Forum

Ecography 30: 328–330, 2007
doi: 10.1111/j.2007.0906-7590.04779.x

Subject Editors: Robert Colwell and Carsten Rahbek. Accepted 19 February 2007

Does species diversity really drive speciation?

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It has been hypothesized that total speciation rate may depend on species diversity (Seposky 1978), population sizes (Hubbell 2001), and island area (Losos and Schluter 2000). In a recent paper, Emerson and Kolm (2005) tested the hypothesis that species diversity might promote speciation, by comparing the proportion of endemics in a taxon with the number of species in that taxon, in the Canary Islands and the Hawaiian Islands. They show that the number of species of the taxon is a good predictor of the island endemics in that taxon, and suggest that this result demonstrates the role of species diversity in speciation. We propose an alternative explanation: that the same abiotic variables that control species diversity also influence speciation, and that this phenomenon may render the analysis of Emerson and Kolm circular.

Emerson and Kolm performed a stepwise regression of the speciation rate of a taxon, measured as the proportion of endemics of that taxon, against a set of independent variables comprising abiotic factors and the number of species of that taxon. However, as we shall see, if the number of species itself is dependent on the same set of abiotic variables as the speciation rate, then the stepwise regression will select the number of species as the explanatory variable for the speciation rate and lead to the wrong conclusion that the abiotic variables are less important. This statistical artefact happens because the number of species accounts for the compound effect of the abiotic variables. Cadena et al. (2005) point out a particular case of this artefact which happens when both species richness and endemism depend on attributes of islands that influence the average age of resident populations and reduce extinction rates, such as area. Here we show that the statistical artefact can occur more generally for any type of abiotic variable that influences both species richness and speciation or extinction rates.

In both the Canary Islands and the Hawaiian Islands species diversity of arthropods and plants is well explained by abiotic variables (Table 1). While the abiotic variables explaining species diversity in each of the archipelagos differ, the most important variables are the same for both taxon in each archipelago (elevation and island age for the Canary Islands, and area for the Hawaiian Islands). Therefore it is not surprising that there is a tight correlation between species diversity of arthropods and of vascular plants in the Canary Islands ($r = 0.96$, $p = 0.01$) and in the Hawaiian Islands ($r = 0.89$, $p < 0.001$).

To see how the effect of the abiotic variables can be hidden in a stepwise regression, consider the regression of the species diversity of arthropods against a set of variables including abiotic factors and the diversity of vascular plants. For the Canary Islands the stepwise regression selects the number of vascular plants as an explanatory variable ignoring all the abiotic variables, and in the Hawaiian islands only one of the two significant abiotic variables remains (Table 2). Similarly, if we perform a stepwise regression of the species diversity of vascular plants against abiotic factors and the diversity of arthropods, the only selected explanatory variable in the Canary Islands is the diversity of arthropods while in the Hawain islands again only one of the two significant abiotic variables remains (Table 2). This suggests that while species diversity in a given taxon is controlled by abiotic variables, the effect of each abiotic variable can go undetected in a stepwise regression that includes species diversity of another taxon as an independent variable (which implicitly includes the effect of abiotic variables). This statistical problem shades doubt on the analysis of Emerson and Kolm of the relationship between proportion of endemics and species diversity. The proportion of endemics

Table 1. Stepwise forward multiple regression analyses were performed for the number of species of each taxon for each island group as a function of abiotic variables only. The abiotic variables used were island age, island elevation, island area and distance to nearest island. All the variables were log transformed. A tolerance level of 0.1 was applied to prevent colinearity between independent variables. β is the standardized regression coefficient.

Islands	Dependent variable[1]	n	r^2	p	Independent variables[2]	β	p
Canary Islands	Arthropods	7	0.92	0.007	Elevation	0.99	0.003
					Age	0.61	0.017
	Plants	7	0.98	0.003	Age	0.81	0.002
					Elevation	0.55	0.016
					Distance	0.58	0.018
Hawaiian Islands	Arthropods	17	0.75	<0.001	Area	1.09	<0.001
					Distance	0.34	0.116
	Plants	18	0.91	<0.001	Area	1.14	<0.001
					Age	0.25	0.082

[1]The number of species in the taxon as the dependent variable.
[2]Independent variables included in the final model.

is well explained by abiotic variables alone (Table 3). The redundancy of including species diversity as an independent variable is apparent in comparing regression models for the proportion of endemisms considering only abiotic variables (Table 3) and models considering both the abiotic variables and species diversity (Table 1 in Emerson and Kolm): in the Canary Islands for arthropods we have $r^2 = 0.99$ using only abiotic variables vs $r^2 = 0.80$ using both abiotic variable and species diversity; for plants, $r^2 = 0.97$ vs $r^2 = 1.0$; in the Hawaiian Islands for arthropods we have $r^2 = 0.79$ vs $r^2 = 0.93$; and for plants we obtain $r^2 = 0.80$ vs $r^2 = 0.79$. A similar comparison using the Schwarz Criterion (SC; also known as a Bayesian information criterion, Hilborn and Mangel 1997) that penalizes the number of variables in the model gives the same qualitative results (i.e. the model that had the highest r^2 also has the lowest SC value). While the Schwarz Criterion would put at advantage models that include a compound variable such as species diversity accounting for the joint effect of a set of abiotic variables, even that a priori advantage is not enough to give those models better SC scores.

While we do not argue against a role for species diversity on speciation, we do not think that the analysis of Emerson and Kolm can ascertain such role. On the other hand, we can think of many ways in which the same abiotic factors promoting speciation also influence species diversity (Whittaker et al. 2007). For instance, island age allows for accumulation of colonizer species, but also allows for more time for intra-island speciation to occur (Borges and Brown 1999). Elevation permits the coexistence of more species as more ecological niches exist (Kocher and Williams 2000), but the existence of more ecological niches and terrain barriers to dispersal also promote intra-island speciation (Losos and Schluter 2000). Island area increases the number of individuals and the number of ecological niches which decreases extinction rate (Mayr 1965, MacArthur and Wilson 1967, Cadena et al. 2005) and favours speciation (Losos and Schluter 2000, Hubbell 2001). Finally distance acts in opposite ways on species diversity and proportion of endemisms. A larger distance to the nearest island decreases the probability of colonization, which in turn lowers species diversity (MacArthur and Wilson 1967), but at the same time favours endemism by decreasing the probability that a species originating in a given island will colonize other islands (Brown and Lomolino 1998). However, distance is never the first variable to enter the stepwise regression models, suggesting it has less importance than elevation and area in these two datasets. In conclusion, the Hawaiian and

Table 2. Stepwise forward multiple regression analyses were performed for the number of species of each taxon for each island group as a function of abiotic variables and the number of species of the other taxon. All the variables were log transformed. Tolerance level as in Table 1.

Islands	Taxon[1]	n	r^2	p	Independent variables[2]	β	p
Canary Islands	Arthropods	7	0.91	0.001	Plants	0.96	0.001
	Plants	7	0.91	0.001	Arthropods	0.96	0.001
Hawaiian Islands	Arthropods	17	0.83	<0.001	Plants	1.11	<0.001
					Distance	0.32	0.064
	Plants	17	0.96	<0.001	Area	0.77	<0.001
					Arthropods	0.24	0.029

[1]The number of species in the taxon as the dependent variable.
[2]Independent variables included in the final model.

Table 3. Stepwise forward multiple regression analyses were performed for the proportion of single-island endemic species of each taxon for each island group as a function of abiotic variables only. Independent variables were transformed using log transformation and the dependent variable was transformed using arcsin transformation. Tolerance level as in Table 1.

Islands	Dependent variable[1]	n	r^2	p	Independent variables[2]	β	p
Canary Islands	Arthropods (% End)	7	0.99	0.001	Age	0.84	0.001
					Distance	0.77	0.003
					Elevation	0.37	0.021
	Plants (% End)	7	0.97	0.009	Age	0.64	0.012
					Distance	0.60	0.040
					Elevation	0.57	0.037
Hawaiian Islands	Arthropods (% End)	17	0.79	<0.001	Distance	0.79	0.001
					Elevation	0.71	0.005
					Area	0.67	0.016
	Plants (% End)	18	0.80	<0.001	Distance	0.79	<0.001
					Area	0.78	0.002
					Elevation	0.58	0.009

[1]The proportion of endemics species in the taxon as the dependent variable.
[2]Independent variables included in the final model.

Canary islands datasets clearly suggest that the same abiotic effects which influence species diversity also promote speciation, and this reality confounds the examination of the role of species diversity in speciation.

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