Biogeographical and Ecological Determinants of Land Snail Diversification on Islands

Biogeographical and ecological determinants of land snail diversification on islands*

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Abstract: The equilibrium theory of island biogeography as originally proposed by R. MacArthur and E. O. Wilson relied on the ecological processes of colonization and extinction to determine the species diversity of islands. Although they were well aware of the potential contribution of speciation within-island to species diversity, MacArthur and Wilson's equilibrium model was purely ecological and did not incorporate the evolutionary process of diversification. This might seem surprising given that the best-known examples of adaptive radiation, the diversification of a single ancestral species into descendant species occupying a wide variety of ecological niches, are found on island systems. Recently, it has become possible to quantify the relative contribution of between-island colonization and within-island speciation to species diversity with the use of molecular phylogenies. By providing an estimate of the historical relationship among species, phylogenies can be used in combination with information on species' geographical distributions to infer the geographical zone of origin of species. Here I use this process-oriented analysis to determine the main predictors of diversification in three unique insular land snail lineages: the Galápagos Bulimulidae, the Hawaiian Succineidae and the Hawaiian Achatinellinae. I find that in Galápagos bulimulid land snails, species richness resulting from between-island colonization is mainly driven by island area and insularity, whereas species richness resulting from within-island speciation is mainly determined by habitat heterogeneity. In contrast, I find that within-island species diversification is driven by island area in Hawaiian succineids, and the probability of speciation via between-island colonization in this group is significantly greater on younger islands. None of best multiple regression models proposed to explain variation in Hawaiian Achatinellinae species diversity were significant.

Key words: Achatinellinae, Bulimulidae, Succineidae, Galápagos, Hawaii

For years biologists have recognized the unique value of oceanic islands for the study of ecological and evolutionary processes. If part of an archipelago, islands become a series of replicates within a large evolutionary natural experiment, making them scientifically even more appealing. Over the years, research focusing on island biotas has led to the development of ideas within a wide range of fields including biogeography and the formation of species.

The theory of island biogeography as initially proposed by MacArthur and Wilson (1963, 1967) stated that variation in rates of inter-island colonization and extinction generates and maintains island species diversity. Less isolated islands presumably receive a high number of colonists and, therefore, reach higher equilibrium diversity. Larger islands carry species with larger population size, and because larger populations are less likely to be driven to extinction by stochastic processes, larger islands are expected to maintain higher equilibrium diversity. Larger islands often also have greater habitat heterogeneity, which in turn could allow for the co-existence of more species diversity. However, because island area and habitat heterogeneity are frequently correlated, it has been difficult to disentangle the roles of habitat heterogeneity and island area. Since the original formulation of the theory of island biogeography, numerous studies have shown that island insularity and area (and sometimes habitat heterogeneity) are significant predictors of total island species richness (Triantis *et al.* 2008).

Though MacArthur and Wilson's ecological theory of island biogeography includes the process of speciation (MacArthur and Wilson 1963, 1967), the empirical tests of their model most often assumed that the only source of species diversity is colonization from external pools. However islands are also known as natural laboratories of evolution, and many of the most famous cases of island diversity are the result of within-island formation of new diversity via speciation (Losos and Ricklefs 2009 and references therein). Until recently it has been impossible to determine the relative contribution of speciation due to between-island colonization and within-island speciation to total island species richness, and therefore impossible to disentangle the effects that biogeographical

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factors (such as island area) have on colonization versus speciation. However, the increasing accumulation of molecular phylogenies has prompted a new approach to the species-richness problem with the integration of evolutionary history in community assembly studies. Here, phylogenies can be used in combination with geographical distributions and simple parsimony to infer the geographical zone of origin of species. In insular contexts, this implies that the processes of within-island speciation versus speciation due to between-island colonization can be differentiated, quantified, and studied separately (Fig. 1). By partitioning species diversity into these two components, it becomes possible to separately evaluate the importance of biogeographical factors (such as island insularity, area, habitat heterogeneity, and age) on within-island speciation and between-island colonization (Parent and Crespi 2006). This is a novel, conceptually simple approach to a very old and general problem about how environmental variation (here, species richness) arises. This approach should inform us of the ecological and evolutionary processes involved in the formation of species at the community level, as well as the relative importance that various biogeographical and ecological factors have on these processes.

Many organisms have diversified within archipelagos, and, in general, invertebrate lineages have evolved into great numbers of species. However, land snails are of particular interest: with their low dispersal ability over short temporal and spatial scales, combined with their potential for long distance dispersal over longer time scales, they are ideal candidates for diversification on islands. Not only can land snails reach very isolated islands, once established they will usually diversify

and multiply, presumably as a result of the combination of geographical isolation and local adaptation.

In this paper, I first outline a methodological approach combining phylogenetic and biogeographical data to partition species richness on islands into its driving processes. I then use this approach to evaluate the importance of biogeographical and ecological factors in generating species richness on islands via speciation *in situ* and speciation due to between-island colonization in three endemic lineages of insular land snails: the bulimulid land snails of the Galápagos, and the amber snails (Succineidae) and tree snails (Achatinellinae) of the Hawaiian Islands. I conclude the paper with a discussion of the prospects and limitations of the approach to the study of island diversity presented here.

STUDY SYSTEMS

Galápagos Islands

The Galápagos Islands are located in the Pacific Ocean, about 960 km west of the South American coast, straddling the equator at the 90th meridian west. The Galápagos archipelago is composed of 13 major islands larger than 10 km^2, and numerous smaller islands, islets and rocks, for a total of about 8000 km^2 of land spread over 45 000 km^2 of water (Snell *et al*. 1996). Of these islands, Isabela is the largest (more than the total area of all the other islands combined) with an area of 4588 km^2 and the highest, with a maximum elevation of just over 1700 m. Isabela is formed by six volcanoes interconnected mostly by barren lava flows, that may represent a geographical barrier to dispersal analogous to open water for land snails.

The Galápagos Islands are a young, oceanic, volcanic archipelago with a relatively well-understood geological history (Nordlie 1973, Swanson *et al*. 1974, Bailey 1976, Cox 1983, Hall 1983, White *et al*. 1993, Geist 1996). Potassium-argon (K-Ar) age determinations and marine fossils indicate a maximum age of the oldest currently existing island on the order of 3 million years (Myr) ago, whereas geological plate motion models set a maximum age of emergence around 4 Myr ago, depending on the velocity of the Nazca plate (White et al. 1993, Geist 1996). In contrast to the roughly linear arrangement by age of the Hawaiian Islands (Price and Clague 2002), the Galápagos Islands are clustered into groups of similar age (White *et al*. 1993). Vegetation on Galápagos can be separated into six (or seven) 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).

Like that of many other isolated oceanic islands, the Galápagos fauna is impoverished and taxonomically unbalanced
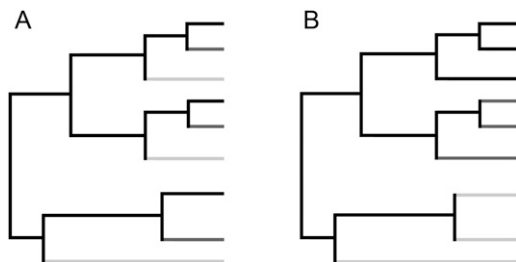
Figure 1. Phylogenetic partitioning of within-island speciation and speciation due to between-island colonization. Species branches are shaded according to island where they are found (three shades of gray corresponding to three putative islands). If branching is associated with shift in shading, we infer speciation due to between-island colonization; if there is no shift in shading, we infer within-island speciation. Six species in scenario **A** are the result of between-island colonization and 3 are the result of within-island speciation; scenario **B** depicts 3 speciation events due to between-island colonization and 6 following within-island speciation events.

when compared to Neotropical source areas. Because of their isolation and arid climate, the Galápagos Islands have been successfully colonized by only a subset of the diverse flora and fauna of the closest continent. Although relatively few lineages of Galápagos terrestrial fauna have diversified within the archipelago (associated with adaptation or not), the species resulting from this diversification process constitute a large proportion of the terrestrial fauna of the islands.

Galápagos Bulimulidae

With 71 described species grouped in one genus, the radiation of Galápagos bulimulid land snails is the most spectacular in the biota of these islands in terms of species number (Chambers 1991, Parent *et al*. 2008). Of the nine other land snail genera that have colonized the islands, only one radiated and gave rise to 4 species (Smith 1966). All Galápagos bulimulid species are endemic, and current phylogenetic evidence based on multiple independent molecular markers (mitochondrial and nuclear DNA genes, as well as microsatellite markers) suggests that all species studied in detail are single island endemics (Parent and Crespi 2006, Parent 2008).

Bulimulids have colonized all of the major Galápagos Islands, and they are found at all elevations except on shorelines composed mainly of sandy beaches and lava rocks. Many species have limited and patchy distribution range, most often restricted to a single vegetation zone. Past records indicate that up to 11 species could be found at a single location (Coppois 1985), but finding four or five coexisting species in a given habitat is more common. Galápagos bulimulid species vary remarkably in shell morphology (size, shape, color, and color pattern), and this phenotypic variation has been found to be associated with various aspects of ecological variation, including vegetation zones, related moisture levels, and microhabitat (Coppois and Glowacki 1983, Parent 2008). 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 2008). Since plants provide food and shelter, and probably most importantly, habitat structure, land snails can potentially adapt to different plant species for feeding, hiding, or resting.

Parent and Crespi (2006) found a combination of within and between-island speciation in Galápagos bulimulid snails. Polyphyletic land snail assemblages were found on islands centrally located in space and time (Isabela, Santa Cruz, Pinzón, Santiago), whereas the more isolated (again in both space and time) islands of Española, San Cristobal and Floreana were mostly occupied by monophyletic assemblages resulting from within-island diversification.

Hawaiian Islands

The Hawaiian islands are an archipelago of eight major islands, several atolls, numerous smaller islets, and seamounts in the Pacific Ocean, located about 3,000 km from the nearest continent. The islands were formed as the Pacific plate moved northwestward over a stationary "hot spot" in the earth's mantle. Generally the islands are divided into two categories: the young and high islands versus the old and lower islands. Currently, the oldest island is Kure Atoll (29 Ma) and the oldest high island is Kauai (5.1 Ma), whereas the youngest island, Hawaii, is less than 0.6 Ma and still in volcanically active. For the case studies presented in this paper I have restricted the analyses to biotas found on the young and high islands.

Similarly to Galápagos Islands, the Hawaiian archipelago is the host of unique organisms that are the products of evolution in isolation over tens of millions of years. The islands' extreme isolation, diversity of habitats, and dynamic geology have given rise to remarkable organismal diversity (Ziegler 2002). Over 750 described non introduced land snail species are found in Hawaii, and over 99% of these species are unique (endemic) to the islands (Cowie 1995, Cowie *et al*. 1995).

Below I test for the effect of island area, elevation, habitat diversity (measured as the total number of plant species), isolation, and age on total island species diversity, species diversity resulting from within-island speciation and species diversity resulting from between-island colonization. Similarly to the Galápagos Islands data set, I first tested for pairwise correlations among the independent variables, and then determined tolerance levels for the pair of independent variables that were significantly correlated. The only significant correlation was found between-island area and elevation ($r = 0.893$, $t = 4.434$, $P = 0.007$), so that larger islands are also higher. Tolerance value for elevation regressed on area (Tolerance = $1-R^2 = 0.202$) is too low for both variables to be included in the same model (Quinn and Keough 2002), and therefore I excluded island elevation from all further analyses on the Hawaiian data sets.

Hawaiian Succineidae

There are 42 recognized Hawaiian succineid species. All Hawaiian succineids are endemic, and 35 of them are thought to be single-island endemics (Cowie *et al*. 1995). Initially the Hawaiian succineids were thought to be monophyletic (Zimmerman 1948), but more recent molecular work suggests that this group might in fact be the result of multiple colonization events Rundell *et al*. (2004). However this does not affect the inference of the mode of diversification as presented in this paper; island clades that are monophyletic are still inferred to be the result of within-island speciation, whereas species that have their closest relative on another island or somewhere outside the archipelago are considered speciation events due to colonization. The Hawaiian Succineidae have radiated into a diverse array of habitats, from the very dry coasts to highland rainforests (Cowie 1995, Cowie *et al*. 1995). Holland and Cowie (2009) noted that there is an association

between shell morphological variation and ecological variation suggesting that diversification within this group might be at least partly adaptive. If this is the case, I expect island habitat diversity to be a significant contributor of species richness in this group, particularly when considering species resulting from within-island speciation.

Holland and Cowie (2009) found weak support for the progression rule of successive colonization from older to younger islands. However, the highest diversity in this group of land snails is clearly not found on the older islands: the island of Hawaii is less than 0.6 Ma old, and harbors 22 of the 42 recognized species (Cowie *et al*. 1995), suggesting that increasing island age might not be associated with greater species diversity.

Hawaiian Achatinellinae

With their remarkable phenotypic diversity, for years the Hawaiian tree snails (Achatinellinae) have fascinated professional and amateur biologists alike. There are 99 recognized species in the group distributed in 4 genera and all are considered to be single-island endemics (Cowie *et al*. 1995, Holland and Hadfield 2004). Presumably the diversification in this group is not adaptive but rather is associated with geographical isolation. Most species are now endangered or extinct, and the phylogenetic relationship among the species in this group is therefore inferred based on a very limited number of species. I used the molecular phylogeny presented in Holland and Cowie (2009), which was first published by Holland and Hadfield (2004) to quantify the processes of diversification in this group.

Biogeographical and ecological correlates of diversification

The extent of within-island and between-island speciation in any taxonomic group with multi-island distribution on an archipelago can be determined by combining information about the geography and phylogeny of the species. For islands with at least one species, we can infer at least one speciation event due to inter-island colonization (phylogenetic information is not needed). For islands with more than one species, the existence of distantly related species on the same island suggests speciation as a result of colonization (Fig. 1). On the contrary, *in situ* speciation is indicated by a clade of sister species on an island where a clade originated by the colonization of a single species that diversified into multiple species thereafter (Fig. 1). The above inferences are the most parsimonious explanations for the observed patterns given the data at hand, and do not necessarily correspond to what happened. For example, mitochondrial (mt) DNA introgression could potentially lead to the erroneous inference of within-island speciation (Losos 2011). Indeed, if colonizing individuals happen to interbreed with individuals of an already

established population of another species, their descendants' mtDNA could leave a signature of within-island speciation on the phylogeny. This particular type of erroneous inference can be avoided if the phylogeny used to infer speciation processes is based on multiple independent genetic markers (as opposed to exclusively rely on mtDNA). Another possibility is that multiple colonization events coupled with extinction of the ancestral species on the source island would leave the erroneous inference of within-island speciation on the colonized island. Although this scenario of double colonization followed by extinction is certainly a possibility, it seems unlikely to account for large groups of species since it would require several extinction events (Losos and Parent 2009). Unfortunately, the latter erroneous inference cannot be avoided by adding molecular data, and unless there is a good fossil record for the studied species (which is rarely the case for species occurring on volcanic oceanic islands), it is impossible to empirically rule out the double-colonization followed by extinction scenario.

Once the extent of within-island vs. between-island diversification is quantified, it becomes possible to test specific predictions related to the relative importance of biogeographical factors on the processes of diversification (Table 1). Large island area is considered an important factor promoting speciation *in situ* by providing more opportunity for isolation within an island, so that populations that become geographically isolated have the potential to diverge and split into different species. The greater habitat heterogeneity of larger islands can also affect the rate of within-island speciation by providing additional opportunity for diversification through what is 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 species that can escape the burden of competition by adapting to unoccupied habitats. In addition to area and insularity, island age can affect the total island species richness since older islands have had more time to accumulate species through colonization and speciation. In the colonization-extinction equilibrium context, age should only have a short-lived effect, with colonists filling up ecological space as it becomes available on islands. However, species diversity resulting from the presumably slower process of within-island speciation might be affected by island age, with older islands having more time to accumulate habitat diversity, and in turn more time to accumulate more species via this evolutionary process. Finally, the species diversity equilibrium is dynamic and changes through time because islands themselves change (Whittaker *et al*. 2008). Island age can therefore have indirect effects on oceanic island species richness by its effects on island area and elevation (volcanic islands shrink and sink over time), and island insularity (e.g., the geographical configuration of the archipelago is likely to change over time). Table 1 is a

Table 1. Predictors of land snail species richness, and the description of their predicted direct and indirect effects. The process(es) of species formation or maintenance each predictor is affecting is indicated in parentheses (S = within-island speciation; C = inter-island colonization; E = extinction), along with the direction of the predicted relationship with an increase in the value of the predictor (+ for positive; - for negative). § This effect is likely to become less significant as niches on islands are filled by colonists and newly formed species. Modified from Parent and Crespi 2006.

Species Richness Predictor	Description	
	Direct Effect(s)	Indirect Effect(s)
Island Area	- larger target for colonists (C+) - increased opportunities for isolation by distance (S+) - reduced extinction risk by potentially sustaining larger population size (E-)	- increased habitat diversity (S+, C+)
Island Elevation	- better target for colonists (C+)	- increased habitat diversity (S+, C+)
Island Habitat Diversity	- increased potential for adaptation (S+) - increased probability that colonists will find suitable habitat (C+)	none
Island Age	- more time to be colonized (C+)§ - more time to speciate (S+)§ - more time to go extinct (E+)	- increased (S+, C+) and followed by decreased (S-, C-) habitat diversity as island decreases in area - decreased island elevation and area due to erosion and subsidence (S-, C-, E+)
Island Isolation	- target harder to reach for colonists (C-)	- decreased habitat diversity because of lower colonization rate by plants (S-, C-)

comprehensive list of the potential direct and indirect effects different biogeographical and ecological factors might have on the processes of within-island speciation, speciation due to between-island colonization, and extinction.

RESULTS

Galápagos Bulimulidae

I re-analyzed data from Parent and Crespi (2006) to determine 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. Because collinearity between independent variables might confound the analyses I checked for redundancy by investigating tolerance levels for the independent variables. I first tested for pairwise correlations among the independent variables, and then determined tolerance levels for the pair of independent variables that were significantly correlated. The significant correlations were found between-island area and elevation (correlation coefficient $r = 0.690$, $t = 3.302$, $P = 0.006$), island area and habitat diversity ($r = 0.765$, $t = 4.114$, $P = 0.001$), island area and isolation ($r = 0.741$, $t = 3.824$, $P = 0.002$), and island elevation and age ($r = -0.638$, $t = -2.874$, $P = 0.014$). Tolerance values for all of these pairwise regressions (Tolerance = $1-R^2 > 0.45$) were adequately high (Quinn and Keough 2002), and

all variables could therefore be included in the regression models.

I used a phylogeny based on multiple independent DNA markers (updated from 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, I also included species that are the sole inhabitant of islands, because even if they are not represented on the phylogeny, they can safely be inferred as being the result of between-island colonization. Following this method I inferred 25 colonization and 15 speciation events for a total of 40 species distributed over 14 islands.

The best multiple regression model explaining the total bulimulid species richness among Galápagos islands includes island habitat heterogeneity and age (Table 2). Therefore, a richer fauna of bulimulid land snails is found on older islands harboring a more diverse range of habitats. When considering species richness resulting only from speciation due to between-island colonization, the best model includes island area and isolation. Larger islands presumably represent easier to reach targets for potential colonists. Moreover, larger islands have greater habitat diversity, and there is therefore a greater chance that a dispersing land snail will find a suitable habitat and establish on larger islands. The habitat diversity on islands is the only significant predictor of species richness due to *in situ* speciation (Table 2). This positive relationship between habitat and species diversity suggests that diversification

Table 2. Results of multiple regression analyses. The sample size (*N*) is provided for each model, as well as the standardized regression coefficient (*β*), the standard error for the regression standardized coefficient (*S.E. of 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 follow: † $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Snail group	Dependent variable	N	Independent variables	β	S.E. of β	t
Galápagos Bulimulidae	Total species richness Adjusted R^2 = 0.433**	26	island habitat diversity***	0.539	0.122	4.423
			island age	0.111	0.081	1.364
	Between-island speciation Adjusted R^2 = 0.543**	14	island area**	0.173	0.0425	4.07
			island isolation**	-0.00000621	0.0000017	-3.662
	Within-island speciation Adjusted R^2 = 0.487**	14	island habitat diversity**	0.00442	0.00121	0.00332
Hawaiian Succineidae	Total species richness Adjusted R^2 = 0.989**	8	island area**	5.332	0.546	9.757
			island habitat diversity**	-0.0176	0.00292	-6.018
			island isolation	1.349	0.720	1.874
			island age	-0.778	0.372	-2.089
	Within-island speciation Adjusted R^2 = 0.608*	8	island area*	0.633	0.184	3.441
Hawaiian Achatinellinae	Total species richness Adjusted R^2 = 0.330	8	island habitat diversity†	0.0814	0.0353	2.308
			island isolation	-10.369	7.164	-1.447
	Between-island speciation Adjusted R^2 = 0.578†	8	island habitat diversity*	0.00603	0.00192	3.144
			island isolation*	-1.048	0.390	-2.689
	Within-island speciation Adjusted R^2 = 0.479†	8	island habitat diversity*	0.00536	0.00194	2.769
			island isolation†	-0.838	0.393	-2.134

within-island is associated with habitat shifts in this group of land snails. Island area is often related to habitat diversity (Whittaker and Fernández-Palacios 2007), but number of plant species can provide a more direct measure of habitat diversity for land snails or other animals whose ecology is directly related to plant diversity (Triantis *et al.* 2003, Triantis *et al.* 2005). Different faunal groups can differ in their responses to area and habitat diversity, so that area, habitat diversity or a combination of both have a strong effects on species richness depending on the biological traits of the different taxonomic groups. Galápagos bulimulid land snail species have adapted to the different vegetation zones, and most species are found on specific plants or defined microhabitats (Coppois and Glowacki 1983, Parent 2008). 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.

Hawaiian Succineidae

I used the phylogeny published in Holland and Cowie (2009) to quantify the relative proportion of within-island and between-island speciation events on each Hawaiian young and high island (8 islands in total). The sample size for the Hawaiian Islands is much smaller than for Galápagos (8 islands compared to 14 for the partitioned analyses), and so is the associated statistical power to detect any significant trend. Nonetheless, the strongest trends can be detected. First, a

model that includes island area, habitat diversity, isolation, and age (Table 2) significantly predicts total species richness of Hawaiian succineids. Island area is a significant positive predictor of island species richness in this model, and total succineid species richness is found to significantly decrease with greater island habitat diversity. This trend is contrary to what would have been predicted if ecological differences were a major contributor of species diversification in this group.

The best model predicting species richness of Hawaiian succineids due to within-island speciation includes island area as the only explanatory variable (Table 2). Therefore, larger islands support higher within-island diversification rates. In line with the finding that habitat diversity *per se* was not an important contributor to species richness, the association of within-island diversification with island area suggests that diversification might proceed via geographical isolation in Hawaiian succineids.

Finally, maybe because of the limited species representation on the phylogeny, there is never more than one speciation event inferred to be the result of colonization on each island, so that the variation in species richness due to between-island colonization cannot be tested using standard multiple regression. I therefore tested if the probability of speciation due to between-island colonization was associated with any of the biogeographical variables used in previous analyses. I find that the probability of an island to harbor a species resulting from a colonization event is significantly greater on younger islands (logistic regression coefficient =

-3.039; $z = -2.039$, $P = 0.041$). This surprising finding suggests that younger islands are more likely to harbor species resulting from between-island colonization. Younger oceanic islands tend also to be generally larger (although the association between-island area and island age is not significant), but in the case of the succineids island area per se was not found to be a significant predictor of the probability of colonization.

Hawaiian Achatinellinae

Although the multiple regression analyses for the Hawaiian Achatinellinae did not generate any model explaining a significant proportion of the variation in species richness, whether total or partitioned, the results present some interesting trends. The variation in species richness due to between-island colonization suggests that less isolated islands and islands with greater habitat diversity harbor more species. In addition, islands with greater habitat diversity had more species resulting from within-island diversification. Finally, within-island diversification rate tends to be lower on more isolated islands. Although not significant, the latter trend is expected since more isolated islands generally support less habitat diversity, and therefore provide lower ecological opportunity for diversification within-island.

DISCUSSION AND CONCLUSIONS

Together, the results of these case studies emphasize the importance of considering both speciation due to between-island colonization and within-island speciation processes in parallel when trying to determine what factors contribute to species diversity. The relative contribution of speciation due to between-island colonization and within-island speciation to total island species richness remains to be specifically quantified for larger (geographical, temporal, and taxonomical) scale studies, but this first comparative study reveals that species richness is not driven by the same processes, even in taxonomic groups that are biologically very similar.

The relative magnitudes of within-island speciation and speciation due to between-island colonization differed among the studies presented here: whereas only about 38% of island species richness of bulimulids and 40% Hawaiian succineids was inferred to be the result of the process of within-island speciation, 70% of the Hawaiian Achatinellinae represented on the available phylogeny are the result of this evolutionary process. The Galápagos snail study reveals that island area and insularity are significant correlates of speciation due to between-island colonization, whereas island habitat heterogeneity is the only significant correlate of within-island speciation. In succineids, island area is a significant predictor of both total species richness and within-island diversification

rate. This highlights a potentially important difference between these two groups of species: whereas bulimulids have clearly adapted to the diverse habitats found on Galápagos and this adaptation might be associated with diversification in this group, the potential for geographical isolation might be a more important contributor to species diversification in Hawaiian succineids. With their thicker and heavier shells, bulimulids are likely to be poorer disperser than succineids. It is possible that this lower dispersal ability has allowed for the local adaptation, phenotypic evolution, and habitat associated within-island speciation that characterize Galápagos bulimulids, whereas the higher dispersal ability of Hawaiian succineids might have damped their potential for phenotypic diversification along environmental variation. However, for the succineids, within-island speciation might become possible on islands large enough to support geographically isolated populations.

The case study of the Hawaiian Achatinellinae highlights some of the limitations of the approach presented here. First, although the method seems robust (in the sense that it generates significant trends in the cases both of the Galápagos bulimulids and the Hawaiian succineids despite the incomplete sampling of these groups), it is possible that the limited species representation on the Hawaiian Achatinellinae phylogeny makes it difficult to detect any significant models. Unfortunately, given the high extinction that has devastated the Hawaiian Achatinellinae, their phylogeny will most likely always suffer from poor taxon sampling and limit the potential for inference of diversification patterns. It would be possible to test the robustness of the presented method by simulating phylogenies with various degrees of taxon sampling and analyzing the resulting trends. Second, while the diversification processes are quantified based on parsimony, and, as explained in the methods section, it is possible that the inference of speciation and colonization events does not correspond to reality. I am currently developing a maximum likelihood method to quantify the rates of *in situ* and between-island speciation, which will more fully use of the information from the phylogeny to hopefully generate estimates of the rate of these processes closer to reality. Third, the method presented here assumes that the phylogeny is the true reflection of the diversification of a lineage (i.e. there are no uncertainty at the nodes where speciation events occur). This assumption disregards the available nodal support (in the form of bootstrap replicate numbers, Bayesian probabilities or others), and the method could therefore be extended to take into account the uncertainty associated with each splitting event. Finally, not a shortcoming of the method, but the possibility remains that the diversification in the Hawaiian Achatinellinae is simply not driven by any ecological and biogeographical correlates tested here.

The results presented in this paper demonstrate that the partitioning of island species richness among diversification processes is crucial if we are to test for factors that are important in determining species diversity across biogeographical contexts and taxonomic groups. The framework I propose therefore extends the classical theory of island biogeography in two significant ways. First, by adding the evolutionary origin of species to overall island species richness, it becomes possible to disentangle the roles of ecological and evolutionary processes and their biogeographical correlates in determining species diversity. MacArthur and Wilson's theory assumed that species were neutral, that is species differences did not influence species diversity equilibrium. By considering the attributes of species (such as morphology, dispersal ability, ecological requirements, etc.) forming island communities, this framework will potentially lead to novel insights as to how species traits might be important determinants of community assembly. Because it is suitable for any island-like context, this framework combining phylogenetic and geographic information can be applied to a very broad range of systems, and will lead to a better understanding of what determines species diversity in any natural setting. An important motivation here is that humans are very rapidly transforming the natural world into island-like systems, such that processes involved in determining island biodiversity will become increasingly relevant to global biodiversity. A better understanding of ecological and evolutionary processes on island systems will offer insight into the long-term prospect for global biodiversity. The framework presented here has therefore broad implications for the study of species diversity in general since such process partitioning is likely relevant to many island-like systems and fragmented habitats; such systems are becoming the norm in our modern world.

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