Does species richness drive speciation? A reassessment with the Hawaiian biota

Daniel S. Gruner, Nicholas J. Gotelli, Jonathan P. Price and Robert H. Cowie

D. S. Gruner (dsgruner@umd.edu), Bodega Marine Lab and Section of Evolution and Ecology, Univ. of California, Davis, CA 94923, USA (present address: Dept of Entomology, Univ. of Maryland, 4112 Plant Sciences Building, College Park, MD 20742, USA). N. J. Gotelli, Dept of Biology, Univ. of Vermont, Burlington, VT 05405, USA. – J. P. Price, Dept of Geography and Environmental Studies, Univ. of Hawai'i at Hilo, Hilo, HI 96720, USA. – R. H. Cowie, Center for Conservation Research and Training, Univ. of Hawai'i, Honolulu HI 96822, USA.

Does richness cause speciation?

After MacArthur and Wilson (1967), island biogeographical research focused primarily on processes of colonization and extinction over ecological time scales, but recent work has rejuvenated interest in the generation of diversity in situ over evolutionary time (Lomolino 2000, Losos and Schluter 2000, Gillespie 2004, Cadena et al. 2005). In a recent contribution, Emerson and Kolm (2005) proposed a causal link between species richness and speciation on islands. They suggested that species richness per se might increase the rate of speciation by intensifying competition and suppressing population densities of resident species, thereby allowing for increased genetic drift, greater lability in traits, and increased evolutionary change (Erwin 2005). Alternatively, increased structural complexity and heterogeneity associated with higher richness may stimulate niche diversification and speciation (Tokeshi 1999).

literature. Several rejoinders argued for alternative mechanisms as sufficient but more parsimonious explanations for observed endemism patterns on oceanic islands. Cadena et al. (2005) proposed that the accumulation of endemic species depends primarily on the realized lifespan of islands: older islands have both more opportunity to receive colonists and longer duration in which to accumulate endemics. With their "island immaturity – speciation pulse" hypothesis, Whittaker et al. (2007) extended this model to include geological island ages to older islands, to the senescent islands where the eventual collapse of endemism and richness is observed as islands disappear beneath the sea surface. Pereira et al. (2007) also argued for the primacy of physical variables and time, but further demonstrated the insufficiency of multiple regression analyses as a test of this hypothesis. They showed that total richness and endemism patterns strongly covary with island size, elevation, distance to nearest island, and island age, and with richness of the other taxon (e.g. arthropods for plants) such that it is impossible with this analytical method to ascribe ultimate causation to within-taxon richness. Finally, several authors proposed null models to account for island endemism patterns attributable to statistical properties of random samples (Witt and Maliakal-Witt 2007, Kiflawi et al. 2007, Birand and Howard 2008). Emerson and Kolm (2007a, b) proposed a different (and we argue, inappropriate) null model in response to these criticisms.

In this paper, we revisit the relationship between endemism and species richness in a reanalysis of arthropod (Nishida 2002) and plant (Price 2004) data for the Hawaiian Islands and include a new dataset for land snails (Cowie et al. 1995, Cowie and Holland 2006). We propose distinct null models for endemism patterns in these island datasets. Because the methodological contrasts and findings of these different null models are more clear in the context of our assumptions, methods, and results, we address the specific null models of Emerson and Kolm (2007a, b), Witt and Maliakal-Witt (2007), Kiflawi et al. (2007), and Birand

and Howard (2008) following the discussion of our analyses.

Emerson and Kolm's (2005) original regression analysis rested on the implicit assumption that, in the absence of driving speciation mechanisms, the number or proportion of endemic species should be independent of the total richness on individual islands (this assumption was later made explicit, Emerson and Kolm 2007a). Under this assumption, the statistical null hypothesis is of no correlation between the proportion of SIEs and total species richness. However, a universal property of biodiversity sampling curves is that rare species are disproportionately under-represented in small samples (Gotelli and Colwell 2001). At the biogeographic scale, we expect the proportion of SIEs to escalate with total species richness, even in the absence of mechanisms promoting in situ speciation. Therefore, we formulated two null sampling hypotheses that incorporated the expected non-linearity in SIE proportion with variation in the richness of island species pools.

Null models for island endemism

Model 1: simple random sampling

To investigate this null sampling hypothesis, we analyzed arthropod and plant data (n = 17), and snail data (n = 14; 3 islands with zero native snails) for the Hawaiian islands obtained as species by island inci.6(s)-63ae29.9(no7(1:sis291(w)0ct612.49.2(simple)-3i)-71)-9.7(ed)-326.88.2(of)-ng

contradict the hypothesis that diversity per se drives speciation, although they may have been affected by the possibility of randomly sampling the same SIE species by replacement. For the plant and arthropod data sets, the expected value of the index in the Model 1 simulations remained roughly constant across most of the range in observed richness, then increased gradually as larger random samples accumulated a greater fraction of rare taxa (Fig. 1A). For snails, the expected values fell initially, but this reflects the extremely low richness on these islands (<5 native species on 7/14 islands), which distorts the ratios and also leads to wide confidence intervals.

Similar results were obtained with Model 2 (Fig. 1B); however, two clear differences emerge. When the model is constrained not merely to the same richness total per island (assumption 4, above), but also the occurrence frequency of each species is fixed to that observed in the dataset, the confidence intervals adhered more narrowly and the slopes of the expected values steepened in the upper tails of richness (Fig. 1). Endemism on most islands remained within or below the 95% confidence intervals, suggesting the observed arcsine-transformed index of speciation was generally weaker or within expectation from random

sampling. However, Kaua'i, the richest island for plants, contained more SIE plants than expected by chance in both simulations, and contained more SIE snails than expected with Model 2 simulations. The index for O'ahu, richest for

mass only 20 000 yr ago (Price and Elliot-Fisk 2004). We would expect that the recent connectance of this island group would enhance dispersal and genetic introgression among divergent races, thereby driving the observed SIEs of these islands below the null model expectations (Fig. 1B). On balance, the few departures from random sampling are consistent with phylogenetic and community ecological work that implicates island size and geological history as the ultimate drivers of evolutionary species accumulation in the Hawaiian Islands (Cowie 1995, Gillespie 2004, Price 2004, Cadena et al. 2005, Gruner 2007, Whittaker et al. 2007).

The slopes of arcsin-transformed index versus species richness relationships appear somewhat steeper at the richest tails of the observed versus the simulated Model 1 data (Fig. 1). ANCOVA analysis of these relationships grouped by the observed versus expected island endemism indices as a categorical covariate showed a significant interaction between total richness and the covariate for arthropods and plants, but not snails (Table 1). These subtle patterns could perhaps be interpreted as support for diversity-driven speciation hypothesis. However, the two linear regressions of the observed and expected indices cross each other at island richness totals that are larger than the most species-rich island observed for each taxon in the Hawaiian archipelago (Fig. 2; arthropod total richness = 7161, plants = 5137, snails = 907). In other words, even this result cannot account for the observed pattern of endemism in the richness range of the Hawaiian archipelago.

The regression analysis presented by Emerson and Kolm (2005), questioned already for its power to demonstrate causation (Pereira et al. 2007), presents the endemism index as a ratio of the form y/x regressed against x (SIEs/total species number versus total species number). Although Emerson and Kolm (2005) ran diagnostics to evaluate the independence of their richness variables, Brett (2004) cautioned that regressions incorporating predictors in the response variables can lead to spurious statistical correlations. The arcsine-transformation of the proportional index introduces additional distortion in observed and expected

values at small sample sizes (snails, Fig. 1), and the assumption of normal error distribution for the parametric regression model can be violated. The null models that we have used here directly account for these possibilities because randomization methods do not depend on the assumption of normality, and they take into account the non-independence of y/x when regressed against x. A more natural index is simply the observed number of SIEs per island. When the data are plotted as observed and expected number of SIEs on log-log axes, the emergent result remains: the number of SIE taxa found on most islands is either about the same or slightly less than would have been expected by chance (Fig. 2). ANCOVA analysis applied to log-transformed total SIE showed no difference in the slopes of expected and observed relationships for plants and snails, and a weak interaction for arthropods with convergence beyond the observed richness of any island (Fig. 2, Table 1).

Other null models

Several recent papers have also used null model methodology to address the problem of island endemism. Witt and Maliakal-Witt (2007) argue that it is a tautological property that two lists of island species with shared and unshared elements will always have a greater proportion of endemics on the more species-rich island. When the argument is extended to N-species lists, it is possible to construct special cases that violate this inequality, but we agree with their general point that most random re-arrangements of island species lists will contain a greater proportion of endemics in larger faunas. Witt and Maliakal-Witt's (2007) null models (which they developed independently of our analysis) illustrate that point and are most similar to our Model 1 (simple random sampling), which also uses sampling with replacement, but does not restrict endemics to single occurrences. Our Model 2 (fixed-fixed) simultaneously preserves the occurrence frequency distribution and the

Table 1. ANCOVA results for the relationships between endemism and total richness in Hawaiian arthropods, plants and snails. ANCOVA models test the relationship of $\log_{10}$ native species richness and the group covariate with the (a) arcsine-transformed proportion of single island endemics (SIEs) (Emerson and Kolm's [2005] "index of speciation") and (b) $\log_{10}$ richness of SIEs. The covariate was defined by whether the datapoint was an observed or expected value generated from null Model 1 (random sampling) simulations.

Source		(a) asin [SIEs/total S]			(b) $\log_{10}$ [SIEs +l]		
	DF	SS	F	p	SS	F	p
Arthropods							
$\log_{10}$ total richness	1	0.2969	51.522	<0.0001	30.7146	1717.63	<0.0001
Group	1	0.5781	100.314	<0.0001	0.7086	39.629	<0.0001
Richness × group	1	0.1285	22.304	<0.0001	0.1863	10.417	0.003
Error	30	0.1729			0.5365		
Plants							
$\log_{10}$ total richness	1	0.1001	20.039	0.0001	17.7496	185.498	<0.0001
Group	1	0.2055	41.142	<0.0001	1.4446	15.0977	0.0005
Richness × group	1	0.0309	6.180	0.0187	0.0192	0.2000	0.6576
Error	30	0.1498					
Snails							
$\log_{10}$ total richness	1	0.0009	0.008	0.9319	18.4592	926.790	<0.0001
Group	1	0.8048	6.292	0.0193	0.1306	6.5586	0.017
Richness × group	1	0.1995	1.560	0.2238	0.0147	0.7383	0.398
Error	24	3.0700					

observed species richness per island, ensuring that the number of endemic species in the simulated archipelago exactly matches the number in the real data.

In their critiques of the null models of Witt and Maliakal-Witt (2007) and Kiflawi et al. (2007), Emerson and Kolm (2007a, b) offer an alternative null model that was based on our freely available EcoSim software (Gotelli and Entsminger 2004). Emerson and Kolm (2007a: 336) stated that: ''we have carried out simulations maintaining observed values for the number of species per island, but allowing species within an island to 1) go locally extinct, 2) successfully colonise another island, or 3) undergo either anagenetic or cladogenetic speciation. Importantly these events are random, with local extinction being balanced by either colonisation or speciation to maintain species number.''

However, the EcoSim randomization software produces classical null model tests, which are stochastic randomizations of observed data that do not incorporate specific biological processes (Gotelli and Graves 1996). EcoSim algorithms do not include any explicit processes of extinction, colonization, or speciation. In some cases, mechanistic models such as the neutral model can be interpreted as a kind of null model (Gotelli and McGill 2006), but the claim (Emerson and Kolm 2007a) that these models include extinction, colonization and speciation processes is incorrect. In contrast, both Witt and Maliakal-Witt (2007) and Birand and Howard (2008) presented null models in

and would also expect from Witt and Maliakal-Witt's (2007) framework. Because the null model of Emerson and Kolm (2007a, b) seems flawed, their slope test does not provide valid support for their hypothesis that species richness promotes endemism.

Conclusions

There is little debate that in situ speciation is a dominant process generating biological diversity on oceanic islands (Darwin 1859, Grant 1998, Whittaker 1998). In general, more research is required to determine which factors stimulate speciation, and the ''diversity-driven speciation'' hypothesis is one possibility that deserves further attention. However, such efforts should state clear null hypotheses that can distinguish a robust increase in SIE proportion with richness from a spurious result generated by sampling. Emerson and Kolm (2005: 1017) write of an ''overlooked prediction of island biogeographic theory: as species number in an area increases, so should the rate of speciation.'' As demonstrated by our analyses, however, a positive relationship can be expected simply from the sampling properties of species pools. We found consistent results using data for three different assemblages (arthro-