
The Speciation-Area Relationship

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The species-area relationship is often referred to as the closest thing to a rule in ecology (Schoener 1976). . . . The pattern appears to be so common that it would be much more expedient to report the few exceptions . . . than the many hundreds, and possibly thousands of studies reporting this pattern.

—Lomolino 2000

INSPIRED IN PART BY THE SPECIES-AREA RELATIONSHIP, MacArthur and Wilson (1967) proposed the equilibrium theory of island biogeography, which relied on the ecological processes of colonization and extinction to determine the species diversity of islands. Although widely influential, theirs was not the only ecologically oriented explanation of insular species richness. Lack (1976), for example, believed that island diversity was determined by the habitat diversity on islands; more distant islands had lower diversity because they tend to be impoverished in terms of habitat heterogeneity. These ideas, particularly the MacArthur and Wilson theory, dominated thinking about island species diversity throughout the latter part of the twentieth century.

Islands are also widely recognized as natural laboratories of evolution, ideal localities in which to study evolutionary processes and their long-term consequences (e.g., Carlquist 1974, Grant 1998, Losos and Ricklefs, 2009). One area that has been particularly influenced by research on islands is the study of adaptive radiation, the idea that a single ancestral species diversifies, producing descendant species that occupy a wide variety of ecological niches. Many of the most famous cases of adaptive radiations—Darwin's finches, Hawaiian silverswords, African Rift Lake cichlids—occur on islands or islandlike settings. One consequence of adaptive radiation, if it occurs *in situ*, is that the diversity of an island is a result not just of colonization and extinction, but also of the evolutionary input of species resulting from within-island or within-archipelago speciation (cladogenesis); for example, the tiny island of Rapa in the South Pacific (size=40 km²) harbors 67 species of *Miocalles* weevils, all the presumed descendants of a single ancestral colonist (Paulay 1985).

MacArthur and Wilson (1963, 1967) were not unaware of the potential significance of evolutionary processes occurring on islands. Indeed, the final chapter of their monograph was entitled, “Evolutionary Changes Following Colonization.” Nonetheless, it’s fair to say that for more than three decades after the book’s publication, little attention was paid to evolutionary issues as research focused on the ecological factors affecting species richness.

However, times have changed and in recent years researchers have begun to pay attention to the role of evolutionary factors in generating and maintaining insular species richness. This work—like much of the renaissance in macroevolutionary thinking—has been sparked by the increased availability of phylogenies and of comparative methods based on phylogenetic information.

The goal of this chapter is simple: to investigate the extent to which evolutionary diversification may be responsible for generating species-area relationships. Few explicitly phylogenetic studies have addressed such questions, and we will focus here on two case studies, Caribbean lizards in the genus *Anolis* and Galápagos snails in the genus *Bulimulus*. These two groups occur on island groups that differ greatly in age, size, and isolation. Moreover, the two groups have been studied with different approaches (though using the same conceptual methodology discussed below). Despite these differences, the similarity in general pattern of evolutionary diversification is striking. In addition to these case studies, we will discuss evolutionary processes that may serve to obscure species-area relationships.

Methods

Our approach is straightforward: by examination of the geography of species in a phylogenetic context, we can estimate the extent to which the species on an island arrived there by colonization versus originating *in situ* by a speciation event in which one ancestral species divided into two descendant species. For islands with more than one species, colonization is indicated by the existence of distantly related species on the same island (figure 15.1A). The most parsimonious explanation of such a pattern is that the species are the descendants of independent colonization events. Conversely, the existence of a clade of species on an island suggests that the clade originated by the colonization of a single species that subsequently diversified *in situ*, producing many descendant species on that island (figure 15.1B). A clade of n species on an island would suggest the occurrence of at least $n - 1$ speciation events—“at least” because, of course,

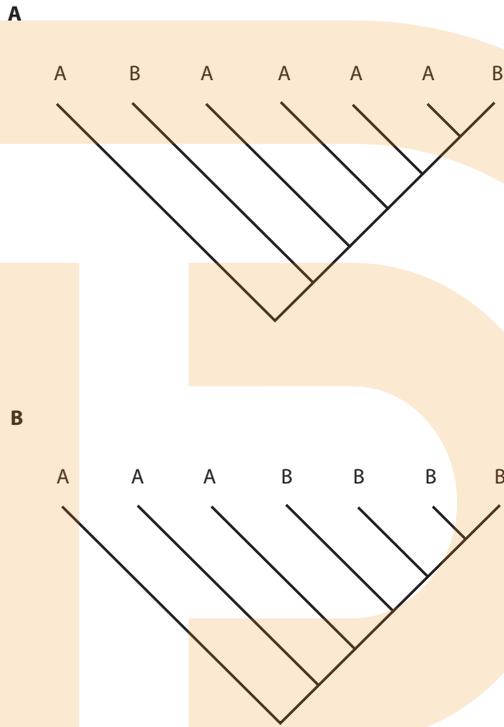


Figure 15.1. Reconstruction of colonization and within-island speciation from a phylogeny. In (A), two distantly related species occur on island B. The most parsimonious explanation is that they independently colonized the island. By contrast, in (B), a clade of species all occur on island B. The most parsimonious explanation in this case is that B was colonized once, followed by a number of speciation events on that island.

evidence of some speciation events may have been lost due to subsequent extinction.

Of course, this method is not infallible. For example, multiple colonization events followed by extinction of related species in the external source area may leave the descendants as sister species among extant taxa, thus erroneously implying the occurrence of within-island speciation (figure 15.2A). Although this alternative explanation is a possibility, it seems unlikely to account for the existence of large clades, such as in figure 15.1B, because it would require the extinction of so many related species on the ancestral island. On the other hand, within-island diversification could be mistaken for colonization if members of the radiating clade



Figure 15.2. Examples of how phylogenetic interpretations can be misleading. In (A), two species independently colonized island B, as in figure 15.1. However, subsequently, other species on island A went extinct, thus leaving the two species on island B as sister taxa among extant taxa, which would falsely suggest that they were the result of within-island speciation subsequent to a single colonization event. In (B), within-island speciation on island B produced a number of species as in Figure 1. Subsequently, however, several of these species sent off colonists to other islands, so that the species on B are no longer each other's closest relatives. As a result, evidence for within-island speciation on island B becomes less clear-cut.

send off colonists to other islands or back to the source area, thus breaking the monophyly of the species on the ancestral island (figure 15.2B).

The hypothesis we wish to test is simple: the extent of within-island diversification is a function of island area, with larger areas experiencing higher rates of diversification. A related question, should such a pattern be detected, concerns the cause of the relationship. Ecological investigations of the species-area relationship focus primarily on two explanations: increased habitat heterogeneity on larger islands may create a corresponding

increase in the number of different ecological types that can be supported, and island size per se may directly affect the number of species on an island, for example by the decreased extinction rate of the larger populations that may occur on larger islands (Ricklefs and Lovette 1999).

In a corresponding way, the same two factors may lead to a speciation-area relationship: On one hand, large islands may have more ecological heterogeneity, either directly sparking increased rates of speciation, as suggested by current ideas commonly referred to as “ecological speciation” (e.g., Rundle and Nosil 2005, Funk et al. 2006), or as a result of greater persistence (lower extinction rates) of newly speciated taxa which can avoid competitive exclusion by adapting to different habitats. Alternatively, larger islands may provide greater opportunity for populations to become isolated by geographical means (rivers, mountains, inhospitable habitat, etc.); the resulting higher speciation rates may lead to higher species richness, irrespective of any ecological differences among islands.

Anolis Lizards of the West Indies

Anolis is the second most species-rich genus of vertebrate, only slightly surpassed by frogs in the genus *Pristimantis* (Hedges et al. 2008). Currently, approximately 361 species are recognized, of which 155 occur in the West Indies and the rest in mainland Central and South America, plus one species native to the southeastern United States. In the West Indies, anoles are found on almost every emergent landmass more than a few square meters in area; species diversity ranges from one on many islands to more than 60 on Cuba (for a review of anole ecology and evolution, see Losos [2009]).

Examination of the species-area relationship for West Indian *Anolis* reveals a significant relationship, but one not well fit by linear regression (Rand 1969; Losos 1996). By contrast, a breakpoint regression indicates the existence of two lines, one which covers the majority of the range of island sizes and which fits the data poorly, and the second which includes the four large islands of the Greater Antilles and which fits the data extremely well (figure 15.3).

Species-Area Relationship on Smaller Islands

The poor fit of the regression for the smaller islands is readily explainable. This is a heterogeneous group of islands that have different underlying mechanisms determining their species richness. For example, the islands of the Great Bahama Bank were connected into one enormous landmass, almost the size of Cuba, during the last Ice Age. On the now

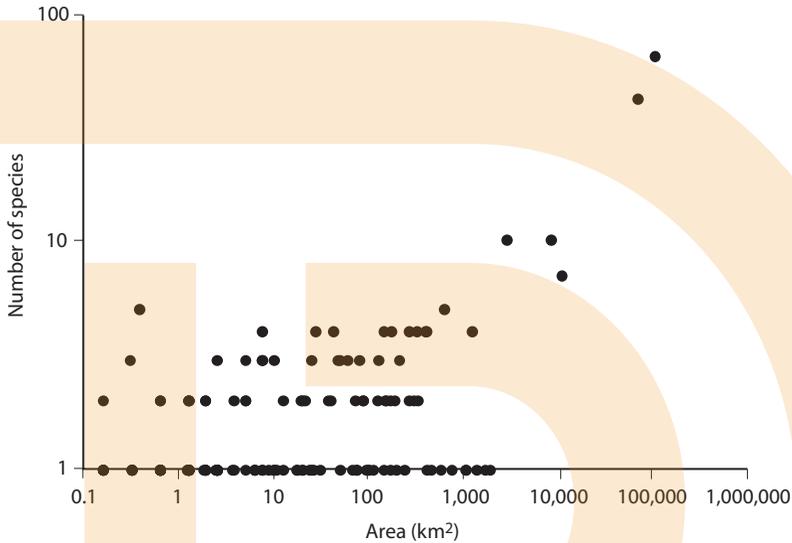


Figure 15.3. Relationship between island area and number of *Anolis* species in the West Indies. A linear regression on ln-transformed data is significant, but only explains 27% of the variation. However, a breakpoint regression finds two lines, one with a shallow slope over the majority of the area range which explains only 11% of the variation, and a second line with a much greater slope that fits the four largest islands and explains 93% of the variation in species numbers in those islands.

fragmented islands of this Bank (termed “land-bridge” islands because they used to be connected to a larger landmass), a very regular species-area relationship exists (figure 15.4A). The occurrence of species on these islands is strongly nested with respect to island area and is a classic example of faunal relaxation: when islands are fragmented, the smaller the island, the greater the number of species that become extinct (Wilcox 1978, Richman et al. 1988). To a large extent, this pattern of extinction is driven by habitat; as islands get smaller, they becoming increasingly less vegetated, and as a result, the more arboreal species vanish. A similar explanation accounts for the species-area relationship among islands that are located near, and formerly were connected to, Puerto Rico, Cuba, and Hispaniola (figure 15.4B). However, because the Greater Antilles have higher species diversity than the large islands of the Bahamas, small islands near the Greater Antilles have greater species richness than islands of similar size on the Bahamas Bank; this difference partially explains the poor predictive ability of area when these islands are considered together.

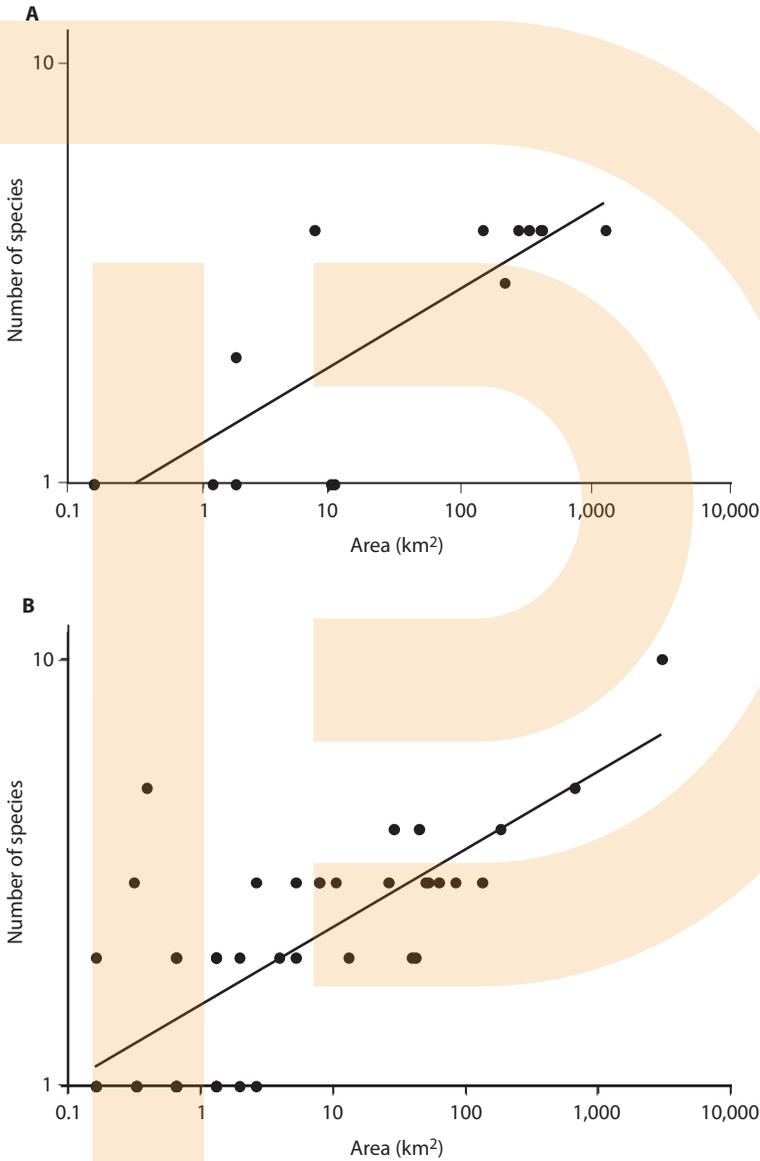


Figure 15.4. Relationship between island area and number of *Anolis* species on subsets of West Indian islands. A. Islands on the Great Bahama bank. B. Islands located near Cuba, Puerto Rico, and Hispaniola which were connected to these larger landmasses at times of lower sea levels (termed “land-bridge” islands). C. Oceanic islands in the West Indies.

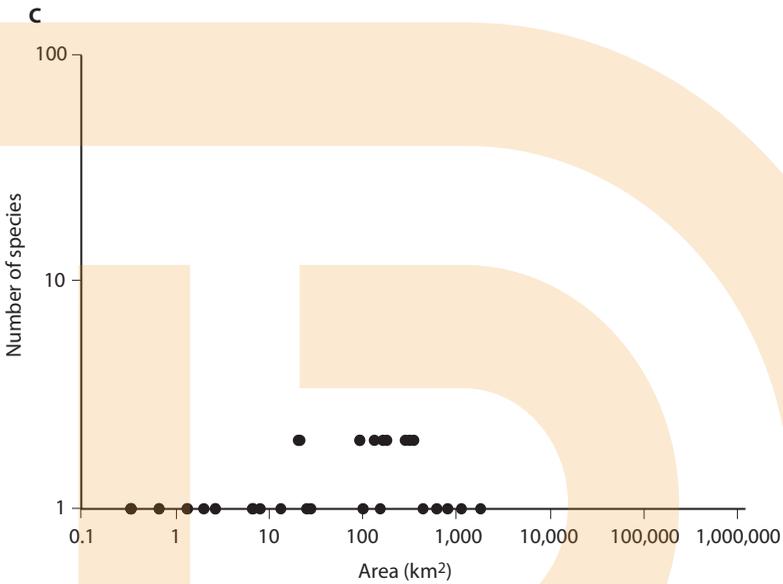


Figure 15.4. (continued)

More important in disrupting the species-area relationship, however, are the oceanic islands of the Caribbean, islands that were never connected to larger landmasses and thus must have received their anoles as a result of overwater colonization. These islands include not only the Lesser Antilles chain, but also islands scattered throughout the northern Caribbean, such as the Cayman Islands, St. Croix, Mona, Navassa, and others. In contrast to the extinction-structured diversity of land-bridge islands, oceanic islands never contain more than two species. Although the distance to the Lesser Antilles might account for this low number, even oceanic islands near the Greater Antilles only contain at most two species, even though some of these islands are much larger than some land-bridge islands that contain 3–4 species. Moreover, no area effect is evident among oceanic islands; in fact, the largest islands in the Lesser Antilles only harbor a single anole species (figure 15.4C).

Speciation-Area Relationship in the Greater Antilles

In contrast to the weak relationship among smaller islands, the four largest Caribbean islands, the Greater Antilles, exhibit a tight species-area relationship with a much elevated slope. What might explain this difference? One obvious possibility is that the species richness of larger islands is being augmented by *in situ* evolutionary diversification.

Examination of the phylogeny of *Anolis* (Nicholson et al., 2005; for review of anole phylogenetics, see Losos [2009]) reveals several patterns. First, ample evidence exists for within-island speciation in the Greater Antilles. For example, six of the seven species on Jamaica are closely related members of the *grahami* series, indicating the occurrence of at least five speciation events on Jamaica.¹ Puerto Rico contains three anole lineages, two of which only contain one species, but the third has eight species. Similarly, Hispaniola and Cuba harbor many lineages, containing 1–33 species.

By contrast, almost no evidence suggests the occurrence of within-island speciation on any island smaller in size than Puerto Rico (Losos and Schluter 2000). This pattern suggests an area threshold below which speciation occurs rarely, if at all. Such a high threshold—approximately 9,000 km²—is unexpected. Although some smaller islands have only been recently isolated, others are geologically very old and, according to molecular estimates, have harbored their anoles for many millions of years (e.g., Malhotra and Thorpe 1994, Schneider 1996). Moreover, many of these islands exhibit great habitat heterogeneity and substantial elevational relief, and even have offshore islets upon which populations might be isolated. Why speciation has not occurred on any of these islands is a mystery, although not a unique one: in a consideration of isolated oceanic islands in the Pacific, Diamond (1977) noted that no island smaller than New Guinea had experienced a within-island speciation event among birds, a finding later corroborated by Coyne and Price (2000).

Examination of the Greater Antilles indicates that the vast majority of the species diversity is the result of within-island diversification; at most 11 between island speciation events are required to explain the distribution of species across islands (unfortunately, uncertainty about Caribbean geology precludes distinguishing between colonization and vicariance as the cause of between island speciation [see Losos 2009]); consequently, more than 90% of the 121 species in the Greater Antilles have resulted from *in situ* evolutionary diversification.

Second, quantitative analysis indicates that the rate of speciation on Greater Antillean islands is strongly correlated with island area (figure 15.5; Losos and Schluter 2000). This result is based on a regression of

¹The *grahami* series has one other member, *A. conspersus* on Grand Cayman. This species is clearly derived from within *A. grahami* itself (Jackman et al. 2002) and thus is clearly a case of a colonization event from Jamaica to Grand Cayman. Thus, the *grahami* series is not, technically, monophyletic on Jamaica. Nonetheless, the phylogeny clearly indicates the existence of multiple speciation events on Jamaica. Similar examples occur in several other of the island clades discussed here (e.g., the *carolinensis* species group on Cuba [Glor et al. 2005]).

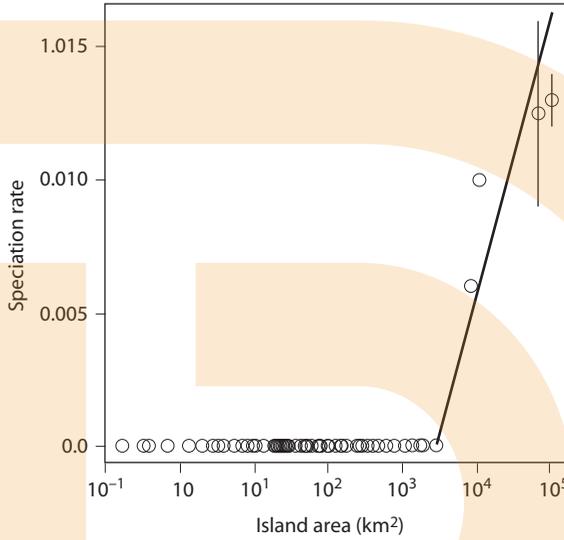


Figure 15.5. Speciation-area relationship in the Greater Antilles. Rates of speciation were estimated from the phylogenetic relationships of Greater Antillean anoles, assuming that the presence of sister taxa on the same island indicates the existence of a within-island speciation events. Error bars on the two larger islands reveal uncertainty in assignment of ancestral locations deep in the phylogeny—essentially, either Hispaniola or Cuba could be the ancestral home from which the other island was colonized multiple times (see discussion in Losos 2009); this uncertainty changes the identification of within-island speciation events deep in the phylogeny, leading to slight changes in estimated speciation rates (Losos and Schluter 2000).

the minimum number of speciation events inferred to have occurred on each island versus island area and is scaled to branch lengths on the phylogeny. These analyses also suggest, using maximum likelihood methods, that the diversification-area relationship results primarily, if not exclusively, from a relationship between speciation and island area, rather than from area effects on extinction rates (Losos and Schluter 2000).

Determinants of the Speciation-Area Relationship

Given that a speciation-area relationship exists for West Indian *Anolis*, the next question is: what drives that relationship? One possibility is that greater ecological specialization occurs on larger islands. To assess this possibility, we consider three components of anole diversity:

1. *Ecomorphs*. The Greater Antilles are famous for the evolution of the same set of habitat specialists on each island, called “ecomorphs” and named for the part of the structural habitat they utilize (e.g., trunk-ground, trunk-crown, twig). Phylogenetic analysis indicates that the ecomorphs on each island have evolved for the most part independently, producing much the same evolutionary end point (Williams 1983, Losos et al. 1998). Although six ecomorph types are recognized (reviewed in Losos 2009), only four occur on all four islands in the Greater Antilles; the grass-bush ecomorph is absent from Jamaica and the trunk ecomorph from Jamaica and Puerto Rico. Consequently, the ecomorph phenomenon contributes in a small way to the species-area relationship, as the larger two islands have six ecomorphs, whereas the smaller two islands have only four and five.

2. *Unique habitat specialists*. In contrast to the ecomorphs, a number of habitat specialists have evolved on only a single island, with no parallel on other islands. These unique types include a species that always occurs near streams and both escapes and forages in the water (*A. vermiculatus*, Cuba); giant, chameleon-like species specialized for eating mollusks and other hard-bodied prey (Chamaeleolis clade, formerly considered its own genus, but now recognized to have evolved within *Anolis*, Cuba); and a leaf-litter specialist from Hispaniola (*Chamaelinorops* clade, also formerly considered its own genus, Hispaniola). Six such types occur on Hispaniola, five on Cuba, one on Jamaica, and none on Puerto Rico. Thus, the evolution of unique types has also contributed somewhat to the species-area relationship.

3. *Within-habitat specialist clade diversification*. By far the largest component of anole species diversity in the Greater Antilles has resulted from species proliferation within clades of microhabitat specialists. Thus, the *sagrei* clade of trunk-ground anoles is comprised of 14 trunk-ground species on Cuba, the *alutaceus* clade of grass-bush anoles contains 14 grass-bush anoles on Cuba, and the *cybotes* clade of trunk-ground anoles sports nine species on Hispaniola. Several unique habitat specialists also have speciated extensively, most notably the five members of the Chamaeleolis clade in Cuba. Overall, 52 of the species on Cuba represent multiple species within clades of habitat specialists (i.e., 63 species on Cuba, minus the 11 independent evolutionary instances of habitat specialization), compared to 29 such species on Hispaniola, five on Puerto Rico, and one on Jamaica.

Some of this within-habitat specialist diversification has involved adaptation to different parts of the environment to permit resource partitioning and coexistence. For example, on all four islands, large and small species

of trunk-crown anole have evolved, presumably to minimize competition for food. In addition, within trunk-ground and grass-bush clades on several islands, species have evolved different thermal physiological tolerances, permitting partitioning of thermal microclimates within localities (reviewed in Losos 2009).

Most within-specialist clade speciation, however, appears more related to geography than adaptive divergence. Many—perhaps most—of these species are allo- or parapatrically distributed and have small geographic ranges, often centered on different mountain ranges. In the *alutaceus* clade, for example, two species are island-wide in Cuba, but the other 12 have very small distributions, mostly in mountainous eastern Cuba. The natural history of many of these species is poorly known, but it seems likely that much of this diversity is the result of the allopatric speciation across the rugged landscape of these islands. The greater speciation rate of these clades on larger islands, then, may primarily be a consequence of the greater opportunity afforded for geographical isolation and speciation on the larger—and very mountainous—landmasses of Cuba and Hispaniola.

To summarize the anole story: islands smaller than the size of Puerto Rico have not experienced within-island speciation; their diversity is solely the result of the ecological processes of colonization and extinction. By contrast, more than 90% of the species on the four large islands of the Greater Antilles have arisen *in situ*. The strong species-area relationship for these islands is thus a consequence of a speciation-area relationship. Although some of this relationship results because more habitat specialists occur on larger islands, the majority of diversity stems from a greater rate of within-habitat specialist speciation on larger islands; this increased rate may result primarily from the greater opportunity for speciation to occur on larger islands.

Bulimulid Land Snails of the Galápagos

With over 70 described species (Chambers 1991), the bulimulid land snails of the Galápagos represent the most species-rich radiation of these islands. The entire group *Bulimulus*, subgenus *Naesiotus* (sometimes considered its own genus) to which Galápagos bulimulids belong includes 162 known species distributed in South America, from Venezuela to Argentina (mostly in the Andean region) and in the southern half of Brazil (Breure 1979). All Galápagos bulimulid species are endemic, and current phylogenetic evidence based on multiple independent molecular markers suggests that all species studied in detail are single island endemics (Parent and Crespi 2006).

Bulimulids have colonized all of the major Galápagos islands, and they are found at all elevations except on the shoreline, which is composed mainly of lava boulders and sandy beaches. Vegetation on the Galápagos can be separated into 6–7 altitudinal zones (Wiggins and Porter 1971, van der Werff 1979), and the plant-species composition of each zone is a reflection of the humidity level of the zone, with moisture level increasing with elevation (McMullen 1999). Galápagos bulimulid species vary remarkably in shell size, shape, color, and color pattern, and this morphological variation in shell morphology is related at least partly to aspects of ecological variation, including vegetation zones, related moisture levels, and microhabitat (Coppo and Glowacki 1983). Furthermore, a significant positive correlation between shell shape (degree of shell roundness) and elevation suggests that snail species have adapted morphologically to the varying moisture levels (Parent, unpublished data). Since plants provide food and shelter, and probably most importantly, habitat structure, land snails have potentially adapted to different plant species for feeding, hiding, or resting.

The geological history of the Galápagos archipelago is relatively well understood, with individual islands formed as the Nazca plate moved over a single active hot spot, presumably currently located under the volcanically active Fernandina Island (White et al. 1993). Española, Santa Fe, and San Cristobal are the oldest islands of the archipelago (2.35–3.90 million years [my] old); Santa Cruz, Floreana, Pinzon and Santiago islands form a middle-aged group (0.77–1.52 my old), and finally the most recent group of islands includes Isabela and Fernandina islands (less than 0.7 my old). Isabela Island is formed by six major volcanoes that are separated by extensive barren lava flows. Bulimulid land snails cannot survive without a minimum of vegetation for food and shelter, and thus they are not found at low elevations between the volcanoes forming Isabela. Therefore, each volcano forming Isabela Island can be considered as a separate island with regard to bulimulid land snail distribution.

The colonization sequence of the Galápagos bulimulid lineage (inferred from a molecular-based phylogeny) was found to roughly parallel the geological order of the islands (Parent and Crespi 2006), supporting the progression rule hypothesis with species found on older emerged islands connecting at deeper nodes (see chapters in this volume by Whittaker, and by Gillespie and Baldwin).

We determined the importance of island area, habitat diversity (measured as the number of native plant species), island insularity (measured as distance from the nearest older major island), and island age on island species diversity. We used data from Parent and Crespi (2006) to reanalyze the role that island area has in combination with island habitat diversity, insularity and age on (1) total island species diversity, (2) diversity due to within-island speciation, and (3) diversity due to between-island colonization.

We used a phylogeny based on multiple independent DNA markers (Parent and Crespi 2006) to distinguish species that arose *in situ* on an island from those that arrived by colonization from another island. In these analyses, we also included species that are the sole inhabitant of islands, because even if they are not represented on the phylogeny, we can safely infer that they arose by between-island colonization. Following this method we inferred 25 colonization and 15 speciation events for a total of 40 species distributed over 14 islands.

An examination of the species diversity for Galápagos bulimulids highlights several points:

1. Variation in the total bulimulid species richness among Galápagos islands is significantly explained by island area when considering the total number of species on islands or including only species resulting from *in situ* speciation. However, the species-area relationship is not significant when only species resulting from between-island colonization are considered (figure 15.6).

2. The speciation-area relationship in bulimulid land snails suggests that there is an island area threshold below which *in situ* speciation rarely occurs (figure 15.6, solid circles). Neither of the islands smaller than Pinzón (18.1 km²) has experienced an *in situ* speciation event, and very little *in situ* speciation occurred on islands smaller than Floreana (172.5 km²). Interpretation of these trends is complicated due to the confounding factors of island age and vegetational diversity. For example, the four islands larger than Pinzón that do not have species resulting from *in situ* speciation have particularly low plant species diversity for their area due to either their low elevation (Marchena and Española) or geologically young age (Fernandina, and volcanoes Darwin and Wolf on Isabela Island).

3. The young islands of Fernandina and Isabela together form over 60% of Galápagos total land area, but only 12 of the 71 described bulimulid land snail species (about 17%) are found on these islands. Although the total species-island age relationship is marginally nonsignificant (adjusted $R^2=0.15$, $p=0.097$), this pattern suggests that at least some of the youngest islands have not reached their equilibrium species diversity (cf. chapter by Gillespie and Baldwin).²

4. When we focus on the total species-area relationship, linear regression does not fit the total species diversity data very well (figure 15.6). However, the species-area relationship fits the data much better when cor-

²Unfortunately, the geological history of the Caribbean is too complicated and poorly understood to allow comparable analyses for *Anolis*. However, phylogenetic information indicates that three of the four Greater Antillean islands have been occupied for long and roughly similar amounts of time, which suggests that age effects may not be of primary importance in determining species richness, a point further reaffirmed by the failure to speciate of some old lineages in the Lesser Antilles (for review, see Losos 2009).

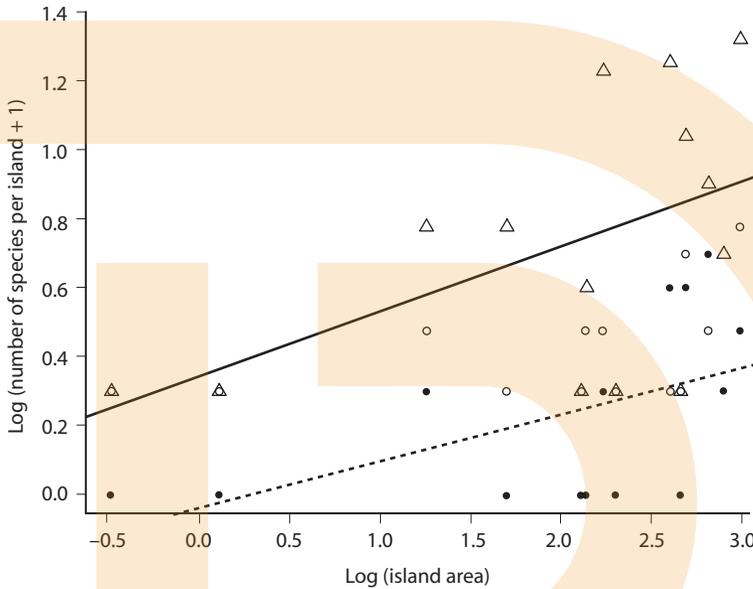


Figure 15.6. Regression of island area against the total number of bulimulid land snail species (open triangle; adjusted $R^2=0.20$, $p=0.062$), the number of species inferred to have resulted from within-island speciation (filled circles; adjusted $R^2=0.22$, $p=0.053$), and the number of species inferred to have resulted from between-island colonization on the Galápagos Islands (open circles; adjusted $R^2=0.071$, $p=0.183$).

recting total species diversity for island age (using the standardized residuals of island species diversity against age; figure 15.7; table 15.1). Likewise, the speciation-area relationship fits the data better once the number of speciation events is corrected for island age (figure 15.7; table 15.1).

5. Although island insularity does not have a significant effect on total island species richness on its own or combined with other biogeographical factors, we found that it does contribute to the species richness resulting from interisland colonization (figure 15.7; table 15.1), as predicted by MacArthur and Wilson. Indeed, we find that the colonization-area relationship fits the data better once the number of colonization events is corrected for island insularity (table 15.1).

6. The species-habitat diversity and speciation-habitat diversity relationships (both corrected for island age as above) provide an even better fit to the species diversity data (figure 15.8, table 15.1) than the species-area relationship corrected for island age (figure 15.7). Island area is often related to habitat diversity (Ricklefs and Lovette 1999, Whittaker and Fernández-Palacios 2007), but the number of plant species can provide a

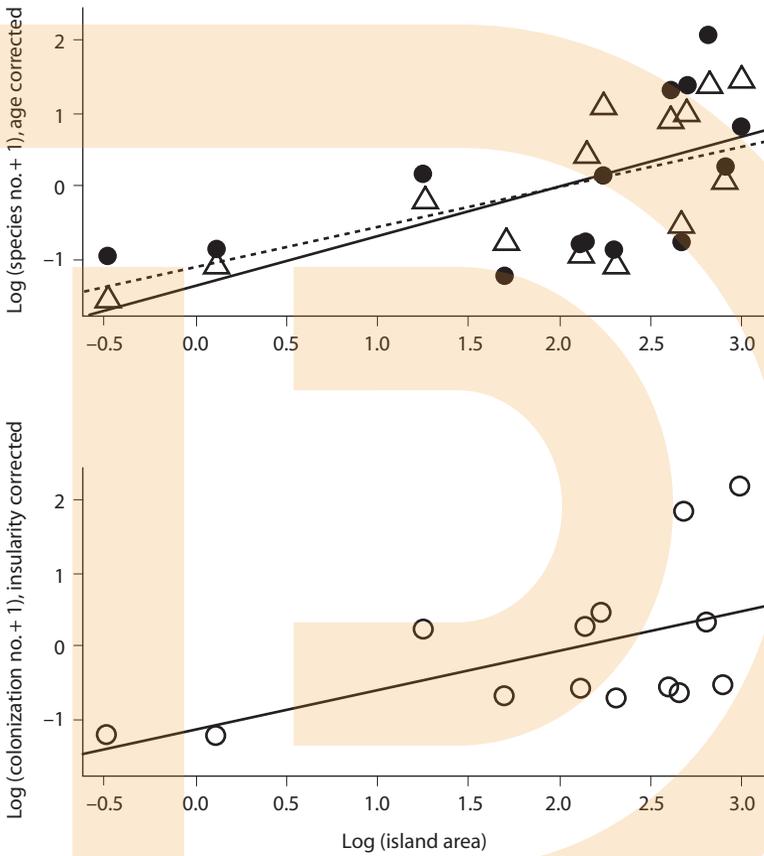


Figure 15.7. Regression of island area against the total number of Galápagos bulimulid land snail species (top panel; open triangle; adjusted $R^2=0.43$, $p=0.006$), the number of species inferred to have resulted from within-island speciation (top panel; filled circles; adjusted $R^2=0.24$, $p=0.044$), both corrected for island age, and the number of species inferred to have resulted from between-island colonization, corrected for island insularity (bottom panel; adjusted $R^2=0.24$, $p=0.043$).

more direct measure of habitat diversity for land snails or other animals whose ecology is directly related to plant diversity.

The significant “speciation-area” relationship compared to the much weaker “colonization-area” suggests that the overall species-area relationship is primarily the result of the contribution of within-island speciation to total island species diversity. Nevertheless, habitat diversity explains a

TABLE 15.1
 Results of Forward Stepwise Multiple Regression Analyses for Different Models

<i>Model</i>	<i>Independent variables</i>	<i>n</i>	β	<i>SE of β</i>	<i>t</i>
Overall species diversity	Island area	26	0.23***	0.058	3.93
Adjusted $R^2=0.37^{**}$	Island age		0.23*	0.093	2.45
Within-island speciation	Island area	14	0.036**	0.011	3.14
Adjusted $R^2=0.39^*$	Island age		0.59	0.44	1.34
Overall species diversity	Island habitat diversity	26	0.54***	0.12	4.41
Adjusted $R^2=0.43^{***}$	Island age		0.11	0.084	1.34
Within-island speciation	Island habitat diversity	14	0.0044**	0.0012	3.46
Adjusted $R^2=0.44^*$	Island age		0.10	0.41	0.24
Between-island speciation	Island area	14	0.026*	0.0091	2.86
Adjusted $R^2=0.35^*$	Island insularity		-0.00001*	0.0000042	-2.42

Notes: The number of bulimulid land snail species is used as dependent variable for all models considered. All variables were transformed to meet the assumptions of parametric statistics. The sample size (*n*) is provided for each model, as well as the standardized regression coefficient (β) and the test statistic (*t*) for each independent variable entered in each model. *P* values for adjusted R^2 and β values are indicated as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

greater proportion of the variation in number of age-corrected speciation events than island area (figure 15.8). In fact, multiple regression analysis reveals no area effect once habitat diversity is considered (Parent and Crespi 2006). This result, combined with the lack of detection of a habitat diversity effect for between-island colonization diversity, implies that an island with more plant diversity will accumulate more species mainly because it will be more likely to provide more opportunity for species differentiation and speciation, rather than offering more suitable habitat for colonizing

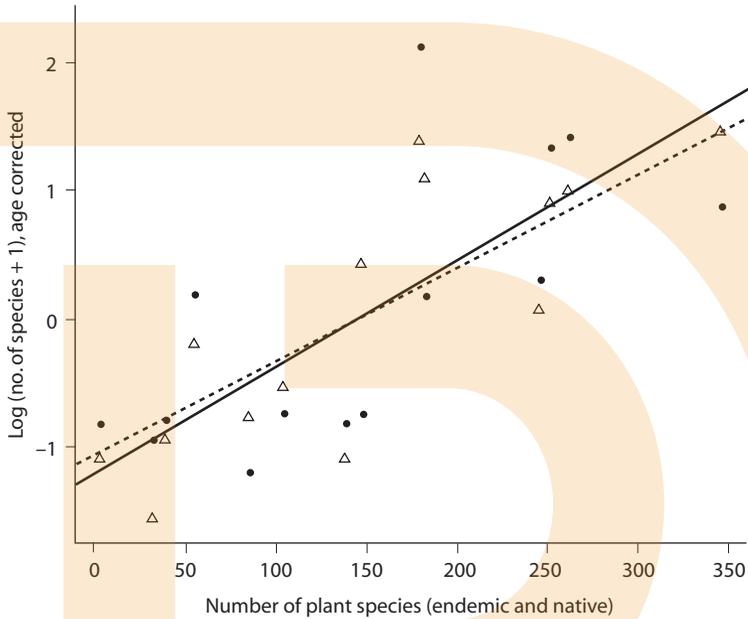


Figure 15.8. Regression of the total number of Galápagos bulimulid land snail species (open triangle; adjusted $R^2=0.65$, $p=0.0003$) and the number of species inferred to have resulted from within-island speciation (filled circles; adjusted $R^2=0.45$, $p=0.005$), both corrected for island age, against island habitat diversity measured as the number of endemic and native plant species.

species. Different faunal groups can differ in their responses to area and habitat diversity, so that area, habitat diversity or a combination of both have strong effects on species richness depending on the biological traits of the different taxonomic groups (Ricklefs and Lovette 1999). Galápagos bulimulid land snail species have adapted to the different vegetation zones, and most species are found on specific plants or defined microhabitats (Coppo and Glowacki 1983, Parent, unpublished data). Thus adaptation to specific vegetation types apparently provides the opportunity for bulimulid snails to differentiate within-island and partition the niche space to allow species to co-occur and accumulate on a given island.

To summarize the bulimulid story: in contrast to *Anolis*, colonization accounts for more species diversity than speciation in bulimulid species diversity. Nonetheless, like *Anolis*, the species area relationship primarily results from greater amounts of within-island diversification on larger and more habitat diverse islands. Unlike *Anolis*, habitat diversity, rather than area effects on speciation per se, seem to account for the speciation-area relationship.

Other Evolutionary Factors Besides Area Affecting Species Diversity on Islands

In addition to island area, a number of other factors could affect the rate of species diversification on islands. For the most part, these factors are independent of area; thus, to the extent that they are important, these factors may tend to diminish the relationship between island area and rates of within-island diversification.

Isolation

Classically, island isolation acts to decrease the rate of colonization and thus, in the MacArthur and Wilson theory, to lower the equilibrium number of species expected on an island, as we found with bulimulid snails. Moreover, to the extent that distant islands are impoverished faunistically and, particularly, floristically, they may be less able to support other species (Lack 1976).

By contrast, for several reasons, isolation may serve to increase the rate of within-island speciation (e.g., MacArthur and Wilson 1963, 1967, Heaney 2000, 2007):

1. More distant islands are likely to experience less ongoing gene flow, thus increasing the likelihood that an island population could diverge and speciate from its ancestral population and subsequently diversify *in situ*.
2. More distant islands, being impoverished biotically, may harbor fewer competitor species, thus facilitating adaptive radiation of a successful colonist.
3. Moreover, the disharmonic nature of distant island faunas—with some mainland taxa represented and others not—is likely to substantially alter patterns of natural selection stemming from interspecific interactions, thus driving ecological adaptation, and enhancing the likelihood of speciation.

We are unaware of any studies that have demonstrated any of these phenomena, but they certainly are plausible in principle.

Island Configuration

MacArthur and Wilson (1963) noted: “adaptive radiation takes place as species are generated within archipelagoes, disperse between islands, and, most importantly, accumulate on individual islands to form diversified associations of sympatric species.” This view encompasses the classic view of adaptive radiation, exemplified by Darwin’s finches of the Galápagos: allopatric speciation occurring on separate islands in an archipelago followed by secondary reinvasion can result in the build-up of

species richness and adaptive radiation. The importance of island configuration is clearly seen in Darwin's finches (e.g., Grant and Grant 2008, this volume). In contrast to the great diversity of this clade in the Galápagos, the only other Darwin's finch, on isolated and vegetationally diverse Cocos Island in the Pacific Ocean, has failed to diversify, despite having occurred there for a long period of time. Presumably, the lack of opportunity for allopatric speciation has prevented speciation on Cocos and facilitated it in the Galápagos.

We are unaware of any quantitative treatment of this subject, but again it seems likely that diversification would be greater in an archipelagic setting, particularly for species, such as birds, which are unlikely to speciate on single, isolated islands.

Such speciation would not constitute within-island speciation; rather, in the MacArthur and Wilson framework, it would result in an evolutionarily increasing pool of potential colonists.³ That is, usually the source pool of species is considered to be the number of species on the nearby mainland. With intra-archipelagic speciation, the source pool for each island in the archipelago would be enhanced by the species that evolved on the other islands, thus leading to a higher equilibrium number than would occur on isolated islands.

Age

Time might be related to evolutionary diversification in several different ways. On one hand, one might expect that the longer a clade has occurred on an island, the greater the opportunities for speciation and the greater the number of resulting species would be (Heaney 2000), as appears to be the case for bulimulid snails. A similar positive association between *in situ* speciation and island age has been suggested in a preliminary study of diversification in Galápagos beetle genus *Galapaganus* (Sequeira et al. 2008). This expectation seems reasonable, particularly for isolated islands which might not reach their carrying capacity of species.

On the other hand, long-jawed spiders (*Tetragnatha*) in the Hawaiian Islands reach their greatest diversity on middle-aged (and middle-sized) islands. Gillespie (2004) suggested the following scenario: young islands have not had enough time to generate their equilibrium number of species.

³As figure 15.2b demonstrates, understanding the geography of speciation in an archipelago may be challenging. If an ancestral species diverges into two species on one island, but then the two species each colonize other islands in the archipelago, then the initial within-island speciation event may not be evident on a phylogeny because each species has as its closest relative a species on another island.

Middle-aged islands have been colonized by a number of lineages, each of which has diversified. However, the descendants of such species have not had time to disperse widely, and as a result, the descendants of different colonists have not yet come into contact. Given enough time, as has occurred on older islands, these species do increase their range and come into contact with each other. At that point, interspecific interactions—probably primarily competition—lead to the elimination of some species (see the chapter by Gillespie and Baldwin for a broader discussion of age effects in diverse Hawaiian lineages).

Although direct evidence of interaction-driven extinction on older islands is not available, such an ecological overshoot is also seen in recolonization experiments over ecological time (Simberloff and Wilson 1969); other workers have suggested that a similar evolutionary phenomenon occurs in other systems (Gillespie 2004, Gavrilets and Vose 2005, Seehausen 2006).

Finally, islands themselves evolve through time. Whittaker (this volume) suggests that volcanic islands may go through a life cycle in which species number is maximized early in the history of the island and then decreases through time as the island subsides and erodes. Such a phenomenon is seen in *Tarphius* beetles in the Canary Islands (Emerson and Oromi 2005). Interestingly, the hump-shaped pattern of species richness through time in these beetles is entirely determined by the number of species generated by within-island speciation, as the number of colonization-derived species per island is roughly constant. Situations such as this and the Hawaiian *Tetragantha* also are among that small group of case studies alluded to by Lomolino in the opening quote that do not exhibit a species-area relationship; they represent situations in which age-dependent effects on species richness outweigh area effects.

Conclusion

This is an exciting time for those interested in the determinants of species richness on islands. Thanks in large part to the great current interest in applying phylogenetic approaches to the understanding of macroevolutionary questions, as well as to a desire by many to integrate ecological and evolutionary thinking (e.g., Whittaker and Fernández-Palacios 2007; Emerson and Gillespie, 2008), the opportunity to understand the evolutionary aspect of species richness has never been greater.

At this point few studies exist in which we can quantitatively assess the relative significance of ecological and evolutionary processes, but this situation is likely to change soon with the flood of phylogenetic information

that is rapidly becoming available. With this information, we will be able to answer questions such as:

- What circumstances determine the relative importance of ecological and evolutionary processes?
- How common are island threshold sizes below which *in situ* diversification does not occur?
- Under what circumstances do isolation, configuration, and age effects predominate?

By the time the MacArthur and Wilson theory reaches its fiftieth anniversary, we predict that a rich and varied data base will exist to provide answers to these questions and many more, and thus to fully integrate evolutionary considerations into island biogeography theory, a goal clearly articulated by MacArthur and Wilson (1963, 1967), but only now being realized.

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