, several chapters in Woods 1989a; Sergile and Woods 2001).

### **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 and Wilson (1967, Figure 2, page 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 the logarithm of area has been given particular significance in many analyses (e.g., May 1975; e.g., Connor and McCoy 1979), but in fact provides relatively little information about the processes responsible for diversity patterns. MacArthur and Wilson emphasized the relationship between extinction rate and island area, arguing that larger populations were less vulnerable to extinction from random factors. 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. According to Lack, extinction had little to do with the species-area relationship. Thus, Lack believed that islands were ecologically saturated with species whereas MacArthur and Wilson held that the diversity of an island of any given size was colonization limited and that the number of species at the steady state depended on the replacement of extinct species by new species from continental sources of colonization. Because this debate concerns historical processes that cannot be observed directly, the controversy remains largely unresolved (Ricklefs and Bermingham 2004b).

Lack's idea predicts that diversity should be directly related to the diversity of ecological opportunities on islands. Ricklefs and 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. The Lesser Antilles exhibit sufficient uncorrelated variation in area and habitat diversity that the effects of each can be identified statistically. The partitioning of variation in number of species (Figure 2) showed that the relative influence of area *per se* and habitat diversity varied among faunal groups. The species richness of bats, which show little habitat specialization, was sensitive primarily to island area, whereas that of reptiles and amphibians, which partition habitats more finely, were influenced uniquely only by habitat diversity. Birds and butterflies were sensitive to both. These analyses provide support both for Lack and for MacArthur and Wilson, but they also emphasize the importance of understanding ecological distributions of species in trying to interpret larger-scale patterns of species richness.

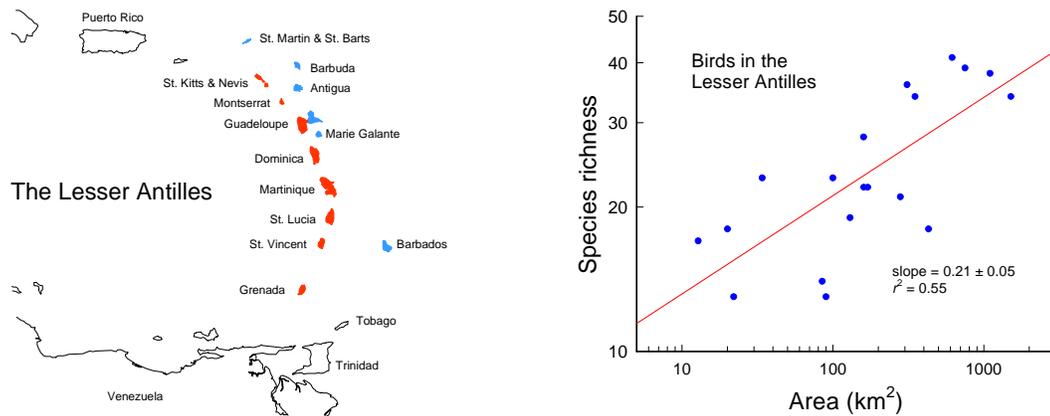
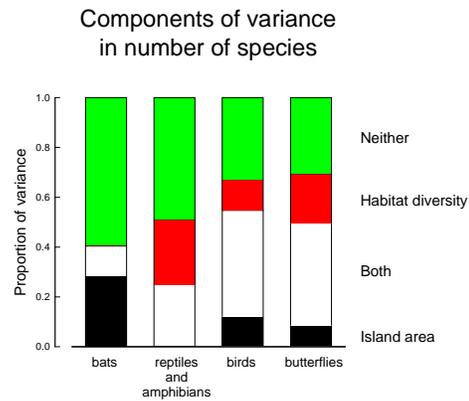


Figure 2. Species-area relationship of birds in the Lesser Antilles. High (red) and low (blue) islands, which have high and low habitat diversity, are distinguished in the map at top. Species richness of birds as a function of island area shows a typical species-area relationship with a slope of  $0.21 \pm 0.05$  (top right). The bar diagram at right shows the proportion of the total variance in species richness among areas that is statistically associated with island area (black), habitat diversity (red), correlated variation in both variables (white), and unexplained by either (green). The large amount of unexplained variance for bat species richness probably reflects the poor state of present knowledge of bat distributions in the Lesser Antilles. Birds and butterflies are much better known, and factors in addition to area and habitat diversity clearly influence their diversity on islands. From Ricklefs and Lovette (1999).



The number of species on an island is influenced by colonization and extinction, but also by the production of new species within an island, giving diversity an additional historical and evolutionary dimension. 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  $3,000 \text{ km}^2$  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 an important process. Considering this, Losos and Schluter (2000) showed that extinction on the larger islands is negligible and that speciation rate increases with island area, with the exponential rate of diversification increasing with a slope of  $0.76 \pm 0.09$  relative to the logarithm of island area. This approach emphasizes that we must consider underlying processes in order to understand more fully patterns of island diversity and distribution. In this area, studies in the West Indies have made considerable progress in recent years.

Ecological and phylogenetic studies of island faunas are beginning to unravel the processes that influence the diversity of island faunas and floras. These processes include colonization, extinction, and evolutionary radiation within and between islands. Ecological and evolutionary manifestations of the changes following colonization and the diversification of island biotas include ecological release, that is, increased habitat breadth and niche space use within habitats, ecological shifts, and morphological divergence.

### **Vicariance versus dispersal biogeography**

One of the most fundamental issues 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 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 1970's, overland dispersal to islands required land bridges, now submerged, in the distant past (Wallace 1876; Darlington 1957). Overland dispersal and subsequent vicariance resulting from continental drift was first argued by Rosen (Rosen 1976; Rosen 1978; Rosen 1985) for freshwater fish and other land-locked organisms (Chakrabarty 2006; Echelle et al. 2006), and strongly defended by Savage (Guyer and Savage 1985) and others for such land-bound taxa as lizards and snakes and terrestrial mammals (Davalos 2004). The resolution of the vicariance and dispersalist views depended on the timing of colonization. If this were close to the beginning of the Tertiary, a land route to the proto Greater Antilles would be possible through what is now southern Mexico; if later, the biota would have to have crossed a widening water gap. Unfortunately, fossils of terrestrial organisms in the West Indies are rare and limited primarily to more recent formations, including the famous Miocene ambers of Hispaniola (Wilson 1985; Iturralde-Vinent and Macphee 1996).

The first attempt to resolve the dispute using molecular methods to assess the timing of dispersal events was S. Blair Hedges' application of calibrated immunological distances between island forms and their mainland relatives (Hedges 1996b; Hedges 1996a; Hedges 1996c; Hedges 2001). Immunological distance between two taxa is based on the cross-reaction between antibodies formed in response to antigens from one taxon and antigens from the second. The more similar the protein sequences, presumably reflecting the relationship between the taxa, the stronger the reaction and the smaller the immunological distance. Immunological distance can be calibrated using taxa with divergence times known from fossil evidence.

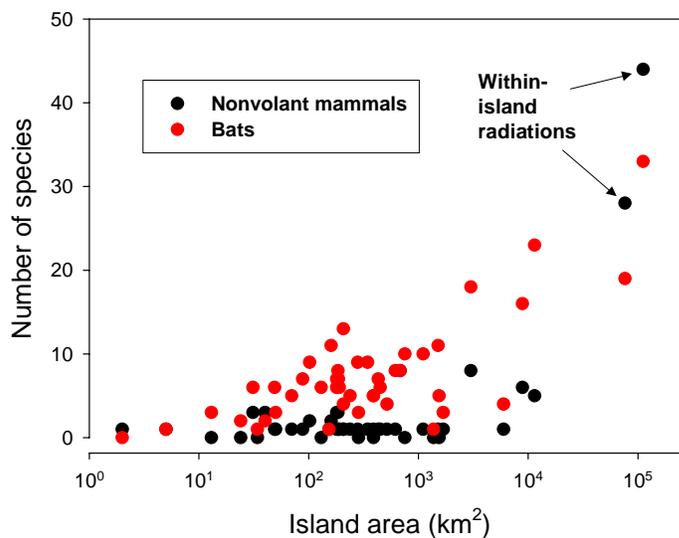
Based on immunological distances, Hedges suggested that most colonization times of reptile and amphibian lineages in the Greater Antilles were too recent to allow for overland dispersal from what is now southern Mexico followed by vicariant isolation. However, MacPhee and Vinent-Iturralde (1999) suggested a way around this impasse by postulating a continuous land connection (GAARlandia, [GAAR from Greater Antilles-Aves Ridge]) about 33-35 million years ago between northern South America and the Greater Antilles by way of the Aves Ridge. This feature, which now lies deeply submerged, was at least partly exposed during the early Oligocene (Holcombe and Edgar 1990), but 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 around 34 Ma is evident in Hedges' immunological distances (Hedges 2001).

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, about 25 million years ago, the Amazon River flowed north and entered the Caribbean Sea in western Venezuela (<http://www.geo.vu.nl/users/pal/Climazonia/landscap.htm>). 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 3). Most islands, including Jamaica and Puerto Rico, have fewer than 5 lineages of non-volant mammals. The large numbers of species on Cuba and Hispaniola represent radiations of a small number of rodent lineages (Woods 1989b).

Figure 3: Species-area relationship for mammals, distinguishing between flying and non-flying mammals to show the effects of dispersal ability, but also reflecting the effect of adaptive radiation on the islands of Cuba and Hispaniola. Data are from (Woods 1989b, table 5).

Influence of dispersal ability on number of lineages of mammals  
From data in Woods (1989).



### Colonization-extinction dynamics

From the ages of colonization events, one can describe the dynamics of colonization and extinction within the framework of the MacArthur and Wilson equilibrium model. Accordingly, 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 equal to the rate of extinction. Thus, the cumulative distribution of colonization times should exponentially approach the equilibrium number of lineages in the islands (Figure 4). 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 colonization time ( $t$ ) is  $L(t) = (C/E)(1 - \exp[-Et])$ , and the equilibrium number of lineages  $L(\infty)$  is equal to  $C/E$ .

This curve is fitted to immunological distances determined by Hedges for endemic reptiles and amphibians in Figure 4. The fitted coefficients for the reptile and amphibian age accumulation curve in Figure 4 are  $C = 1.31 \pm 0.05$  events per million years, and  $E = 0.029 \pm 0.002$  per species per million years. The equilibrium number of lineages in the Greater Antilles is  $C/E = 45.2$ , which is somewhat greater than the observed number of 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 about 25 Ma and between 0 and 5 Ma. 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  $1/0.029 = 34.5$  million years! Because the number of lineages is short of 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.

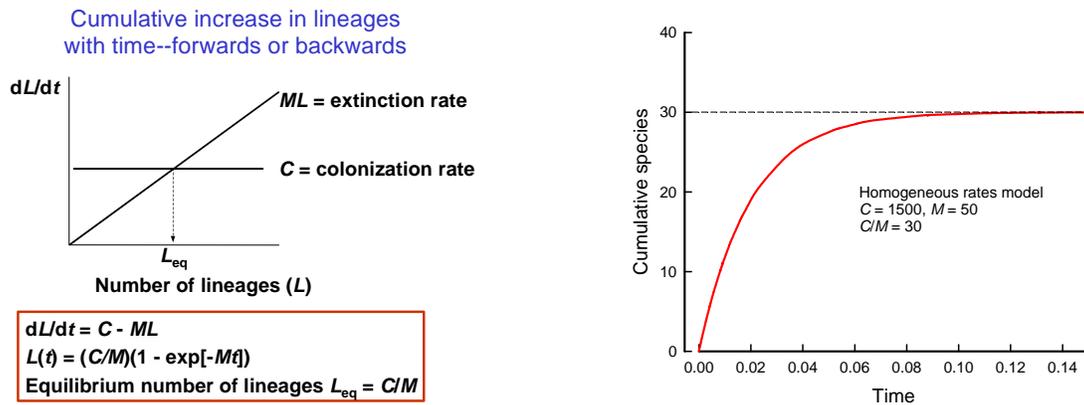
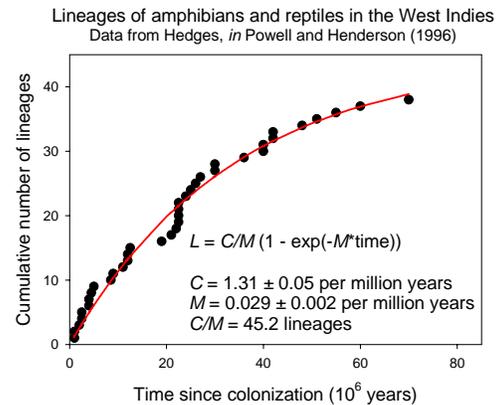


Figure 4. A simple model of diversity dynamics within the West Indies with uniform colonization, which is independent of the number of species within the archipelago, and a constant probability of extinction per species (above). Over time, looking either forward or backward from the present, the cumulative number of species approaches an equilibrium value exponentially (top right). The colonization-extinction model is fitted to Hedge's (1996b) data for the colonization times of reptiles and amphibians in the West Indies (right), revealing very low rates of both colonization and extinction.



Ricklefs and Bermingham (2004a, Figure 5) applied a similar analysis to 22 lineages of land and freshwater birds of the Hawaiian Archipelago, obtaining values of  $C = 387.7 \pm 29.2$  colonization events and an extinction rate of  $15.1 \pm 2.4$  per unit of mtDNA sequence divergence. Assuming a 2% sequence divergence per million years (Lovette 2004), these rates are  $C = 7.8 \pm 0.6$  and  $M = 0.30 \pm 0.05$  per Ma. The expected equilibrium number of lineages would be 25.7, only slightly higher than the current level, and the expected lifetime of a lineage in the archipelago would be 3.3 Ma. 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 curvature of the lineage-time relationship, of lineage extinction (quadratic term,  $F_{1,15} = 1.85$ ,  $P = 0.19$ ; linear slope  $161.9 \pm 7.3$  per unit mtDNA sequence divergence (3.2 per Ma).

Ricklefs and Bermingham (2001) analyzed 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 5). Thus, conditions affecting colonization, extinction, or both, apparently have not been homogeneous over the approximately 10-million-year history of 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 about 0.5-1.5 Ma, 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 disappear, 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 and Bermingham 2001). Because lineage extinction appears to be rare, the maximum colonization times of ca. 10 Ma may represent the first colonists of the Lesser Antilles and indicate the time that these islands first became suitable for surviving avian populations.

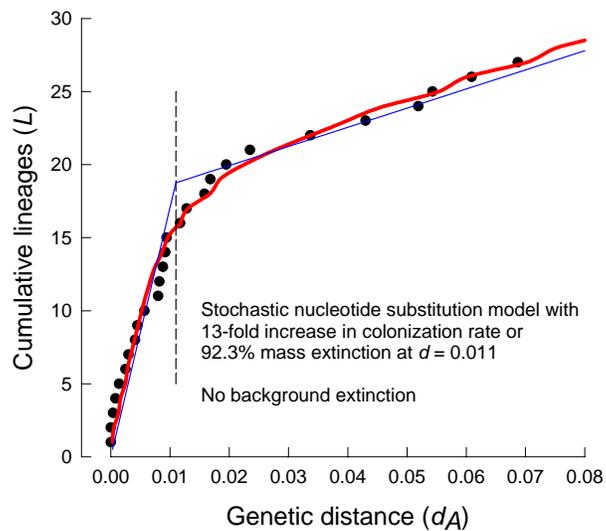


Figure 5. The cumulative number of lineages as a function of increasing genetic distance ( $d$ ) in the terrestrial avifauna of the Lesser Antilles (Ricklefs and Bermingham 2001). Genetic distances are based on divergence in the mitochondrial ATPase 6 and 8 gene region between lineages in the Lesser 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  $d > 0.02$  indicates that the archipelago-wide rate of extinction is close to zero.

### Adaptive radiation (*Anolis* and other groups)

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 and Schluter 2000; Glor et al. 2003; Glor et al. 2004) and *Leiocephalus* (Hedges et al. 1992; Pregill 1992; Hass et al. 2001) iguanid lizards, *Sphaerodactylus* geckos (Hass 1991), *Eleutherodactylus* frogs (Hass and Hedges 1991), capromyid rodents (Woods 1989b), and *Lyonia* (Ericaceae) trees and shrubs (Judd 2001). The anole radiations have been analyzed in detail and reveal repeated and independent diversification of ancestral lineages into a series of parallel ecological types on each of the major Greater Antillean islands (Losos et al. 1998; Glor et al. 2003) (Figure 6). Thus, adaptive radiation appears to be ecologically deterministic when conditions promote the differentiation of geographically or ecologically isolated lineages to the level of species.

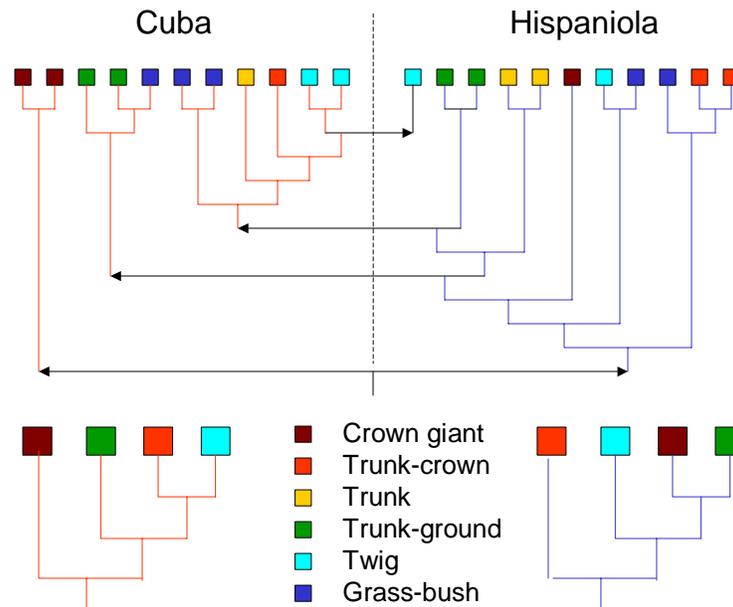


Figure 6: Phylogenetic trees for several Cuban and Hispaniolan radiations of *Anolis* lizards with repeated production of same ecological and morphological types. The black arrows indicate inferred colonization events. The diagrams extracted at below left (Cuba) and right (Hispaniola) show that although each island now has the same array of ecological types, the sequence of their evolutionary origins differs. Adapted from Losos et al. (1998).

The Lesser Antilles present a similar range of ecological opportunities, but they appear to be too small to support the formation of new species of *Anolis* or other vertebrates within islands (Thorpe and Malhotra 1996; Malhotra and Thorpe 2000). Furthermore, dispersal between islands is apparently too infrequent to allow the build up of a fauna through allopatric speciation and secondary sympatry within the archipelago as a whole. Although the Lesser Antilles have a similar geographic 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 and 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. This radiation might have occurred before many other birds had colonized the islands (Hunt et al. 2001). 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 and Sytsma 1997; Givnish 1999; Schluter 2000). Thus, the dispersal abilities of organisms must be “tuned” to distances within an island or archipelago to provide the right conditions for adaptive radiation.

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. This can be tested for reptiles and

amphibians within the West Indies (Figure 7), among which there is a significant positive relationship between number of species and age of lineage. The relationship has considerable scatter, but this is to be expected of an essentially random, haphazard process such as the splitting of lineages within an archipelago (Nee et al. 1992; Harvey et al. 1994; Nee et al. 1994; Ricklefs 2003). If we assume that this is a completely random process, with each lineage having an equal probability of splitting per time interval, the logarithm of species richness should increase 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 ( $S$ ). When lineage diversity ( $S$ ) in Figure 7 is normalized by the predicted value from the log species-time regression, the standard deviation of the normalized values was 6.9 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 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.

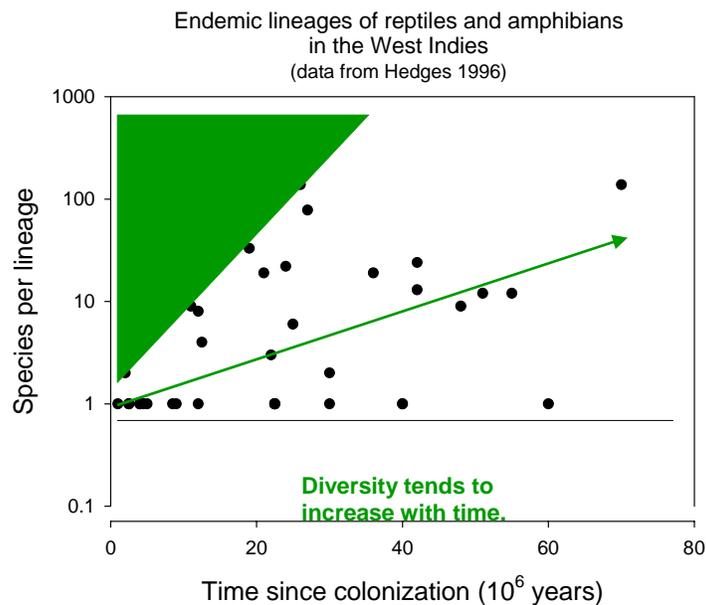


Figure 7. Relationship between species richness within the West Indies and age of taxon for endemic reptiles and amphibians. The slope of the regression line passing through the origin (time = 0, species = 1), which is the average rate of diversification of the lineages, has a slope of 0.022 ( $\pm 0.003$ ) per million years ( $F_{1,36} = 41.7$ ,  $P < 0.0001$ ,  $R^2 = 0.537$ ). Data from Hedges (1996b).

### 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 never escape (Carlquist 1974). While this has almost certainly been the case for remote archipelagoes such as the Galapagos 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.

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 region, the most parsimonious explanation for the direction of colonization is from the region having the ancestral branches (Figure 8). For example, the *Icterus cayanensis* and *I. chryscephalus* 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 8).

Similar evidence of colonization from the West Indies to the mainland of South America has surfaced for bananaquits *Coereba flaveola* (Seutin et al. 1994; Burns et al. 2002) and *Amazona* parrots (Russello, 2003). The catbird (*Dumetella carolinensis*) of North America also could be an offshoot of the West Indian ancestor of the present-day Lesser Antillean thrashers (Hunt et al. 2001). The fact that several of these “reverse” colonization events have been identified by phylogeographic reconstruction within the relatively depauperate Lesser Antillean avifauna, along 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.

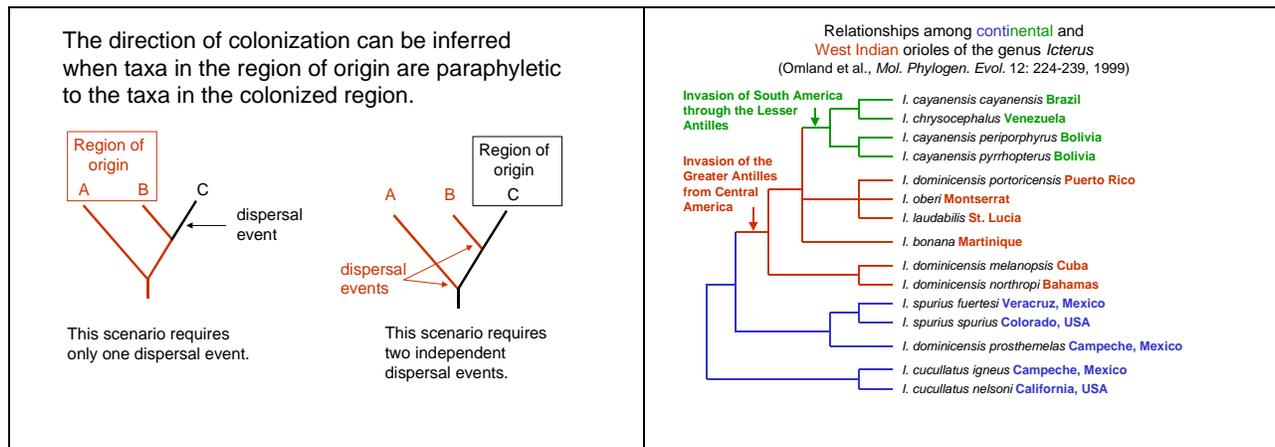


Figure 8. The phylogenetic nestedness of island and continental lineages indicates the most parsimonious reconstruction of the direction of colonization (left). The relationships among continental and West Indian orioles of the genus *Icterus* suggest that the *I. cayanensis*-*I. chryscephalus* clade of South America originated from the Lesser Antilles. Based on Omland (1999).

### Ecological changes in species over time.

The dynamics of species within the West Indies include changes in ecological distribution as well as geographic distribution. 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 have entered the West Indies through such marginal habitats as well, as inner forest and montane species tend to be poor colonists. Ricklefs and 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 toward extinction was called the “taxon cycle” by Wilson, and was described in detail for West Indian birds by Ricklefs and Cox (1972; 1978) and Cox and Ricklefs (1977). 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 and 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 leaf 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 and Cox 1978) suggests a level of determinism in the dynamics of island systems. But even though certain ecological rules are evident in these shifts, their occurrence has a random component. For the 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 geographic distribution are not known. Ricklefs and 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 and Bermingham 2001) considerably exceed the most prominent time scales of environmental fluctuation, which are on the order of tens to a few hundred thousands of years (Dynesius and Jansson 2000). Ricklefs and Cox (1972) suggested instead that taxon cycles are intrinsic to ecological systems and are driven by evolutionary 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 and Crawley 2002; Mitchell and 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 geographic 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 in total malaria infections (Apanius et al. 2000) and in infections by individual parasite lineages (Fallon et al. 2003).

### **Extinction, including anthropogenic extinction.**

The ultimate fate of all species is extinction. What is remarkable about island populations is how long they persist. Estimates of archipelago-wide extinction rates based on colonization times are as low as 0.03 per million years for lineages of reptiles and amphibians. 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 because of their isolation from continental centers of evolution and diversification (Ricklefs 2003; Ricklefs 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 and Lovette 1999), but they also tend to resist extinction. Over the archipelago as a whole, Ricklefs and 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. Persistence times of populations of small land birds on individual islands in the volcanic core of the Lesser Antilles average approximately two million years. The longer duration of lineages in the archipelago as a whole undoubtedly can be attributed to recolonization of islands during expansion phases of the taxon cycle. The shorter persistence times of birds in the Lesser Antilles compared to reptiles and amphibians in the Greater Antilles might be attributed to the smaller size of the Lesser Antillean islands, lower population densities of birds, and the higher rate of colonization, hence 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 and Bermingham in the curve of lineage accumulation of Lesser Antillean land birds over time (Figure 5) might have been caused by a mass extinction event approximately 0.5-1 Mya. As one can see in Figure 9, 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 extremely 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 created greater area of open habitat at low elevation through which most colonization apparently takes place.

Although the mass extinction model is intriguing, 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 population 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 immigrant populations would evolve independently and diverge at a more rapid rate. This would result in the observed heterogeneous lineage accumulation curve, as shown in Figure 9. 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 and Bermingham 2004a). Nevertheless, molecular phylogenetic evidence of repeated brief phases of dispersal among islands in the past suggest that migration between islands is episodic rather than continuous and that the speciation-threshold model is not generally applicable.

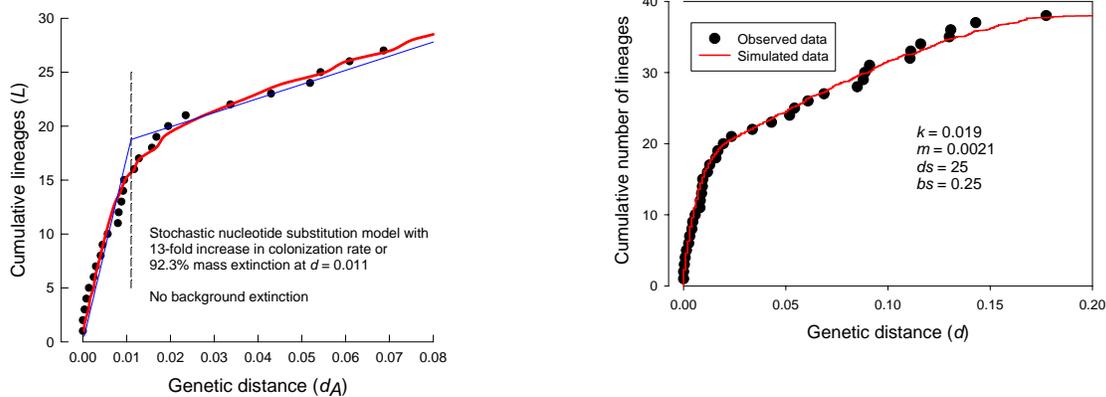


Figure 9. Lineage accumulation curve fit by a stochastic nucleotide substitution model incorporating a mass extinction event (92.3% of lineages) at a genetic distances of 0.011 and a speciation threshold model with a migration rate of 2.1 events per million years, mtDNA genetic divergence rate of 1.9% per million years, and a speciation threshold of 2.5% mtDNA sequence divergence (Ricklefs and Bermingham 2004a).

Barring mass extinction, the long-term prospects for island populations appear to be excellent when left alone. However, we are now witnessing on islands greatly accelerated extinction at the hand of man. 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 or 18 genera of endemic West Indian rodents have disappeared (Woods 1989b), all but 12 of as many as 50-60 species of parrots are gone (Williams and 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 (White and MacPhee 2001). Earlier extinctions, revealed only by fossil data, include primarily large terrestrial species hunted for food by native islanders. Since European colonization, however, 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 programs on smaller islands in other parts of the world (Bloomer and 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 and 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. 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 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.

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 island populations of birds in the West Indies, one pattern stands out, and that is that 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 10). This pattern is the same, but more extreme, 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.

Historical Extinctions of Island Populations

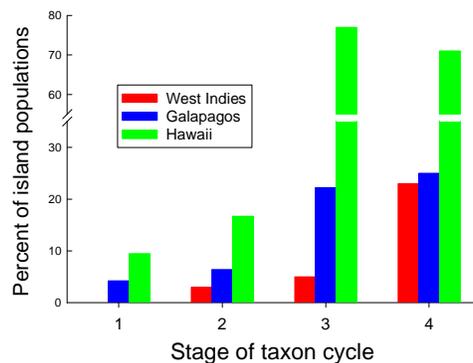


Figure 10. The probability that an island population has suffered extinction or has critical conservation status relative to its stage in the taxon cycle. Also shown is the relationship between the ecological breadth (diversity of habitats occupied) and population density with respect to the taxon cycle in birds of

the Lesser Antilles. From Ricklefs and Bermingham (1999); population status from Stattersfield et al. (1998) and Stattersfield and Capper (2000).

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. (1) 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. (2) 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 and Williams 1989). The cause of pervasive 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 resolved. (3) 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 and 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. (4) Natural catastrophic events, including hurricanes and volcanic eruptions, are commonplace in the West Indies, but their effect on populations 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 and Wunderle 1993; Arendt et al. 1999; Hilton et al. 2003). (5) It is fairly clear that American natives, who began to colonize the West Indies as early as 3500-4000 B.C. (Wilson 2001), caused the rapid extinction of large and terrestrial vertebrates (Morgan and 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). (6) 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 (a semi-natural introduction).

The future of diversity in the West Indies depends on the efforts of conservationists, managers, and researchers both from within the archipelago and from 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 1989a; e.g., Raffaele et al. 1998; Sergile and 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 more 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 buildup of diversity within a region. One of the most surprising findings of studies on West Indian animals and plants 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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