

ECOLOGY

Is speciation driven by species diversity?

Arising from: B. C. Emerson & N. Kolm *Nature* 434, 1015–1017 (2005)

Emerson and Kolm¹ show that the proportion of species endemic to an island is positively related to its species richness and, assuming that endemism indexes speciation rate, they infer that greater species diversity accelerates diversification. Here we demonstrate that the same correlation between species richness and percentage endemism can arise even if within-island speciation is negligible, particularly when both endemism and species richness depend on attributes of islands (such as area) that influence the average age of resident populations. Island biogeography theory indicates that, where the average time to extinction is relatively long, diversity increases through

colonization, irrespective of whether new species are formed²; at the same time, islands on which populations persist for longer accumulate more endemic species as local populations differentiate and populations on neighbouring islands become extinct^{3,4}. We therefore suggest that species richness and endemism are correlated fortuitously owing to their mutual dependence on the life spans of populations on islands, which is unrelated to speciation itself.

If the scenario we propose is correct, islands richer in species and with higher endemism would also have older populations. This prediction is supported by data for birds in the

West Indies, a system in which the occurrence of within-island speciation is an extremely rare event: the proportion of endemic species increases linearly with species richness, and species-poor islands with few endemics have populations that are younger on average than those of species-rich islands with higher endemism (Fig. 1). We argue, therefore, that the correlation between species richness and endemism does not imply a causal relationship between these two variables, but rather that they respond in parallel to the effect that area and other island attributes have on population persistence times. Accordingly, the slope of the species–area relationship is much steeper for old endemics that are largely absent from small, species-poor islands, than for recent colonists, which are similarly diverse on all islands⁵. The fact that large (that is, species-rich) islands have populations with longer persistence times, as indicated by genetic-distance data, is consistent with island biogeography theory for systems where species richness is influenced primarily by rate of extinction⁶.

Our reasoning implies that per cent endemism will often be an inappropriate surrogate for speciation rate because it is strongly influenced by differentiation between island populations and extinction (see also ref. 7). Our analysis also contradicts Emerson and Kolm's assertion that extinction on neighbouring islands would inflate the proportion of endemic species more strongly for species-poor islands. This assertion follows from their argument that high species diversity drives a high rate of extinction. Although total extinctions per unit time rise as diversity increases on an island over time², the rate of extinction per species, hence the average species life span, is relatively insensitive to species richness. Moreover, theory² and observation (Fig. 1) indicate that the rate of extinction per species is inversely related to species richness in comparisons between islands.

The data shown in Fig. 1 support our proposed scenario but disagree with a prediction of Emerson and Kolm's hypothesis — namely that, if speciation rate accelerates as local diversity increases, the rate of turnover under speciation–extinction equilibrium should be higher and the average duration of populations should therefore be shorter on more diverse islands. Some insular endemics are of recent origin^{8,9}, but whether they arose on islands on which populations persist for relatively longer (because of larger island size, increased habitat diversity, milder weather or other factors) can only be addressed with data on persistence times for multiple lineages and

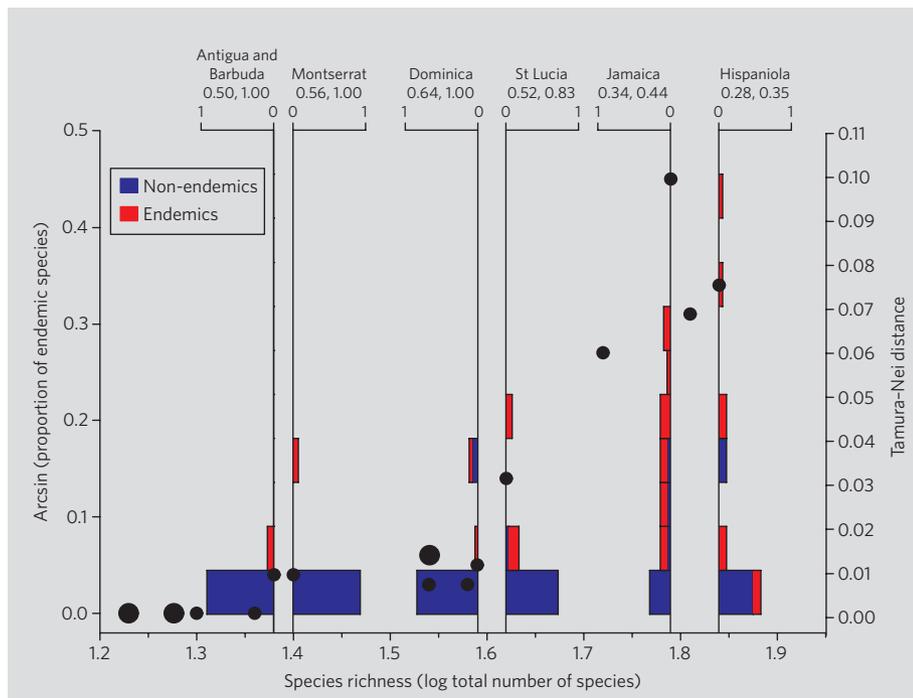


Figure 1 | Relationship between species richness, endemism and persistence times of populations of resident land birds on Caribbean islands. Black dots indicate values of species richness and endemism; larger dots indicate values shared by two different islands. Histograms show relative frequency distribution of persistence times of non-endemic and endemic populations on six islands (Antigua and Barbuda are considered as a single island), measured as mitochondrial DNA Tamura–Nei distance to the node uniting them with their nearest conspecific population or sister taxon. Numbers above the histograms are the proportion of the total species and of endemic species for which we obtained genetic distance data for each island. The vertical axes of histograms cross the dots that correspond to the species richness and endemism of the islands for which they portray genetic distance data. As with plants in the Hawaiian archipelago¹, species richness and island area are highly correlated ($r = 0.928$) and their effects on endemism cannot be separated. When area is excluded from the analysis, as in one of the examples in ref. 1, species richness is the only variable that explains endemism in a forward multiple regression that includes maximum elevation and distance to the nearest island as additional independent variables ($r^2 = 0.723$, $F = 41.671$, $P < 0.0001$, $\beta = 0.593 \pm 0.09$ s.e., $t = 6.46$). Populations on species-rich islands are significantly older than those on species-poor islands (Kruskal–Wallis $\chi^2 = 38.1$, d.f. = 5, $P < 0.0001$), and endemics are older than non-endemics on each of the six islands (Kruskal–Wallis χ^2 , 4.9–13.6; d.f. = 1; P , 0.0002–0.027). Data on mitochondrial genetic differentiation are for 113 populations of 60 bird species on six islands with varying numbers of species and degrees of endemism. Further details are available from the authors (www.umsl.edu/~cdc35b).

islands. In the absence of this information, and of meaningful estimates of intervals between speciation events, Emerson and Kolm's approach to the idea that species diversity might drive diversification is inconclusive. This hypothesis might be plausible in systems where speciation events take place readily within islands, including those described by Emerson and Kolm. However, the influence of diversity on species formation can be properly addressed only by considering variation in per-lineage speciation rate, estimated from phylogenetic reconstructions^{10,11}, across areas with varying species richness.

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Emerson & Kolm reply

Replying to: C. D. Cadena, R. E. Ricklefs, I. Jiménez & E. Bermingham *Nature* **438**, doi:10.1038/nature04308 (2005)

Cadena *et al.*¹ question our conclusion that species diversity can positively influence speciation rate on the basis of their analysis of a data set for West Indian land birds, in which an additional variable is added — lineage age. Here we clarify our hypothesis and show why their system is not suitable for testing whether species diversity can drive speciation.

Cadena *et al.* find that lineage age is correlated with species diversity and per cent endemism. However, as they point out, a fourth variable, island area, is also strongly collinear with species diversity and endemism, and so with lineage age. A similar collinearity between island area and species diversity occurs for one of our four analyses, Hawaiian plants, and we recognized the difficulty of disentangling the effect of these two variables.

For West Indian land birds, island area is likely to be the causative agent for the observed levels of endemism, perhaps because bigger islands contain older species assemblages that have had more time to accumulate endemics, as Cadena *et al.* suggest. Hence, if island area and not species diversity is driving diversification of the avifauna of the West Indies — a likely scenario, given its non-equilibrium state with an imbalance between colonization and extinction² — Cadena *et al.* risk comparing apples with oranges.

MacArthur and Wilson's classic theory³ is traditionally interpreted in terms of colonization and extinction, but we pointed out that it also makes predictions for speciation⁴. Even in the simplest scenario of anagenetic speciation only, the theory of island biogeog-

raphy predicts that, all other things being equal, islands with more species will have a greater proportion of endemics (Fig. 1a). Here the proportion of endemics does provide an index of speciation (and extinction) rate, contrary to the assertion of Cadena *et al.*¹. Similarly, all other things being equal, larger islands are expected to have a smaller proportion of endemics than smaller islands (Fig. 1b). This discrepancy with the results of Cadena *et al.* is consistent with the non-equilibrium nature of the West Indian avifauna, where colonization does not yet seem to be balanced by extinction². Our predictions are expected for the systems we used⁴, where there is a balance between colonization, speciation and extinction (as seen in Canary Island arthropods⁵, where island area and age are not positively related to the proportion of endemics).

Cadena *et al.* also point out that predictions regarding lineage age made from the theory of island biogeography can be tested by molecular phylogenetics. However, lineage age is better determined using age estimates for the most recent common ancestor of monophyletic groups within islands (see ref. 6, for example). This provides a conservative minimum age estimate to allow for extinctions between the most recent common ancestor of island species and that connecting an island clade to a sister lineage on another land mass⁷. Extinctions between the nodes that involve taxa outside the island will inflate the true population age. Hence, the lineage age estimation of Cadena *et al.* may be misleading, particularly in view of taxon-cycling theory as applied to the West Indian avifauna, which supports a relationship between endemism and sister lineage extinction⁸.

We agree that our theory of how species richness drives diversification may be less important in systems that are not under equilibrium conditions. But the analysis by Cadena *et al.* does little to bring into question our conclusion that species diversity may be an important driver of speciation.

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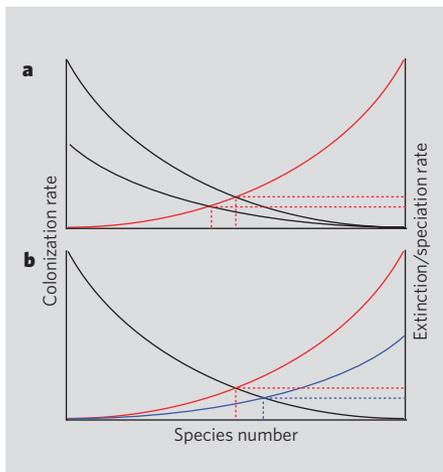


Figure 1 | The theory of island biogeography and speciation rate. **a**, The number of species on an island is a balance between the arrival of colonizing species to an island (black lines) and extinction (red line)³. For two islands of the same size but with differing colonization rates, the island receiving more colonists is expected to contain more species. As the same factors that influence extinction rate also influence speciation rate⁴, the model can predict speciation rate: the island with more species should have a greater proportion of endemics because of a comparatively higher speciation rate. **b**, For two islands with a similar colonization rate but having different numbers of species because of their different sizes, the smaller island (red line) should have a greater proportion of endemic species than the larger island (blue line).

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