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

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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 extinction[2] — Cadena *et al.* risk comparing apples with oranges.

MacArthur and Wilson's classic theory[3] is traditionally interpreted in terms of colonization and extinction, but we pointed out that it also makes predictions for speciation[4]. Even in the simplest scenario of anagenetic speciation only, the theory of island biogeography 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 extinction[2]. Our predictions are expected for the systems we used[4], where there is a balance between colonization, speciation and extinction (as seen in Canary Island arthropods[5], 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 mass[7]. 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 endemicity and sister lineage extinction[8].

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.

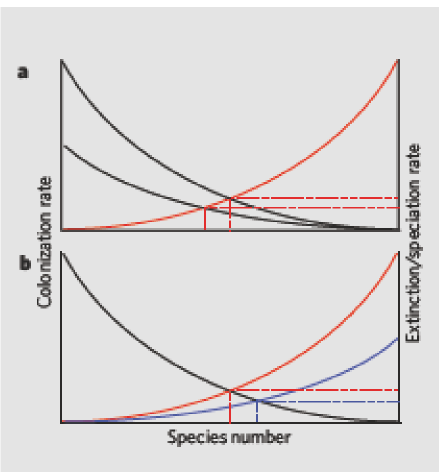

Figure 1 | The theory of island biogeography and speciation rate. **a**, The number of species on an island is a balance between the arrival of colonizing species to an island (black lines) and extinction (red line)[3]. For two islands of the same size but with differing colonization rates, the island receiving more colonists is expected to contain more species. As the same factors that influence extinction rate also influence speciation rate[4], 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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