Species Differences Drive Nonneutral Structure in Pleistocene Coral Communities

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ABSTRACT: Although ecological assemblages frequently depart from neutral model predictions, these discrepancies have not been unambiguously attributed to neutral theory’s core assumption: that community structure is primarily the result of chance variation in birth, death, speciation, and dispersal, rather than the manifestation of demographic differences among species. Using coral communities in Barbados from four time periods during the Pleistocene, we demonstrate that the neutral theory cannot explain coral community similarity distributions, species’ regional abundance distributions, or their local occupancy. Furthermore, discrepancies between the neutral theory and the observed communities can be attributed to violation of the core assumption of species equivalence. In particular, species’ variable growth rates are driving departures from neutral predictions. Our results reinforce an understanding of reef coral community assembly that invokes trade-offs in species’ demographic strategies. The results further suggest that conservation management actions will fail if they are based on the neutral assumption that different coral species are equally able to create live coral cover in the shallow-water reef environment. These findings highlight the importance of developing biodiversity theory that can parsimoniously incorporate species differences in coral reef communities, rather than further elaborating neutral theory.

Keywords: island biogeography, paleontology, linear growth rates, community assembly, coral reefs, Barbados, Caribbean.

Introduction

Understanding the factors that influence the coexistence of species is an ongoing ecological problem and is particularly salient for assemblages whose species compete for a small number of shared limiting resources (Hutchinson 1961; Armstrong and McGehee 1980). Traditionally, species coexistence and community structure have been explained by stabilizing mechanisms, all of which invoke, in various ways, differences among species that give species a fitness advantage when they are rare, thus reducing the risk of extinction (Chesson 2000; Siepielski and McPeek 2010). Such mechanisms include classic niche partitioning (Case and Gilpin 1974; Schoener 1974), in which species’ resource uses only partially overlap but extend to include temporal and spatial variability. For example, environmental fluctuations or competition-colonization trade-offs can promote coexistence by stabilization, even when species that occupy the same habitat have the same relative fitness throughout that habitat (Chesson and Warner 1981; Connolly and Muko 2003). These stabilizing mechanisms of species coexistence are often collectively termed “niche theory.”

In contrast to niche theory, neutral theory proposes that species coexistence is driven by demographic stochasticity and dispersal limitation (Bell 2000; Hubbell 2001; Alonso et al. 2006). According to neutral theory, differences in species’ demographic characteristics play a negligible role in promoting species coexistence, and thus neutral models typically seek to explain patterns of commonness, rarity, and biodiversity by assuming that all individuals are demographically equivalent, regardless of species (Clark 2009; Purves and Turnbull 2010). Neutrality is not a stabilizing mechanism; rather, coexistence is transient. The number of coexisting species at the local (metacommunity) scale reflects the balance between immigration (speciation) and extinction, and their relative abundances are the result of neutral “drift” at both scales. Despite a limited set of assumptions, neutral community models, such as Hubbell’s unified neutral theory of biodiversity and biogeography (NTB; Hubbell 2001), can produce community characteristics that resemble those of empirical data, including species abundance distributions (Alonso et al. 2006; McGill et al. 2006; Rosindell et al. 2011), long-term community dynamics (Olszewski and Erwin 2004; Allen and Savage 2007; Tomasovych and Kidwell 2010), and the
structure of phylogenetic trees (Jabot and Chave 2008). Neutral theory’s ability to generate many realistic patterns of community structure challenges long-held ecological assumptions about the importance of species differences; in doing so, it has focused attention on the fact that ecologists’ confidence that niche processes are major drivers of community structure may exceed the supporting evidence (Siepielski and McPeek 2010).

In the marine realm, coral reefs have been an important model system for coexistence studies, and Caribbean coral assemblages in particular have provided important insights into community structure (Karlson 1999; Pandolfi 2002). Early research revealed that, in contrast to considerable small-scale variation in community structure on Indo-Pacific reefs (Connell 1978), Caribbean community structure was predictable at larger spatial scales. Striking, persistent patterns of relative abundance in different reef zones became apparent, some of which were overwhelmingly dominated by single species (Porter 1972; Kinzie 1973; Geister 1977). Until the 1980s, shallow-water (0–12 m) Caribbean coral communities consisted primarily of branching species (the “elkhorn” and slightly deeper “stag-horn” Acropora zones, which frequently represent more than 90% of a site’s live coral cover), whereas foliaceous and massive species were the more abundant growth forms in deeper water (Jackson 1991). This pattern has been replicated over thousands of kilometers of the southern Caribbean with remarkable stability since the Late Pleistocene (Pandolfi 2002; Pandolfi and Jackson 2006). The earliest explanations for these patterns were based on traditional environmental niches defined by gradients in light availability and exposure to environmental stressors (particularly wave action and storms; Goreau 1959; Geister 1977; Huston 1985a). The dominance of Acropora species in the shallow-water community was thought to reflect their much higher calcification rates, which allowed them to outcompete other species through shading and overtopping (Huston 1979; Lang and Chornesky 1990; Boulon et al. 2005). However, the superiority of the Acropora species was inverted during high-energy disturbances, when branching corals experienced disproportionately high mortality (Rogers et al. 1982; Huston 1985a). Given sufficient frequency and intensity, such disturbances prevent branching corals from excluding weaker competitors in the shallow-water environment (Connell 1978).

Although this highly niche-structured conceptualization of coral community structure is plausible, neutral theory has been proposed as an alternative (Hubbell 1997; Volkov et al. 2007). Indeed, because corals have a sedentary adult phase and occupy distinct habitat patches that are connected by propagule dispersal, they are particularly well suited to the assumptions that classical neutral models typically make about community dynamics (Hubbell 1997; Chave 2004; Dornelas et al. 2006). However, applications of neutral theory to Indo-Pacific coral assemblages have drawn markedly different conclusions. In particular, the studies disagree about whether neutral models can adequately reproduce the relative species abundance of coral communities at local and metacommunity scales (Volkov et al. 2007) or whether they can adequately reproduce patterns in community similarity (Dornelas et al. 2006; Volkov et al. 2007). It has also been proposed that neutral theory can provide reasonable estimates of species’ lifetimes and speciation rates (Rosindell et al. 2010). However, there is presently no consensus about whether these conflicting conclusions are due to differences between studies in the strength of tests applied (McGill 2003; Ruokolainen et al. 2009; Chisholm and Pacala 2010) or whether they are due to differences in ancillary assumptions made that are unrelated to neutrality (e.g., disturbances, speciation, or spatial structure; Economo and Keitt 2008; Connolly et al. 2009; Rosindell et al. 2010).

In this article, we evaluate niche and neutral explanations of coral community structure by investigating patterns of species turnover and relative abundance from four different time periods during the late Pleistocene in Barbados (fig. 1). Paleoecological evidence allows community ecologists to test hypotheses at large spatial and temporal scales, with data sets that were recorded before substantial anthropogenic disturbance (Jackson 2001; Pandolfi 2001). Contemporary reef coral communities have exhibited rapid and unpredictable changes at decadal timescales, mostly in response to anthropogenic impacts, most strikingly in the Caribbean with the catastrophic loss of previously dominant Acropora species (Hughes 1994; Gardner et al. 2003; Pandolfi et al. 2003). Thus, present-day assemblages are likely to depart much more severely from the quasi-equilibrial assumptions of niche and neutral models of species’ relative abundances. The fossil record offers a contrasting perspective that, although not directly observable during human lifetimes, allows investigation of natural ecological patterns from before such effects.

Our analyses are structured to overcome the limitations of previous tests of neutral theory on coral assemblages by directly assessing whether coral community structure and relative abundance can be explained by demographic differences between species. We demonstrate that neutral communities can reproduce neither observed regional species distributions nor species turnover patterns across local communities. We pay particularly close attention to whether these conclusions are robust to numerous common ancillary assumptions of neutral theories. We then focus on neutral theory’s core assumption of demographic equivalence by assessing whether the demographic attributes of different species can explain their relative abundance in the coral community. Specifically, we focus on
whether species’ departures from neutral theory predictions can be explained by their colony growth rates, consistent with the classic niche-based explanations of coral community structure.

Material and Methods

Observed Pleistocene Communities

The interaction between local tectonic uplift and sea level change during the Pleistocene resulted in a series of well-preserved, raised coral reef terraces in Barbados, which form the basis for our analyses. Fossil reefs provide a high-quality record of paleoecological communities across thousands of years (Jackson 1992; Pandolfi 2002). Their durable calcium carbonate skeletons are readily preserved and can be identified to species level within specific reef habitats. Fossil coral assemblages accurately represent time-averaged Pleistocene community diversity (Pandolfi and Minchin 1995), and comparative studies show that fossil coral assemblages retain key characteristics of depth zonation and relative abundance from their living state (Pandolfi and Jackson 2006). Importantly, the comparatively lower species richness of the Caribbean means that demographic information is available for a large proportion of the fauna, which allows us to assess the extent to which demographic differences among species can explain discrepancies between the data and neutral model predictions.

Fossil assemblages were recorded from the leeward reef crest habitat in up to 7 × 40-m-long line intercept transects (separated by 0.5–1.0 km), sampled at three sites along 25 km of the western and southern Barbados coastline (fig. 1). Samples were taken from four different time periods, radiometrically measured as dating from 104, 125, 195, and 220 thousand years before the present (ka), which
allowed each of our analyses to be replicated four times. The data sets for each time period therefore contained multiple local communities (13, 19, 18, and 12 communities, respectively), and coral colonies intercepting the line transects were identified to the species level. Of the 32 species currently found in the Caribbean’s shallow-water “reef crest” community (≤3 m water depth), 31 unique species were encountered in the Pleistocene transects: 20 species in the 104-ka data set, 17 in the 125-ka data set, 22 in the 195-ka data set, and 12 in the 220-ka data set (Pandolfi and Jackson 2006).

\[ \text{Fitting the Neutral Model} \]

Community assembly dynamics in Hubbell’s (2001) neutral model are determined by two key parameters. At the metacommunity scale, the “fundamental biodiversity number,” \( \theta \), is proportional to the total speciation rate \( (\theta = J_\alpha \nu, \text{ where } J_\alpha \text{ is metacommunity size and } \nu \text{ is the probability that a birth is a speciation). At the local community scale, dynamics also depend on the probability, } m, \text{ that a new recruit to a local community is an immigrant chosen at random from elsewhere in the metacommunity. Immigrants are not sourced preferentially from closer locations, which is an assumption of the NTB that is supported by observation in Caribbean coral communities (Pandolfi 2002). For each time step, an individual in a local community is randomly chosen to die (consistent with the assumption that all species have the same mortality rate) and is replaced by a recruit. If the new recruit is an immigrant, then its identity is determined by a random draw from Fisher’s log series distribution (because relative abundances in the broader metacommunity follow a log series distribution with parameter \( \theta \), and because under the neutrality assumption, species produce propagules in proportion to their abundance; Hubbell 2001; Volkov et al. 2003). If the new recruit is not an immigrant, its identity depends instead on the relative abundances of species in the local community. After a large number of generations, the relative abundance of species in a neutral local community reaches an equilibrium that can be compared with the observed data (Chisholm and Burgman 2004).

For each time period, we fit the NTB to the observed data by finding the combination of \( m \) and \( \theta \) that generates neutral local communities that most closely resemble the relative species abundances in each of the observed communities (i.e., the maximum likelihood parameters). The neutral model was fitted using the expected abundance distribution for a neutral local community, using the maximum likelihood methods implemented in the MATLAB package Palamedes (McGill et al. 2007). There are frequently two very different pairs of neutral parameters that fit species abundance data better than nearby combinations of parameters (i.e., there are consistently two local maxima in the likelihood function). Typically, one parameter set has a low \( \theta \) and a high \( m \), whereas the other has a high \( \theta \) and a low \( m \) (Etienne et al. 2006). We found the parameter estimates that corresponded to both of these peaks (henceforth referred to as the “alternative parameter estimates”).

The NTB is a model based on the abundance of individuals from different species. Hermatypic corals, however, have two levels of organization: clonally produced polyps and colonies of many polyps produced by sexual reproduction, fission, or fragmentation (Highsmith 1982). Previous analyses of extant communities have tended to use numbers of distinct colonies (Connolly et al. 2005, 2009; Dornelas et al. 2006), but these cannot be readily identified in the fossil record. Moreover, colonies can vary in size by orders of magnitude, so a single colony mortality event will not necessarily result in replacement by another single colony, and similarly, portions of larger organisms can die independently, with the dead colony surface colonized by neighboring colonies or new recruits of different species. We therefore transformed the sampled abundance data into pseudocount data by considering the smallest intercept recorded in each transect to be an individual. Larger organisms were thus transformed into colonies with abundance equal to the largest integer multiple of the smallest individual.

\[ \text{Testing the Neutral Model} \]

After fitting the neutral model to the patterns of abundance within local communities, we tested it by assessing the degree to which the fitted neutral model could predict differences in community structure across local communities. To generate neutral metacommunities for comparison with data, we used the maximum likelihood values of \( m \) and \( \theta \) estimated from the analysis of species abundance distributions and used the methods described in Hubbell (2001). To incorporate the potential effects of parameter uncertainty, we estimated the bivariate uncertainty distribution of the neutral model parameters from our maximum likelihood fits to the local relative abundance data (using the matrix of second partial derivatives of the log-likelihood function, following standard likelihood theory; Burnham and Anderson 2002). We then sampled values of \( m \) and \( \theta \) from this uncertainty distribution. For each sampled parameter set, we simulated a neutral metacommunity that had the same number and size of local communities as the Barbados data.

We compared the simulated neutral communities with the observed community data by examining patterns in community similarity, occupancy-abundance relation-
shades, and rank-abundance relationships. Specifically, both for the coral data and for each simulated neutral metacommunity, we calculated Bray-Curtis community similarity between all pairs of sites. We performed a square-root transform of the abundance data before the calculation to reduce the influence of occasional large values; the transformed values were then standardized to unity (Pandolfi and Jackson 2006). We then calculated the mean and standard deviation of similarity across sites, and we asked whether the mean and standard deviation of observed pairwise community similarity patterns differed significantly from those of the simulated neutral metacommunities. In addition, we determined the mean local abundance and percentage of sites occupied by all species in the real data and neutral model simulations. We then used the neutral model simulations to generate a 95% confidence envelope around the occupancy-abundance relationship predicted by the neutral model, and we compared it with the relationship shown by the real data. Finally, we constructed rank abundance relationships. For both the coral data and the neutral model simulations, we pooled the species abundances across all local communities in a single time period. Then we graphed both the rank abundance of the Barbados data and the 95% confidence envelope around the rank abundance distributions of the simulated neutral communities.

To test the alternative, niche-theory-based explanation that demographic differences between species explain differences in species abundance or occupancy, we compared species’ relative abundances in the metacommunity with their colony growth rates, which we compiled from literature sources (table 1). Although these growth rates are measured using recent representatives of the study species, relative colony growth rates are likely to be highly conserved over long time periods. Skeletal growth rates of corals, in particular, show a high level of consistency throughout the Cenozoic (Johnson and Perez 2006). Furthermore, the species’ growth forms (e.g., massive or branching) are unchanged from the Pleistocene (Pandolfi and Jackson 2006), and these constrain the energetic costs and therefore the expected rate of colony growth (Huston 1985a, 1985b).

**Results**

For each of the four time periods analyzed, one of the local maxima in the likelihood function (the one corresponding to high \( m \) and low \( \theta \)) produced species abundance distributions that exhibited substantially better fit than the low-\( m \), high-\( \theta \) maximum, as evidenced by the higher likelihoods of the former (table A1, available online). Moreover, data simulated using these parameters produced community similarity distributions that differed much less from the empirical data than did those distributions produced by the other NTB parameter set (table A2, available online). Therefore, we use the low-\( \theta \), high-\( m \) parameter set of the NTB in all of our comparisons below.

Coral communities from Barbados exhibit community similarity distributions that have a lower mean and higher variance than the NTB can replicate and fall well outside its 95% confidence region (fig. 2). The source of this higher-than-neutral variance can be identified by examining the relative abundance and occupancy of each species across the local communities (fig. 3). These reveal that species observed in Barbados have much lower occupancy than their NTB analogues (i.e., they are consistently less widespread), given their relative abundance in the metacommunity as a whole. Although the rarest species in both the NTB and Barbados communities had comparably low occupancy levels, species with intermediate relative abundance exhibited large discrepancies between observed and expected occurrence.

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**Table 1: Caribbean coral growth rates used to construct figure 5**

<table>
<thead>
<tr>
<th>Species name</th>
<th>Maximum growth rate (mm/year)</th>
<th>Minimum growth rate (mm/year)</th>
<th>Habitat depth (m)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acropora cervicornis</td>
<td>159</td>
<td>30</td>
<td>0–5</td>
<td>Huston 1985b; Boulon et al. 2005</td>
</tr>
<tr>
<td>Acropora palmata</td>
<td>110</td>
<td>25</td>
<td>0–5</td>
<td>Huston 1985b</td>
</tr>
<tr>
<td>Acropora agaricites</td>
<td>17.2</td>
<td>4.8</td>
<td>0–5</td>
<td>Huston 1985b</td>
</tr>
<tr>
<td>Diplopora clivosa</td>
<td>8.8</td>
<td>4</td>
<td>0–5</td>
<td>Huston 1985b</td>
</tr>
<tr>
<td>Diplopora strigosa</td>
<td>10</td>
<td>3.5</td>
<td>0–5</td>
<td>Huston 1985b</td>
</tr>
<tr>
<td>Montastraea annularis</td>
<td>12.2</td>
<td>6</td>
<td>0–5</td>
<td>Huston 1985b</td>
</tr>
<tr>
<td>Montastraea faveolata</td>
<td>9.6</td>
<td>3.6</td>
<td>0–5</td>
<td>Cruz-Pinon et al. 2003</td>
</tr>
<tr>
<td>Montastraea nancyi</td>
<td>12.4</td>
<td>4.4</td>
<td>0–5</td>
<td>Pandolfi et al. 2002</td>
</tr>
<tr>
<td>Montastraea cavernosa</td>
<td>10.9</td>
<td>2</td>
<td>6–25</td>
<td>Huston 1985b</td>
</tr>
<tr>
<td>Porites astreoides</td>
<td>14</td>
<td>2.2</td>
<td>0–5</td>
<td>Huston 1985b</td>
</tr>
<tr>
<td>Porites furcata</td>
<td>22.8</td>
<td>9</td>
<td>0–5</td>
<td>Huston 1985b</td>
</tr>
<tr>
<td>Porites porites</td>
<td>21</td>
<td>6</td>
<td>0–5</td>
<td>Huston 1985b</td>
</tr>
<tr>
<td>Siderastrea siderea</td>
<td>5</td>
<td>1.5</td>
<td>0–5</td>
<td>Huston 1985b</td>
</tr>
</tbody>
</table>
predicted occupancy. In contrast to observed coral communities, occupancy in the NTB increases rapidly with small increases in relative regional abundance. This rapid increase occurs because, even with low levels of migration, neutral dynamics ensure that almost all intermediate-abundance species are present in local communities of reasonable size.

The relative abundance distributions from the observed transects (fig. 4) are dominated by a single species, *Acropora palmata*, which makes up more than 80% of shallow-water coral communities throughout the Pleistocene (Pandolfi 2002; Pandolfi and Jackson 2006). The neutral theory has some success at re-creating this level of dominance, but it cannot simultaneously replicate the observed number of rare species. On average, local communities in Barbados contained twice as many species as their neutral analogues (fig. 4), a difference that is statistically significant ($P < 10^{-4}$ for all four time-periods; Kolmogorov-Smirnoff test). The neutral theory is unable to simultaneously capture the distribution of rare and abundant species, because observed species’ abundances display more heterogeneity than the neutral theory can produce.

Comparing species’ relative abundances with their colony growth rates reveals abundance patterns that are consistent with known demographic differences among coral species found in the Barbados communities. In particular, the species with higher growth rates tend to have higher relative abundances ($r^2 = 0.42; P = .001$) and display higher occupancy ($r^2 = 0.31; P = .03$; fig. 5).

**Discussion**

Our results show that the neutral model fails to capture important aspects of community structure in Caribbean coral assemblages. In particular, it systematically underpredicts the among-species variation in relative abundance within communities, the high variation in community similarity among pairs of sites, and the large occupancy dif-
Fossil Coral Communities Are Nonneutral

Figure 3: Relative abundance of individual species in pooled local communities from the Pleistocene (X-axis, on a log scale), graphed against their occupancy (Y-axis). Open circles indicate observed Barbados species. Lines show Hubbell’s unified neutral theory of biodiversity and biogeography analogues to observed communities (95% confidence intervals from 10^4 simulated neutral metacommunities). Each panel shows a different time period: (a) 104 ka, (b) 125 ka, (c) 195 ka, and (d) 220 ka.

ferences between highly abundant community dominants and the rest of the community. Moreover, the existence of a positive relationship between demographic or competitive ability and species’ relative abundances appears at odds with the core neutrality assumption in particular. However, five ancillary assumptions made by this neutral model could potentially influence neutral predictions about patterns of variation in community structure. These must be considered before we can unambiguously attribute the marked discrepancies between Barbados coral communities and neutral model predictions to violation of the central neutral assumption of species equivalence.

First, the NTB model used here assumes that all local communities are sufficiently close together, relative to dispersal distance, that immigrants to those communities come from a common metacommunity. However, in nature, dispersal among habitat patches in a metacommunity typically exhibits distance decay, with nearby patches being more likely to exchange propagules than distant patches. If the scale of dispersal is the same or smaller than the distance between local communities, then a different neutral model may be required to isolate the assumption of demographic equivalence. This is particularly true given that distance decay in community similarity provides a plausible mechanism for high variance in coral community similarity distributions (Dornelas et al. 2006; Economo and Keitt 2008). Specifically, dispersal limitation results in proximate communities being more similar, whereas distant communities exhibit a dissimilarity that reflects their locally biased immigrants. For tropical reef corals, there is evidence for dispersal limitation in corals at the scale of tens of kilometers (commensurate with the scale of our analysis; Ayre and Hughes 2000; Underwood et al. 2009), so this possibility is worth investigating. Although the taxonomic composition of sampled communities across the Barbados coastline displays considerable variability, it does not exhibit distance decay for any of the four time periods (fig. A1, available online), which indicates that local com-
Figure 4: Rank abundance distributions of pooled observed communities from the Pleistocene (solid line), graphed alongside their neutral analogues (dashed lines indicate 95% confidence intervals of 10^4 replicates). Each panel shows a different time period: (a) 104 ka, (b) 125 ka, (c) 195 ka, and (d) 220 ka. The termination point of the distributions indicates the species richness of the communities. Neutral communities exhibit significantly fewer species in all time periods.

A second ancillary assumption of most neutral models is the absence of environmental stochasticity (Ruokolainen et al. 2009). In particular, episodic disturbances could reset the community dynamics of different local communities at different points in time and thereby influence community similarity (Chisholm and Burgman 2004). Dornelas et al. (2006) hypothesized that this process could theoretically increase the variance of the community similarity distributions. Subsequent analyses of neutral communities in the presence of environmental fluctuations, however, found no evidence for such an effect (Ruokolainen et al. 2009). However, Ruokolainen et al. (2009) simulated disturbances as relatively small fluctuations around equilibrium. Therefore, to explore whether large, episodic events (e.g., cyclones, bleaching events, and disease outbreaks) might produce a different outcome, we explicitly included large stochastic disturbances of varying frequencies into the NTB model and reassessed its fit to the Barbados data (appendix). Large disturbances could affect similarity distributions, but only if they were very common. A high frequency of disturbances increased the rate of immigration, which made all of the local communities very similar to the metacommunity and thus to one another. Frequent disturbances therefore created community similarity distributions with higher means and lower variances and thus increased, rather than decreased, the deviation between neutral communities and the coral data.

Third, fossil data sets represent time-averaged samples...
Fossil Coral Communities Are Nonneutral

Figure 5: Growth rates (linear extension) of coral species from the Pleistocene shallow-water communities in Barbados, obtained from studies of living representatives, graphed against (a) their relative abundance and (b) the proportion of local communities in which each is present. The full range of observed growth rates is shown. Dashed lines indicate best-fit linear model to the midpoint of the log-transformed growth range.

of historical communities (Johnson 1960). A recent study has shown that the degree of time averaging in paleontological communities affects community structure and the apparent rate of community dynamics (Tomasovych and Kidwell 2010). However, time averaging cannot be responsible for the discrepancies that we observe between the Barbados coral communities and the neutral model predictions. Time averaging alters the relative abundance of species in local communities, reduces species dominance, and increases the abundance and occupancy of rare species (Tomasovych and Kidwell 2010). Allowing for such changes to the Pleistocene communities observed in Barbados would only exacerbate the poor fit of the NTB to the occupancy-abundance data (fig. 3). Consistent with this, increasing the degree of time averaging in the NTB simulations creates community similarity distributions with even greater mean similarity and lower variance, which amplifies the discrepancies with the observed fossil communities (appendix; fig. A3, available online).

Fourth, our neutral model assumes point-mutation speciation (Hubbell 2001), whereas alternative speciation processes are also possible (Hubbell 2003; Ricklefs 2003; Rosindell et al. 2010). However, an alternative speciation assumption, with realistic speciation rates, would affect metacommunity dynamics very rarely. In particular, coral speciation was a very infrequent event in the Caribbean during the Pleistocene, and the species pool represented in the Caribbean coral community data set has remained relatively unchanged over the past hundreds of millennia (Pandolfi and Jackson 2006). Thus, it seems implausible that patterns of turnover in species composition at the scale of one island in the Caribbean could be explained by differences in the mechanism of speciation.

Finally, our model assumes that all species have identical birth and death rates, but demographic trade-offs have been argued to be consistent with neutral theory, provided that the trade-offs preserve equal fitness among all species (Hubbell 2001). The biological plausibility of such fitness-equalizing trade-offs has been challenged (Purves and Turnbull 2010). Moreover, the most general neutral model proposed to date, which incorporates such trade-offs, predicts no relationship between species abundance and demographic rates, as in the classical neutral model (Allouche and Kadmon 2009). This prediction is contradicted by the coral data (fig. 5), for which growth rates appear to be important predictors of occupancy and abundance.

In addition, Volkov et al. (2007) proposed an alternative formulation of the neutral model that they argued could reproduce patterns of community similarity in Indo-Pacific coral assemblages. Therefore, we simulated community similarity distributions, as in our baseline similarity analyses, using this model (appendix). Similarity distributions obtained using this model were actually further from the data than were the similarity distributions produced by the neutral model used in our original analyses. In particular, mean community similarity was >0.9, much higher than that exhibited by the data, and the standard deviation of similarity was approximately an order of magnitude smaller than that exhibited by the data. These results further support the conclusion that the discrepancies between our data and the neutral model are likely to be robust to the ancillary assumptions of the neutral model that we used.
The dependence of species abundance and occupancy on colony growth rates suggests that the poor fit of the neutral model is due to violation of the core assumption of species equivalence. This relationship is driven primarily by the higher growth rates and relative abundance of the two Acropora species, which together comprise 95% of the shallow-water Pleistocene communities that we studied in Barbados and whose growth rates are more than five times greater than those of the other species. Growth rates are an important determinant of coral competitive ability (Connell 1978; Stimson 1985), with faster-growing species maintaining competitive superiority by reducing the light and water circulation available to other species, by quickly colonizing available space, by overgrowing and overtopping their slower-growing competitors, and by conferring superior postdisturbance regeneration abilities (Lang and Chornesky 1990). Alongside their increased susceptibility to disturbances, the increased growth rates of Acropora species were traditionally used to explain Caribbean coral community structure. Dornelas et al. (2006) applied this understanding to conjecture that the discrepancies between observed and neutral community similarity distributions from Indo-Pacific reefs resulted from the tendency for local communities to be affected by disturbances independently. To investigate whether such a mechanism could resolve the observed model deviation, we modified the neutral model by adding a competitive hierarchy that is interrupted by random, independent catastrophes, during which competitive dominants experience disproportionately high mortality rates (appendix). These additional community processes allow community similarity distributions whose means and variances can re-create the observed Barbados communities (fig. A4, available online). Although not a comprehensive analysis of the effects of trade-offs between competitive ability and susceptibility to disturbance, this model nevertheless demonstrates that such trade-offs have the potential to decrease mean similarity and increase the variance of similarity on the order required to resemble the empirical data.

A niche-based understanding of community dynamics is the foundation of management in the Caribbean, where coral reef ecosystems have sustained centuries of severe degradation (Jackson 1997; Pandolfi 2002; Pandolfi et al. 2003; Boullon et al. 2005). If coral biodiversity were the result of neutral dynamics, a new management approach would be required (Clark and McLachlan 2003; Dornelas et al. 2006; Daleo et al. 2009). For example, relative species abundance patterns in the Caribbean were fundamentally altered after decades of overfishing followed by the mass mortality of one of the last remaining herbivores, the sea urchin Diadema antillarum, during 1982–1983 (Lessios et al. 1984), and the disease-driven decrease in population of the two dominant Acropora species by >97% across the Caribbean, which drove a collapse in live coral cover (Boullon et al. 2005). At present, recovery of both species is impaired by the high prevalence of diseases to which they remain particularly susceptible (Boullon et al. 2005; Weil et al. 2006). If species differences are critical to the structure of Caribbean coral communities, management efforts should prioritize strategies that can facilitate recovery of these two particular Acropora species, because other species likely lack their ability to rapidly build the complex three-dimensional structures that have been so characteristic of Caribbean reefs through time (Pandolfi and Jackson 2006). Conversely, if species are demographically equivalent and neutral dynamics determine coral community structure, then disease-resistant species can be relied upon to replace Acropora palmata and Acropora cervicornis. Our findings support ecological theory that identifies demographic species attributes as the key drivers of species richness and community structure (Jackson 1991; Tilman 2004; Clark et al. 2007). Such findings suggest that coral reef conservation should not treat species as functionally substitutable, as neutral theory does.

Neutral descriptions of community structure have reinvigorated the study of biodiversity, despite a number of drastic ecological simplifications. They have encouraged an explicit treatment of demographic stochasticity and remain informative as null models (McGill et al. 2005, 2006; Alonso et al. 2006; Dornelas et al. 2006). From a conservation perspective, however, a practical theory of community assembly must approximate real community dynamics well enough to anticipate changes and to evaluate the potential outcomes of alternative management interventions (Clark 2009; Purves and Turnbull 2010). Fossil coral communities in Barbados depart from neutral theory predictions in the same manner as extant Indo-Pacific assemblages (Dornelas et al. 2006) and exhibit higher similarity variance than the neutral theory can explain. These consistent results call into question the utility of a neutral perspective on coral community assembly. However, we show that if we consider demographic differences that ecologists have long believed are influential, this discrepancy may be resolved. These conclusions reinforce the successional-niche explanation of coral community structure, with its emphasis on the importance of interspecific differences in key demographic and competitive attributes. The development of ecological theory that can parsimoniously incorporate such species differences is therefore likely to be more informative than further elaboration of neutral theory (Clark 2009) and to provide a firmer foundation on which to base management of coral reef biodiversity.
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