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Why are diversity and endemism linked on islands?

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Patterns of species diversity on islands have yielded significant insights into evolutionary and ecological processes such as immigration, speciation and extinction. Island species richness and endemism are salient parameters for biologists and conservationists, yet in the voluminous works on island biogeography, the relationship between richness and endemism has not been thoroughly explored. Island biogeography theory suggests that both the species richness of a given island and the percentage of species that are endemic to that island are functions of the island's physical properties and its degree of isolation (MacArthur and Wilson 1967, p. 173). In separate analyses of the floras and arthropod faunas of the Hawaiian and Canary island archipelagos, Emerson and Kolm (2005a) found that species richness was a better predictor of percent endemism than were island size, island age, maximum island height, or distance to nearest neighboring island. On the basis of this result, they inferred that species richness was causing accelerated speciation. However, Emerson and Kolm did not fully consider alternative interpretations, particularly those that do not invoke differences in island-specific rates of speciation. For example, it is possible that diversity and endemism might be linked under a simple null model of island community assembly. In this paper, we demonstrate that a positive correlation between diversity and endemism is an expected outcome of island colonization, and that intrinsic variation among species and islands can amplify the magnitude of that correlation.

Consider two lists, L_1 and L_2, that differ in length such that $L_1 > L_2$. A number of elements, S, are shared between the two lists, while the remainder are unique to one list or the other. The proportion unique to each list is:

$$U_i = (L_i - S)/L_i = 1 - S/L_i$$

It follows that the longer list (island with greater species richness), L_1, will always have a higher proportion unique ($L_1 > L_2$). This is a tautological property that applies to any pair of lists that share some elements. We suggest that it is also true for any set of N lists. In a simple indicidence matrix for S species (rows) in N samples (columns, species lists) where the total number of incidences varies among samples (i.e. species lists vary in richness) and some species are shared among some or all samples, the larger samples will tend to have a greater proportion unique than the smaller ones. We cannot envision a non-random arrangement of incidences among columns that could overcome this expected correlation. Correspondingly, in any set of communities that contains some shared species, more diverse communities will contain a higher proportion of endemic species. Jetz et al. (2004) recognized this phenomenon in an analysis of richness and endemism in the continental African avifauna and corrected for it using a null model. The same principle applies to the colonization of island archipelagos from a finite continental pool of potential colonist species (an infinite pool could eliminate sharing of species between islands). Correspondingly, a stochastic colonization process should cause more diverse islands to contain proportionately more single-island endemic species.

To further demonstrate this point, we used the Hawaiian arthropod dataset (Nishida 2002) that was also used by Emerson and Kolm (2005a). This dataset includes 8068 species on 17 islands, comprising 16 623 island populations. We simulated the colonization of the Hawaiian Islands up to their current levels of species diversity using the list of 8068 species as the pool of potential colonists. Potential colonist species to the simulated archipelago were sampled with replacement, but multiple colonizations to the same island by a given species were only counted once on the island species list. We implemented this procedure using a PERL program (available from the authors upon request). For each simulated archipelago, we quantified the number of species that occurred exclusively on each island. In 10 000 replicate simulations, we found a positive exponential relationship between species diversity and the proportion of single-island species (Fig. 1). The proportion of species occupying only a single island in the simulated archipelago provides a realistic index of the level of species endemism. Consider that colonist species in nature can become endemic over time by one of three paths: 1) extinction of all other populations, 2) speciation by anagenetic change, or 3) speciation by cladogenesis. Species from a continental source that colonize a single island are more likely than multi-island species to become endemic by the first path, and we assume that all colonist populations are equally likely to become endemic by the second and third paths. Because our model does not explicitly include speciation or extinction processes, it effectively yields an index of percent endemism while assuming that diversification rate is invariable among lineages.

We further predict that variation in colonization ability among potential colonist species will increase the tendency for speciose islands to possess higher levels of endemism. Species vary dramatically in dispersal distance (Kinlan and Gaines 2003) and other parameters that affect their ability to colonize islands. The most highly proficient colonist species are likely to occupy many islands (Diamond 1974) and resultantly comprise a higher proportion of depauperate communities than speciose ones. We repeated the simulation of Hawaiian arthropod communities while incorporating different colonization abilities. We used the number of islands on which each species occurs as an index of the probability of an island colonization event. This method provided a conservative estimate of the degree of variation in colonization ability because it did not account for multiple colonizations of a single island that surely must have occurred. The positive correlation between species diversity and endemism was amplified when interspecific variation in colonization ability was taken into account (Fig. 1). We do not explicitly model inter-island colonization, which is surely a common process among Hawaiian island taxa. However, inter-island colonization would have the same effect as increasing the variance in probability of colonization among the potential colonist species. It would increase the percent of species shared among islands, and would therefore further amplify the link between diversity and endemism.

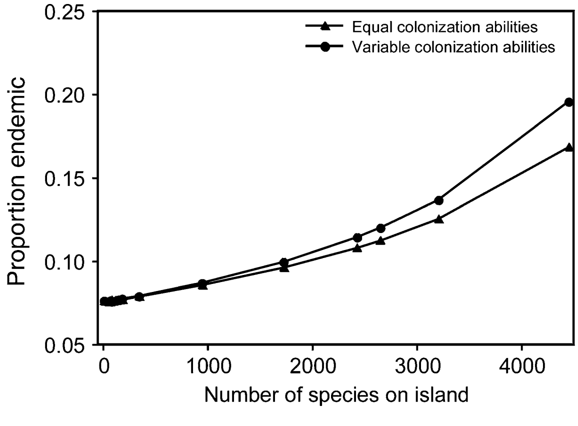

Fig. 1. Percent endemism in relation to species diversity for simulated arthropod communities of the Hawaiian archipelago, based on the mean values from 10 000 simulations. Triangles represent the case of equal colonization rates among species. Circles represent the case of colonization rates proportional to the number of islands currently occupied by each species.

Cadena et al. (2005) demonstrated that species richness and endemism in the West Indian avifauna are both functions of the average age of resident populations, or average time to extinction, which is ultimately determined by the physical properties of islands. Emerson and Kolm (2005b) replied that the West Indian avifauna is a non-equilibrium island system that provides an inappropriate test of the diversity-driven speciation hypothesis. However, equilibrium island biogeography theory is compatible with the observation of Cadena et al. under the condition that inter-island variation in extinction rate exceeds variation in immigration rate. If extinction rate varies while immigration remains constant, theory predicts that higher species diversity will be associated with lower rates of species turnover, regardless of island size or speciation rate (Fig. 2). The implications of species turnover for endemism are clear: higher rates of turnover reduce the average length of tenure for island populations, thereby reducing the proportion of such populations that reach endemic status by one of the three paths listed above. As a result, species turnover is expected to be inversely proportional to percent endemism. If extinction rates vary among islands for reasons other than island size, height, and age, it could explain why species richness was the best predictor of percent endemism in the analysis of Emerson and Kolm (2005a). These simple physical characteristics are known to be coarse indicators of an island's potential equilibrium level of diversity (Johnson et al. 2003). The Hawaiian Islands provide numerous examples of other island-specific properties that can lead to variation in extinction rates, including topographic complexity and susceptibility to volcanism, typhoons, or tsunamis. Furthermore, variation in immigration rate may be

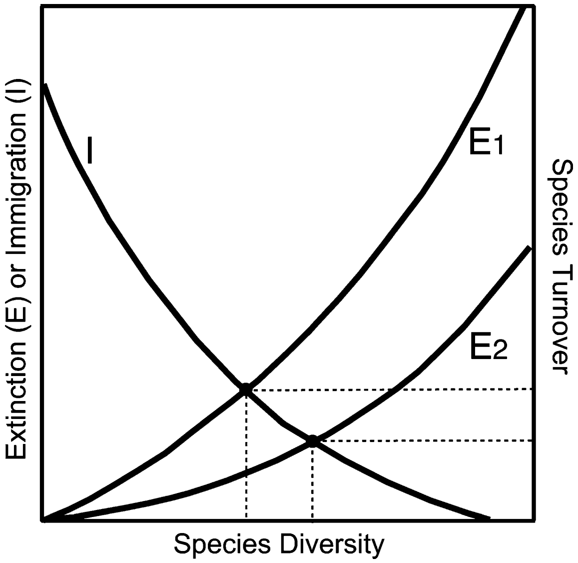

Fig. 2. Island biogeography theory predicts that variation in extinction rate will cause an inverse relationship between species diversity and species turnover. Here the equilibrium levels of diversity and species turnover are plotted for two islands that differ in extinction rate. Adapted from Simberloff (1974).

relatively inconsequential for clustered islands that are roughly the same distance from a continental source.

We have demonstrated three alternative causes for the link between levels of endemism and species diversity on islands: a finite colonist pool, interspecific variation in colonization abilities, and inter-island variation in extinction rate that exceeds variation in immigration rate. Taken together, these may provide a more parsimonious explanation of the observed pattern.

The concept that species diversity drives speciation is powerful and appealing (Erwin 2005). Speciation of parasites and phytophagous insects by host switching or host speciation provides direct examples of diversity begetting diversity (Futuyma and Keese 1992, Clayton et al. 2003, Janz et al. 2006). However, it is doubtful that diversity-driven speciation is a general phenomenon in light of the many examples of adaptive radiations following mass extinctions or island colonizations, each of which implies rapid speciation occurring in a competitive vacuum (Schluter 2000). Recent detailed studies of three-spine sticklebacks (McKinnon et al. 2004) and Hawaiian spiders (Gillespie 2004) suggest that speciation may be both facilitated and limited by niche availability. Our analysis does not negate the possibility that diversity drives speciation, but it indicates that a strong link between endemism and richness is likely to arise through other processes. We maintain that percent endemism is an inadequate index of within-island speciation, and we reemphasize the need for an explicit phylogenetic framework in studies of diversification rate.

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