# Comments

## SPECIES DIVERSITY CAN DRIVE SPECIATION: COMMENT

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### Introduction

The mechanisms that govern spatial patterns in species richness, community composition, and speciation are fundamental issues in community and evolutionary ecology. It has been argued recently (Emerson and Kolm 2005*a*) that, in the Hawaiian and Canary archipelagos, species diversity itself has been driving the speciation rates of endemic plants and arthropods, in accord with island biogeography theory. Here we show that the observed trends in the distribution of endemics within these two archipelagos are in fact consistent with null predictions. Moreover, we show that similar trends are followed by non-endemic singletons (i.e., species not endemic to the archipelago that occur on a single island), despite the different mode by which they first arose in the archipelago. Together, these findings undermine the validity of the "diversity-driven diversification" hypothesis, at least in the systems considered here.

Is biodiversity "simply" the outcome of ecological and evolutionary processes, or could it also be a causative agent in driving speciation? The idea that species can modify their environment, thereby making it available for additional species, is not new (Jones et al. 1997, Erwin 2005). Emerson and Kolm (2005*a, b*) have gone further to suggest that species richness can promote diversification, a prediction they ascribe to the theory of island biogeography (MacArthur and Wilson 1967). Assuming that extinction and speciation rates follow a similar curvilinear dependence on richness, Emerson and Kolm predict that, under equilibrium conditions, the proportional representation of endemic singletons

should increase with richness (but see Cadena et al. [2005]). They then proceed to demonstrate positive relationships between relative endemism and total species richness of the vascular flora and arthropod fauna of the Canary and Hawaiian Islands. Assuming that relative endemism proxies speciation rate, they conclude that diversity drives diversification.

Implied by the "diversity-driven diversification" hypothesis is that the distribution of endemic singletons across islands differ from the distribution expected by chance, given the observed variation in species richness; which itself varies due to differences in island properties such as size, distance from the mainland, and so forth (Table 1). In this note we show that, to a large extent, the trends described by Emerson and Kolm coincide with null expectations generated by random distribution of singletons within archipelagos. Barring the effect of sampling, species richness contributes little in explaining the residual variance in relative endemism; contrary to the "diversity-driven diversification" hypothesis. Consistent with this finding, we show that non-endemic singletons (i.e., species occurring on a single island, but which have been recorded outside the archipelago) follow a similar trend to that of endemics; despite the different mode by which they first arose in the archipelago.

### The null model

Consider an archipelago of $C$ islands, which acquire species through immigration (either from within the archipelago or from without) and speciation. Let $p_j$ be the probability that a given species is currently present on island $j$, such that variation in $p_j$ ensues differences in island traits that affect species acquisition and persistence rates (e.g., size, distance to mainland/closest island, and so on.). Consider next the probability that a species is present on $j$ and nowhere else within the archipelago, $\theta_j$. Assuming that the observed species distribution was structured solely by variation in $p_j$, $\theta_j$ equals $p_j \Pi_{k \neq j}(1 - p_k)$; which is a positive function of $p_j$ (Fig. 1). Normalizing $\theta_j$ by division by $\Sigma_{j=1}^{C} \theta_j$ returns the proportion of singletons on island $j$, which is expected if species (or at least singletons) were randomly distributed across islands. Given $p_j$, we could thus test whether the observed distribution of singletons is significantly different from random by evaluating the 95% confidence interval around the expected proportions. As it is the distribution of singletons that is of ultimate concern, this constitutes a direct test of the diversity-driven hypothesis. Here we let $p_j$ equal island $j$'s relative richness: the proportion of the total species pool found on island $j$.

This model implies that a positive association between relative endemism and species richness is an inevitable

TABLE 1. Results of multiple regression analyses, with total island richness as the dependent variable.

| Location and taxon | Number of islands | Variables in model | β | t | P | Adjusted $r^2$ |
|---|---|---|---|---|---|---|
| Canary Islands | | | | | | |
| Arthropods | 7 | maximum elevation | 1.32 | 6.36 | 0.003 | 0.87** |
| | | distance to mainland | −0.69 | 3.34 | 0.029 | |
| Plants | 7 | maximum elevation | 1.22 | 3.91 | 0.017 | 0.71* |
| | | distance to mainland | −0.61 | 1.93 | 0.125 | |
| Hawaiian Islands | | | | | | |
| Arthropods | 16 | area | 0.86 | 6.34 | 0.000 | 0.72** |
| Plants | 16 | area | 0.96 | 12.42 | 0.000 | 0.91** |

*Note:* β is the standardized regression coefficient.
$*P \leq 0.05$; $**P \leq 0.001$.

consequence of less ubiquitous species experiencing a sharper increase in their probability of island occupancy, which accompanies the increase in the species acquisition and persistence rate of islands ($p$). To see this we need the probabilities of a species occurring on island $j$ and $1, 2, \ldots C - 1$ other islands. The equations for these probabilities are not as trivial as they are for singletons, but the point is easily exemplified using simulation (Fig. 1).

### Methods

*Data set.*—Data for the plants and arthropods of the Canary Islands were obtained directly from B. Emerson and are based on Acebes-Ginoves et al. (2004) and

Oromi and Baez (2004). A list of Hawaiian plants and arthropods was received from the manager of the Bishop Museum. Hawaiian islands included in the analyses are Kure, Midway, Laysan, French Frigate Shoals, Lisianski, Necker, Pearl and Hermes, Nihoa, Niihau, Kauai, Oahu, Molokai, Lanai, Maui, Kahoolawe, and Hawaii. The data analyzed excluded anthropogenic introductions, but included uncertain occurrences.

Island parameters of potential biogeographical importance were compiled from Price (2004; Hawaii: area, maximum elevation, and age) and Fernández-Palacios and Martín-Esquivel (2001; Canary Islands: area, maximum elevation, and distance to mainland); distances to the nearest island were measured using ArcView
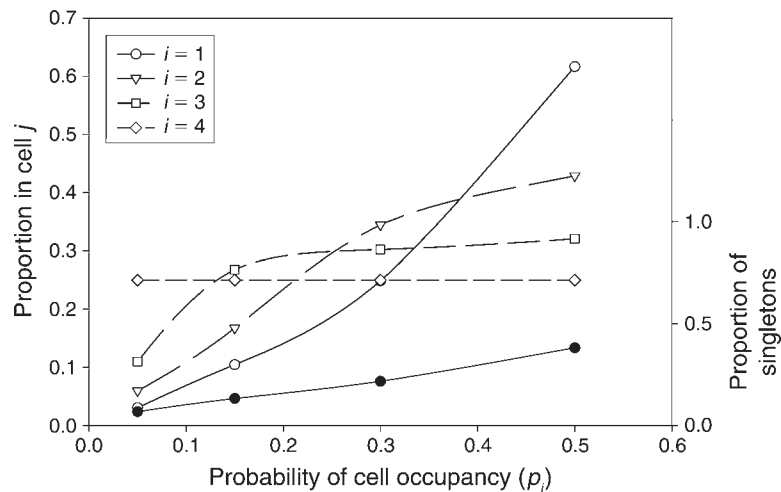


FIG. 1. The proportion of singletons, doublets, triplets, and quadruplets (i.e., species occurring in $i = 1, 2, 3$, and 4 islands, respectively) expected to occur in an island with a probability $p$ of being occupied. The proportions are based on a simulation involving four cells (islands) that vary with respect to $p$ (0.05, 0.15, 0.3, and 0.5). An array of four random numbers was iteratively drawn from a uniform distribution ($0 \geq r \leq 1$). In each iteration, cell $j$ was occupied if $r_j \leq p_j$, and the number of cells occupied was tallied ($i$); iterations with $i = 0$ were discarded. By the end of 10 000 iterations, we calculated the fraction of iterations with $i = 1, 2, 3$, and 4 contributed by each cell ($q_{ij}$; $\Sigma_j q_{ij} = 1$). These fractions are depicted on the first $y$-axis (proportion in cell $j$). Also shown is the proportion of each cell's total occurrences ("richness") that is attributable to singletons: $q_{1j}/\Sigma_i q_{ij}$ (solid circles; second $y$-axis, proportion of singletons).
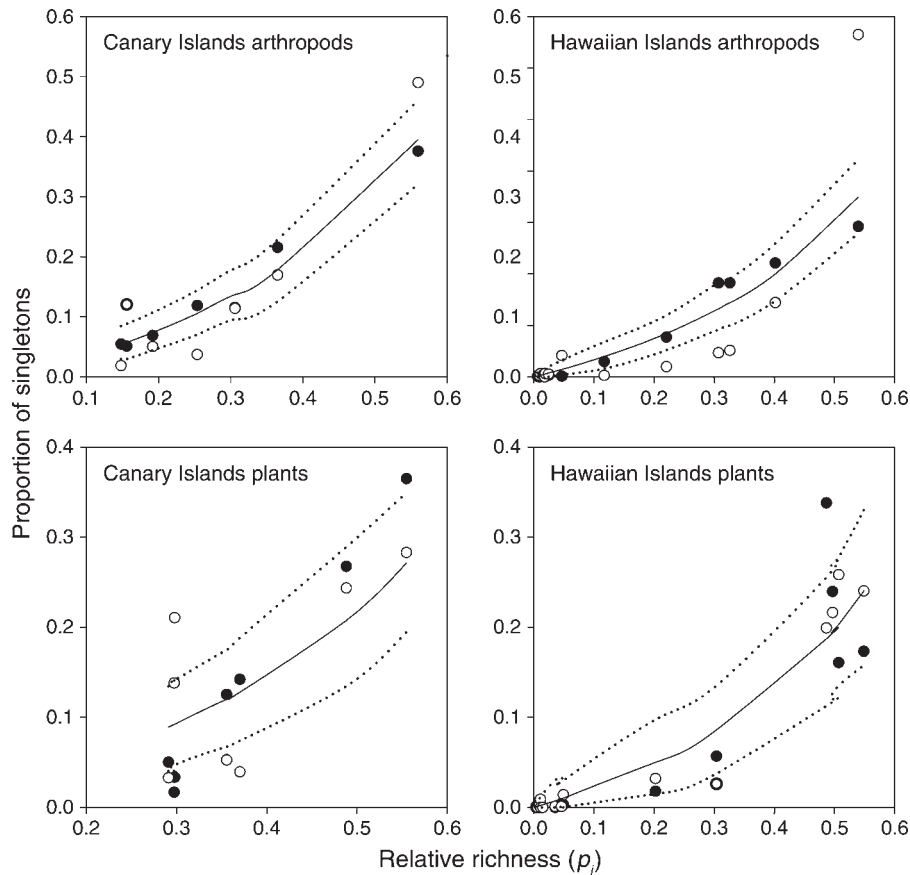
Fig. 2. The observed proportion of the total endemic (solid circle) and non-endemic (open circle) singletons found on each island, along with the proportions expected under the null model (solid line). Relative richness, $p_j$, is defined as the proportion of the total species pool found on island $j$. The 95% confidence interval used to test the null model is depicted by the dotted lines.

GIS 9 (ESRI, Redlands, California, USA) using a U.S. general map (Hawaii) and *The Times Concise Atlas of the World* (Canary Islands; Bartholomew et al. 1986).

*Confidence intervals and hypothesis testing.*—The 95% confidence intervals associated with the expected proportion of singletons were based on numerical estimation of $\theta_j$; the probability that a species is present on island $j$ and nowhere else within the archipelago. Briefly, for each island $j$, a set of $C$ random proportions were iteratively ($n = 1000$) drawn from a uniform distribution ($0 \geq r \leq 1$). Comparing the observed and random proportions, sets with $r_j \leq p_j$ and $r_k \geq p_k$, for all $k \neq j$, were scored as "success." The proportion of successes (out of 1000) constitutes a single estimate of $\theta_j$. The procedure was repeated 1000 times and the ensuing sample used to estimate the confidence interval (i.e., based on the 2.5th and 97.5th percentiles).

As a test of the diversity-driven-diversification hypothesis we (1) evaluated the extent by which observed proportions fall within the expected confidence intervals, (2) evaluated the Spearman rank correlation between island richness and the deviation of the observed proportions from the expected, (3) compared (qualitatively) the trends followed by endemics with those of non-endemics, expecting that presumed differences in evolutionary and ecological histories should result in different distribution patterns.

## Results

To a very large extent, the observed proportion of singleton endemics fell within the range expected by chance (Fig. 2). Indication of a residual positive relationship between richness and endemism, beyond that which is expected by chance, is found only in the case of plants in the Canary Islands (Table 2). Overall, however, the trends followed by endemic and non-endemic singletons are remarkably similar (Fig. 2; Table 2).

## Discussion

The use of null models in the study of community ecology has been an accepted practice for over two

TABLE 2. Spearman rank correlation between island richness and the deviation between the observed and expected proportion of endemic and non-endemic singletons.

| Location, taxon ($n$) | Endemic | | Non-endemic | |
|---|---|---|---|---|
| | $r_s$ | $P$ | $r_s$ | $P$ |
| Canary arthropods (7) | −0.14 | 0.380 | 0.50 | 0.127 |
| Canary plants (7) | 0.89 | 0.003 | −0.18 | 0.351 |
| Hawaiian arthropods (16) | −0.09 | 0.364 | −0.34 | 0.098 |
| Hawaiian plants (16) | −0.43 | 0.048 | 0.17 | 0.267 |

*Notes:* Positive correlations imply that richer islands contain more singletons (and poorer islands contain fewer) than expected by chance. One-tailed significance levels are provided for the correlation coefficients. Sample sizes in parentheses are the number of taxa.

decades and has led to the rethinking of several established hypotheses and paradigms (e.g., Gotelli and Graves 1996, Colwell et al. 2004). Null models do not suggest that evolutionary and ecological processes are not operating, rather that these processes contribute little structure to the variable in question, beyond that which is expected by chance. With respect to the present-day distribution of the Hawaiian and Canary arthropod and plant endemic singletons, we find that it matches null expectations with only minor exceptions (Fig. 2), calling into question the hypothesis that diversity can drive diversification. The similarity in the trends followed by endemic and non-endemic singletons serves only to underscore this conclusion.

It is important to remember that only with respect to topographically and geographically driven variation in $p$ (an island's rate of species acquisition and persistence) does species distribution appear random. In this sense, our findings would be consistent with any other explanation of a positive relationship between relative endemism and richness which invokes differences in island attributes as the sole causative agent (e.g., Cadena et al. 2005). To the extent that the proportion of endemic singletons does indeed proxy local speciation rates, we must conclude therefore that the overriding effect of island attributes affords species richness little contribution to the spatial patterns of diversification beyond the null "sampling" effect.

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# SPECIES DIVERSITY CAN DRIVE SPECIATION: REPLY

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Kiflawi et al. (2007) call into question the analyses of Emerson and Kolm (2005) that demonstrate a positive relationship between species number and diversification. In their paper, Emerson and Kolm (2005) use data for

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plants and arthropods of Canary and Hawaiian Islands to address whether there is a positive relationship between species diversity and the rate of speciation. Even after controlling for other important physical features of islands that are thought to influence speciation rate, they found that speciation rate was strongly related to species number. Kiflawi et al. (2007) rightly point out that the implication of the "diversity-driven diversification" hypothesis is that the distribution of species endemic to single islands differs from that expected by chance. Indeed, if the distribution of single-island endemics is compatible with null expectations, then this negates the need to invoke diversity as a driver of speciation. To this end, they present a null model to address this issue and conclude that, to a large extent, the trends described by Emerson and Kolm (2005) coincide with null expectations. However, here we show that the formulation of their null model is inappropriate for evaluating the conclusions of Emerson and Kolm (2005), providing an unsatisfactory alternative to the statistical null hypothesis of no correlation. However, when expressed in a form comparable to the original data, the null model of Kiflawi et al. (2007) indicates departure from null expectations for the trends described by Emerson and Kolm (2005).

For each of the four original data sets (arthropods of the Canary Islands, arthropods of the Hawaiian Islands, vascular plants of the Canary Islands, and flowering plants of the Hawaiian Islands), the null model of Kiflawi et al. (2007) relates the *proportion of the total pool* of single-island endemics within an archipelago that are found on an individual island to the island's relative richness. Thus, under this null model, the proportion of the total pool of single-island endemic species occurring on a given island becomes a positive function of the total number of species on the island. In other words, islands with more species will have more endemic species. Kiflawi et al. (2007) then generate confidence intervals around their expected proportions of endemics using numerical estimation and find that, for the most part, observed values fall within these confidence intervals.

An important distinction is that the original analyses of Emerson and Kolm (2005) treat the number of endemics on a given island as a proportion of that island's biota, not as a proportion of total pool of endemics across the archipelago, as has been done by Kiflawi et al. (2007). If one views the null model of Kiflawi et al. (2007) in terms of species incidence values, one finds that their null model predicts much lower levels of endemism than are observed, considerably so in most cases. Their null model relates the proportion of single-island endemic species on an island as a proportion of all single-island endemics. For Canary Island vascular plants and arthropods, when these values are converted to species incidence values, their model predicts 72% and 20% less single-island endemic taxa

than are observed. For Hawaiian flowering plants and arthropods, the model of Kiflawi et al. (2007) predicts 71% and 51% less single-island endemic taxa than are observed.

Failure of the null model of Kiflawi et al. (2007) to reject their associated null hypothesis does not constitute a refutation of our original conclusion that species diversity can drive speciation (Emerson and Kolm 2005). Indeed their results support the departure of observed single-island endemic species incidence values from null expectations. Our original approach (Emerson and Kolm 2005) was to look at the number of singletons on an island as a proportion of the total number of species on that island. As such, the null prediction is that this proportion should stay constant as total species number on an island increases. The approach of Kiflawi et al. (2007) has been to look at the number of singletons on an island as a proportion of the total pool of singletons across the archipelago. The null prediction of this model is that this proportion should increase as total species number on an island increases. When the results of the null model of Kiflawi et al. (2007) for the number of single-island endemics on a given island are expressed as a proportion of the total number of species on that island, it becomes apparent that observed values depart from null expectations. In Figs. 1 and 2 we have plotted the null model expectations of Kiflawi et al. (2007) for the proportions of endemic species as a function of island fauna, as opposed to the total pool of single-island endemics. Essentially, both methods of constructing the null model are valid, but our original hypothesis can only be properly tested when single-island endemic data are expressed as a proportion of an island's biota. As can be seen in Figs. 1 and 2, observed patterns are not consistent with null expectations.

As pointed out by Kiflawi et al. (2007), matching of observed data to null expectations suggests that ecological and evolutionary processes contribute little if any structure within the observed data. As such, this would invoke the conclusion that ecological and evolutionary processes are occurring in an unbiased manner across all islands. We test this conclusion further with the use of a null model, including extinction, colonization, and speciation. For vascular plants of the Canary Islands, 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 colonize another island, or (3) undergo either anagenetic or cladogenetic speciation. Importantly, these events are random, with local extinction being balanced by either colonization or speciation to maintain species number on an island. Simulations were carried out using the "fixed column equiprobable row" (Gotelli 2000) randomization procedure as implemented in the software EcoSim (Gotelli and Entsminger 2004). Our analysis is restricted to the
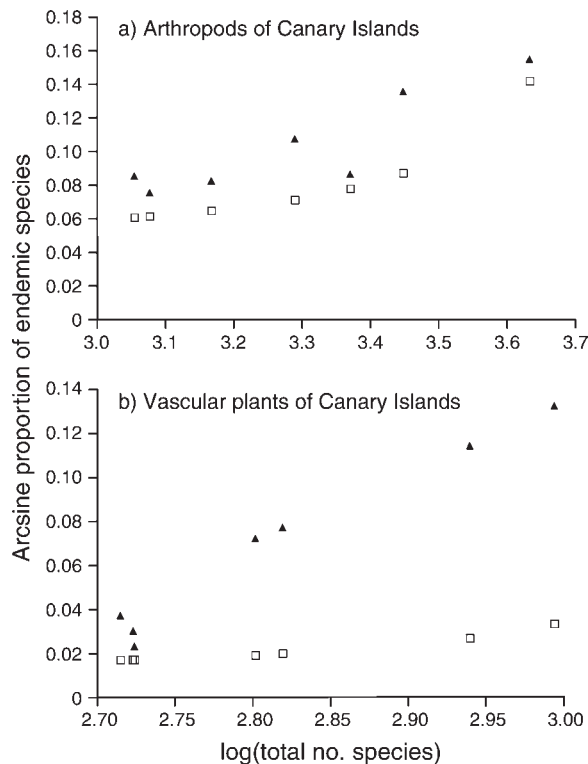
FIG. 1. Bivariate plots for the relationship between the proportion of endemic species on an island and the log-transformed species richness of the island for (a) arthropods of the Canary Islands and (b) vascular plants of the Canary Islands. Solid triangles represent observed values; open squares represent expectations from the null model of Kiflawi et al. (2007).

vascular plants of the Canary Islands because (1) we have the required species–island incidence matrix, and (2) it does not exceed the matrix size limitations of the software. Each simulation was initiated with a matrix corresponding to observed distribution data, and as can be seen from Fig. 3, under a model of stochastic extinction, colonization, and speciation, proportions of single-island endemics are eroded. More importantly, the slope of the relationship between proportion endemics and species richness is steeper for the observed data as compared to data generated from simulation ($t_3 = 6.7$, $P < 0.01$). This suggests that not only do the distributions not overlap, they are also different in shape. Similar to the model of Kiflawi et al. (2007), when expressed as the proportion of an islands total number of species (Fig. 1b), the results of our null model suggest the present-day distribution of the Canarian plant endemic singletons is inconsistent with null expectations.

We have taken a null-model approach by testing if patterns of proportionately more single-island endemics on species-rich islands are maintained when speciation, extinction, and colonization occur equiprobably across

islands. The only parameter we have constrained our model with is the observed number of species on each island. Our results demonstrate the observed pattern disappears, suggesting that observed distributions of single-island endemics depart from null expectations. Further to the analyses of single-island endemic species, Kiflawi et al. (2007) also conclude that the distribution of nonnative species (those also occurring outside the archipelago of interest) restricted to single islands is also compatible with expectations based on their null model (i.e., islands with more species will have more of these taxa). Although the relative proportions of these taxa on islands is not of concern for the conclusions of Emerson and Kolm (2005), it is perhaps not surprising that the distributions of these taxa are a function of the number of species an island contains. However, we would recommend a more robust approach to null modeling to fully evaluate such a conclusion.
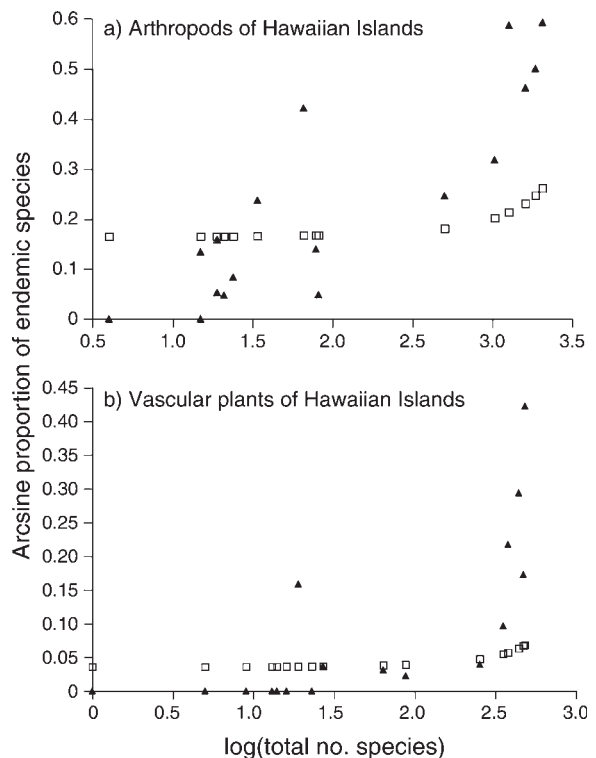
FIG. 2. Bivariate plots for the relationship between the proportion of endemic species on an island and the log-transformed species richness of the island for (a) arthropods of the Hawaiian Islands and (b) flowering plants of the Hawaiian Islands. Solid triangles represent observed values; open squares represent expectations from the null model of Kiflawi et al. (2007).
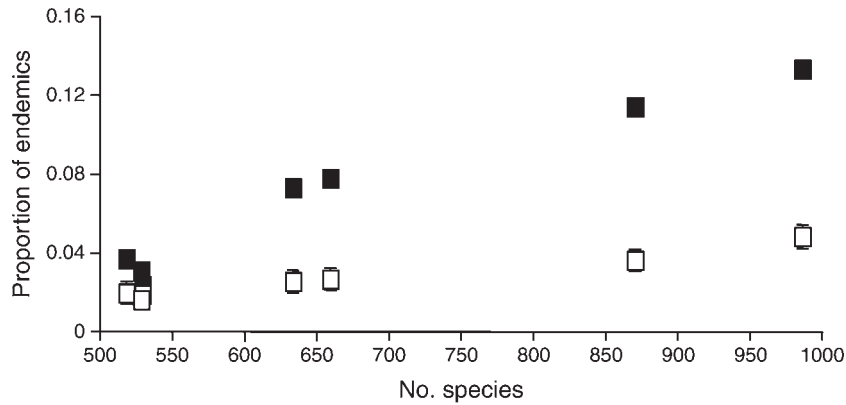
FIG. 3.   Bivariate plot of the relationship between total native species richness and the proportion of single-island endemic species for vascular plants on the Canary Islands (solid squares) and expected values from the null model of stochastic colonization, extinction, and speciation (open squares). The 95% confidence intervals around the predicted values from the null model are shown.

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