

LETTERS

Coral reef diversity refutes the neutral theory of biodiversity

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The global decline of coral reefs^{1,2} highlights the need to understand the mechanisms that regulate community structure and sustain biodiversity in these systems. The neutral theory, which assumes that individuals are demographically identical regardless of species, seeks to explain ubiquitous features of community structure and biodiversity patterns^{3–5}. Here we present a test of neutral-theory predictions with the use of an extensive species-level data set of Indo-Pacific coral communities. We show that coral assemblages differ markedly from neutral-model predictions for patterns of community similarity and the relative abundance of species. Within local communities, neutral models do not fit relative abundance distributions as well as the classical log-normal distribution. Relative abundances of species across local communities also differ markedly from neutral-theory predictions: coral communities exhibit community similarity values that are far more variable, and lower on average, than the neutral theory can produce. Empirical community similarities deviate from the neutral model in a direction opposite to that predicted in previous critiques of the neutral theory^{6–9}. Instead, our results support spatio-temporal environmental stochasticity as a major driver of diversity patterns on coral reefs^{10,11}.

The neutral theory was initially proposed to explain the dynamics of communities that sustain high biodiversity whose species compete for space by a lottery mechanism. This set of assumptions seems, at least superficially, to be better suited to coral communities than to most other animal assemblages¹². Testing the neutral theory against coral biodiversity patterns is therefore essential in assessing its generality and can provide much insight into mechanisms of biodiversity maintenance in these increasingly threatened ecosystems. Most tests of the neutral theory have focused on assessing the fit of a neutral model to relative abundance patterns within local communities, or for a metacommunity as a whole^{4,5,13}. However, it has recently become clear that such approaches, used in isolation, provide only weak tests of community structure models^{14,15}. Therefore, assessing the predictions of a theory at multiple levels¹⁶ is preferable, particularly when competing theories make different predictions. In neutral communities, variability in relative abundances between species is due entirely to demographic stochasticity or 'ecological drift'. Theoretical analyses of neutral models have shown that this process leads to divergence between communities¹⁷, and thus community similarity is determined by the strength of dispersal limitation^{4,17,18}. In contrast, niche apportionment mechanisms have been invoked to argue that higher levels of community similarity should be observed under niche assembly than under neutral dynamics^{6–9}. These contrasting predictions provide an ideal opportunity to test the neutral model against empirical data.

Here we use an extensive data set of species-level abundances on coral reefs to conduct a multiscale test of the hypothesis that the structure of coral assemblages is consistent with the neutral theory. Using neutral-model parameters fitted to abundance distributions

within local communities, we predicted pairwise community similarity statistics for a network of local communities. The predicted similarities are consistently high (Fig. 1a). In contrast, the observed similarities of coral communities are markedly lower, and more variable, than predicted by the neutral theory (Fig. 1b). Furthermore, the neutral model's fit to abundance distributions within local communities is significantly worse than the fit of a Poisson log-normal distribution (model selection supports the Poisson log-normal with more than 99% confidence; Supplementary Fig. S1 and Supplementary Methods). Hence, neither community similarity patterns nor local abundance distributions of reef corals are consistent with neutral-model predictions.

Our finding that observed community similarities are lower than neutral-model predictions is unexpected, and is contrary to the widespread view that high similarity over space and time in empirical data constitutes evidence against the neutral theory^{6–9}. However,

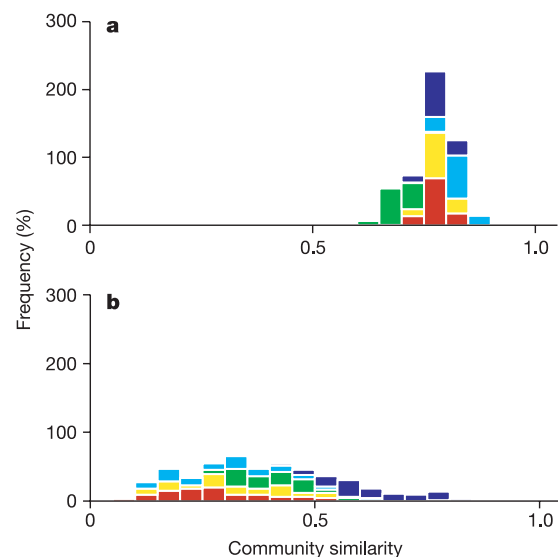


Figure 1 | Frequency distributions of Bray-Curtis similarities.

a, Distributions for local communities simulated with parameters estimated from the data's species abundance distributions; **b**, distributions for observed coral assemblages on reef slopes. Parameter estimates were $m = 0.905, 0.916, 0.915, 0.867$ and 0.748 and $\theta = 25.4, 26.5, 30.6, 10.8$ and 6.3 for Indonesia (red), Papua New Guinea (yellow), Solomon Islands (green), Samoa (light blue) and French Polynesia (dark blue), respectively. The heights of the bars sum to 100% separately for each region, so the stacked bars may exceed 100%. Note the low mean and high variance of the observed distributions in comparison with those of the simulations. Flat and crest assemblages differ from neutral-model predictions in a very similar fashion (Fig. 2).

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others have argued that the neutral theory can produce high similarities^{4,18}. Therefore, to achieve a better understanding of community similarity under the neutral theory, we conducted a comprehensive investigation of neutral-model dynamics. Our results confirm that the neutral theory can produce extremely high similarities, provided that immigration rates from the metacommunity are high, or diversity is very low (Fig. 2, Supplementary Fig. S2 and Supplementary Methods). However, our analyses also reveal that variance in community similarity under neutral dynamics is consistently low, much lower than in our data, regardless of parameter values (Fig. 2, Supplementary Fig. S3 and Supplementary Methods), thereby also confirming that this large discrepancy between neutral-model predictions and our data are robust to uncertainty in parameter estimates.

The higher variance of real coral communities than in neutral-theory predictions indicates a strong role for environmental variability in determining patterns of community similarity on coral reefs. This high variance in community similarity indicates that the data contain a much broader mixture of sites that are very similar and very different, in comparison with the neutral theory. Because habitat differences were minimized by our study design (see Methods), the most likely source of this variability is spatio-temporal environmental stochasticity: the tendency for different local communities to experience fluctuations in environmental conditions differently. On coral reefs, even adjacent reefs can have markedly different environmental histories¹⁹. Such historical differences would tend to decrease mean similarity if species differ in their responses to environmental fluctuations. These mechanisms would also be expected to increase the variability in community similarity values: communities that have experienced similar environmental histories would tend to have a similarity that is higher than average (for example, communities at similar successional stages), whereas communities with markedly different histories would tend to have a similarity that is lower than average. In contrast, neutral models assume that metacommunities are environmentally homogeneous in space and time. Indeed, differences between species in responses to environmental fluctuations challenge a core assumption of the neutral theory: that species are demographically identical.

In addition to the assumptions of environmental homogeneity

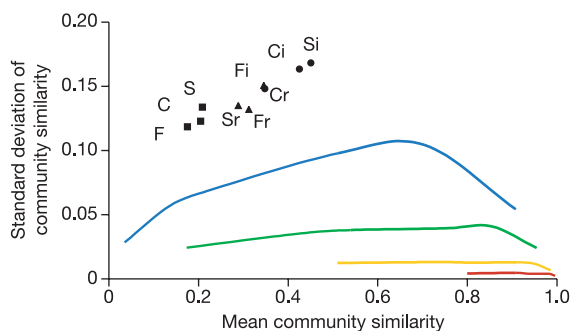


Figure 2 | Bray–Curtis similarity distributions for neutral simulations and coral communities. Because community similarity frequency distributions are approximately normal (Supplementary Information), they can be compared in terms of their mean and standard deviation. Each contour plots the mean and standard deviation of community similarity for $1 < \theta < 500$ (from right to left on each contour) for a particular value of m (0.999 in red, 0.1 in yellow, 0.01 in green and 0.001 in blue). Bray–Curtis similarity distributions for coral assemblages in each habitat are plotted as black points: Si within island slope assemblages, Ci within island crest assemblages, Fi within island flat assemblages, Sr within region slope assemblages, Cr within region crest assemblages, Fr within region flat assemblages, S among all slope assemblages, C among all flat assemblages, and F among all flat assemblages. Note how all data points, regardless of spatial scale or habitat, fall outside and comparably distant from the contours generated by neutral simulations.

and neutrality, which are shared by all neutral models²⁰, there are other assumptions that differ between alternative formulations. We believe these assumptions are less plausible explanations for our results. First, neutral models can have different assumptions about how speciation occurs⁴. However, because speciation occurs rarely, in comparison with changes in relative abundance within species, it seems unlikely that different speciation mechanisms would have a marked effect on community similarity patterns, at least for realistic speciation rates²¹. A second assumption is the ‘mainland-island’ framework: metacommunities are held constant during local community dynamics⁴. An alternative formulation uses an archipelago framework, with the metacommunity changing as local communities change³. Although this might decrease community similarity over time, there is no obvious reason to expect it to increase variance in similarity between local communities, which is a major cause of the discrepancies between coral communities and neutral-model predictions. Last, spatially explicit neutral models predict decreasing similarity with distance^{4,22}. Given that our most distant sites are more than 10,000 km apart, dispersal limitation is certainly occurring within our sampling scale. If dispersal limitation were the principal cause of the discrepancies between our data and the neutral model, the empirical data should converge towards the neutral model (that is, they should move down and to the right on Fig. 2) as the spatial scale at which community similarity is calculated decreases. However, the data do not converge to the model: the high variance in coral community similarity does not decrease as the spatial scale decreases, even when similarity is calculated only for sites less than 10 km apart (Fig. 2).

Because coral communities have been viewed as being among the assemblages most likely to exhibit neutral dynamics^{12,23–25}, our findings challenge the neutral theory’s utility as a general theory of biodiversity and biogeography. The neutral theory was initially proposed as a null model for macroecology, predicting the diversity patterns that could arise from the action of demographic stochasticity and dispersal limitation alone⁴. However, early findings that neutral models can exhibit a close fit to empirical species–abundance distributions rapidly shifted the focus towards whether or not the neutral theory is sufficient, by itself, to explain macroecological regularities, such as species–abundance distributions and species–area relationships^{5,13,16,26}. Although our results do not support the latter hypothesis, they do show how using the neutral theory as a null model can shed light on the mechanisms responsible for macroecological patterns.

In recent years there has been a renewed focus on the use of ecological theory to inform conservation priorities. At the large ecological scales relevant to this endeavour, the prevailing view is that niche apportionment rules stabilize community structure over space and time^{6–9,27}. However, our results support an alternative view in which species’ different responses to spatial and temporal environmental fluctuations are crucial in the maintenance of biodiversity¹⁰. From this perspective, protecting biodiversity requires preserving the patterns of connectivity that allow species to find and exploit suitable environments that are patchy over both space and time. Fluctuation-mediated coexistence has received comparatively little attention in the continuing controversy about the neutral theory, despite the existence of tractable models of the relative abundance of species that explicitly incorporate effects of environmental stochasticity¹¹. Given the accelerating pace of coral reef habitat loss², a renewed focus on these mechanisms and on the body of ecological theory associated with them is urgent.

METHODS

Sampling followed a hierarchical design with three distinct spatial scales: site, island and region²⁸. The five regions encompass a threefold gradient in coral species richness²⁹. There were three islands within each region, four sites within each island, and three local communities at each site: one from each of three reef habitats (flat, crest and slope). Within each local community, ten random

transects 10 m in length were established, and the colonies intercepted by each transect were counted and identified to species.

We estimated the parameters of the neutral model, θ and m (Supplementary Methods), by fitting the predicted species abundance distribution (the 'zero-sum multinomial' or ZSM) to each of the local coral communities, using both simulation-based⁴ and analytical methods^{5,20}. The fit of the ZSM was compared with the log-normal distribution using Akaike's information criterion¹⁴ (Supplementary Methods). We used parameters estimated from fits to local community abundance distributions to simulate the dynamics of 15 metacommunities: one for each habitat type in each region (Supplementary Methods). Bray–Curtis community similarities³⁰ were then calculated for all pairs of simulated local communities within the same metacommunity; these similarities were compared with the distribution of Bray–Curtis statistics for the empirical data. To comprehensively characterize the similarity patterns produced by the neutral theory, we also analysed distributions of community similarity for an exhaustive spectrum of values of θ and m (Supplementary Methods).

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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