Hybrid niche-neutral models outperform an otherwise equivalent neutral model for fitting coral reef data

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HIGHLIGHTS

\begin{itemize}
  \item We evaluate the robustness of the neutral model for coral reefs to niche differentiation.
  \item We compare the goodness of fit of hybrid niche-neutral models and neutral model.
  \item Neutral model for coral reefs remains robust to strong niche structure.
  \item Hybrid niche-neutral models outperform neutral model in coral reefs.
  \item Individual-based abundance distributions are more powerful than species-based ones.
\end{itemize}

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ABSTRACT

Niche theory and neutral theory are two major developments aiming at explaining patterns of biodiversity observed in nature. Both theories have been found relevant either separately or simultaneously in some real communities, and it has been theoretically demonstrated that they can produce similar species abundance distributions. However, it remains controversial whether the two theories can produce similar patterns via different mechanisms, or can interact to jointly produce the observed diversity patterns, or whether the patterns generated by the neutral model are robust to niche structure. Here we show that, although the neutral model proposed for spatially discrete communities remains robust to strong niche structure for high-diversity communities, the inclusion of more realistic niche differentiation modes greatly improves the goodness of fit to Indo-Pacific coral reefs. Actually, the multiple discrete communities’ neutral model, due to its underestimation of the number or abundance of common species, fails to capture the combination of many rare species and a few highly abundant species that characterize the Indo-Pacific coral reef communities. By incorporating niche structure into the multiple discrete communities’ model, the hybrid niche-neutral models can successfully reproduce both the species-based and individual-based abundance distribution patterns observed in the coral reefs. We proposed that both niche theory and neutral theory may be involved in explaining the structure of such communities. Our results also suggest a negative relationship between per capita birth to death ratio and immigration among different guilds of coral species, which clearly deserves further investigation.

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1. Introduction

Up until now, the niche theory and neutral theory are two major developments aiming at explaining species coexistence mechanisms on different temporal and spatial scales (Adler et al., 2007; Gravel et al., 2006). According to the classical niche theory, niche differentiation is necessary for species to co-occur in a certain area (Hardin, 1960; Hutchinson, 1957). In the context of niche differentiation, the whole suitable habitat can be divided into several types (i.e. niches) according to some abiotic factors, and each species performs the best in its matching niche. The classical neutral theory of biodiversity otherwise starts from the extremely simplified ecological equivalence assumption to see what predictions one can get (Bell, 2001; Hubbell, 2001; Rosindell et al., 2011). The neutral theory assumes that the per capita birth, death, immigration and speciation rates are equivalent among individuals of different species in a community. Thus the probability of either success or failure of an individual does not depend on its species identity. Based on this simple and
counterintuitive assumption of ecological equivalence, the best
know neutral model predicts zero-sum multinomial species
abundance distributions (SADs) resembling those in some real
communities, especially in tropical rainforests (He, 2005; Hubbell,
2001; Volkov et al., 2003; Volkov et al., 2005). The structure of a
tropical rainforest can be approximated in which a local com-
munity maintains certain diversity via a balance between local
extinction and successive immigration from the larger and rela-
tively static outer metacommunity. Spatially discrete commun-
ities are typical of another type of community structure (e.g.
Indo-Pacific coral reefs (Connolly et al., 2005; Dornelas and
Connolly, 2008; Dornelas et al., 2006)). In those, different local
communities exchange individuals between each other and the
interaction of local communities produces a metacommunity
(Volkov et al., 2007). Although the classical neutral model has
been rejected for the study of discrete Indo-Pacific coral reefs
(Dornelas et al., 2006), a multiple discrete communities’ neutral
model has been recently developed to account for such a com-
munity structure (Volkov et al., 2007).

Despite the apparent disparity in the starting points between
niche and neutral theories, however, numerical studies have
found that both theories can lead to similar predictions of SADs
(Adler et al., 2007; Chave et al., 2002; Zillio and Condit, 2007).
Volkov et al. (2010) gives rise to exactly the same form of SAD as the pure
niche and neutral theories, however numerical studies have
demonstrated the co-existence of niche differentiation and neu-
tral drift that may potentially contribute to
SADs in spatially discrete communities. We construct hybrid
differentiation and neutral drift that may potentially contribute to
produce the observed diversity patterns, or the patterns gener-
ated by the neutral model are robust to niche structure, are still
necessarily verify the neutral theory in real communities (Harpole
McPeek, 2006). Therefore, whether the two theories produce
similar patterns via different mechanisms, or interact to jointly
produce the observed diversity patterns, or the patterns gener-
ated by the neutral model are robust to niche structure, are still
far from being understood.

Recently, Chisholm and Pacala (2010) demonstrated that the
classical neutral model is robust to strong niche structures, in
which species of different non-overlapping niche classes share the
same per capita demographic rates in large and high-diversity
rainforest-type communities. However, whether the multiple
different communities’ neutral model is robust to niche structures
or whether a hybrid niche-neutral model performs better than the
equivalent neutral model in spatially discrete communities
remains unknown.

In this paper, we investigate the relative importance of niche
differentiation and neutral drift that may potentially contribute to
SADs in spatially discrete communities. We construct hybrid
niche-neutral models for spatially discrete local communities
based on the multiple discrete communities’ neutral model
(Volkov et al., 2007). We find that a hybrid niche-neutral model
with a strong niche structure as adopted by Chisholm and Pacala
(2010) gives rise to exactly the same form of SAD as the pure
neutral model for high-diversity communities. However, hybrid
niche-neutral models of more complex but more realistic niche
differentiation modes outperform the equivalent neutral model in
discrete Indo-Pacific coral reefs.

2. Models

To construct the neutral model for multiple discrete commu-
nities, Volkov et al. (2007) neglect the inter-species interactions
after the community has reached a steady state and assume that
all species are functionally equivalent. They also assume that
the probability of birth and death in a species with \( n \) individuals is
\( b_n = b(n + \gamma) \) and \( d_n = dn \) respectively, where \( b \) and \( d \) denote the
per-capita density-independent birth and death rates and \( \gamma \) is a
parameter for immigration, which is assumed to be species-

\[
\begin{align*}
    p(n) &= \frac{(1-x)^y}{\Gamma(n+y)} \frac{\Gamma(n+1)}{\Gamma(n+y+1)}, \\
    \text{where } x &= \frac{b}{d} \text{ the lifetime reproductive success},
\end{align*}
\]

\[
\begin{align*}
    \phi_{\text{obs}} &= \frac{\Gamma(\gamma)}{\Gamma(n+\gamma)} \\
    \text{where } \theta &= \frac{S_{\text{obs}}}{(1-x)^{\gamma-1} \Gamma(\gamma)} \\
    \text{and } S_{\text{obs}} &= \text{the number of observed species.}
\end{align*}
\]

Now assume that a semi-isolated local community consists of
K nonoverlapping niches, within which a number of species follow
their own neutral rules independent of the other K-1 niches. This is similar to the concept of “emergent group” named
by Herault (2007), which is defined as a set of species having a
similar functional niche owing to convergent ecological strategies.
This may happen if the space is niche differentiated and the
recruitment limitation is not strong. In that case, vacant sites can
almost always be recruited by one of the species having the
matching niche of that site.

By applying the multiple discrete communities’ neutral model to
a single niche of the community, we obtain the expected
number of species with abundance \( n \) in niche \( i \) as:

\[
\begin{align*}
    \phi_{\text{obs}} &= \frac{\Gamma(\gamma)}{\Gamma(n+\gamma)} \\
    \text{where } \theta_{i} &= \frac{S_{\text{obs}}}{\Gamma(1-x)^{\gamma_i-1} \Gamma(\gamma_i)} \\
    \text{is the biodiversity parameter for niche } i \text{, } x_i \text{ is the ratio of per capita birth to death rates}
\]

\[
\begin{align*}
    J_i &= \sum_{n=1}^{\infty} n <\phi_{n,i}> = \sum_{n=1}^{\infty} \frac{n^0 \Gamma(n+\gamma_i)}{\Gamma(1-x_i)^{\gamma_i-1}} \sum_{n=0}^{\infty} n(p n) = \theta_{i} \frac{\Gamma(\gamma_i)}{(1-x_i)^{\gamma_i-1}} \\
    \text{The total expected number of species with abundance } n \text{ in the community consisting of } K \text{ niches is:}
\end{align*}
\]

\[
\begin{align*}
    <\phi_{n,K}> &= \sum_{i=1}^{K} <\phi_{n,i}> \\
    \text{We consider two scenarios for niche differentiation. The first}
\end{align*}
\]
survival, reproduction, and even migration (Hoogenboom and Connolly, 2009). In doing so, we expect that species from different niches possess different positions on the manifold of trade-offs between these two vital demographic parameters of $x$ and $\gamma$.

3. Results

3.1. Hybrid niche-neutral model with same $x$ and $\gamma$ for different niches

For the first scenario that $x$ and $\gamma$ remain the same across different niches, i.e. $x_i = x$ and $\gamma_i = \gamma$, from Eq. (4) we can immediately obtain $\theta_i$ as a function of $J_i$, $x$ and $\gamma$:

$$\theta_i = J_i \left( \frac{1-x^{1+\gamma}}{x^{1+\gamma}} \right)$$

By substituting Eqs. (3) and (6) into Eq. (5), we can obtain:

$$<\varphi_{n}\cdot K> = \sum_{i=1}^{n} \left( \frac{1-x^{1+\gamma}}{x^{1+\gamma}} \right) \cdot \frac{1}{M} \cdot \Gamma(n+\gamma) = \frac{1}{M} \cdot \Gamma(n+\gamma)$$

Eq. (7) is the same as the multiple discrete communities' neutral model (2). Hence, with equal demographic parameters across different niches the expected SADs by the hybrid niche-neutral model are equivalent to those of the multiple discrete communities' neutral model. Note that this conclusion is valid even if the sizes of different niches are different, given that the communities' neutral model. Note that this conclusion is valid even if the sizes of different niches are different, given that the communities' neutral model are equivalent to those of the multiple discrete communities' neutral model. Note that this conclusion is valid even if the sizes of different niches are different, given that the communities' neutral model are equivalent to those of the multiple discrete communities' neutral model. Note that this conclusion is valid even if the sizes of different niches are different, given that the communities' neutral model are equivalent to those of the multiple discrete communities' neutral model. Note that this conclusion is valid even if the sizes of different niches are different, given that the communities' neutral model are equivalent to those of the multiple discrete communities' neutral model. Note that this conclusion is valid even if the sizes of different niches are different, given that the communities' neutral model are equivalent to those of the multiple discrete communities' neutral model. Note that this conclusion is valid even if the sizes of different niches are different, given that the communities' neutral model are equivalent to those of the multiple discrete communities' neutral model. The $n_i$ is the abundance of species $i$, the goodness of fit to SAD and IAD are identical and the difference between the SAD and IAD will be less meaningful (Etienne, 2005).

Chi-Square goodness-of-fit test and the values of $R^2$ are used to compare the goodness of fit of different models. Moreover, because nested models with more parameters often fit the observed data better than those with less freedom, we rank the models using Akaike's information criterion corrected for small sample sizes ($AIC_c$) (Burnham and Anderson, 2002) by calculating the difference between the model's $AIC$ and that of the top-ranked model ($AAIC_c$), and the relative model weights ($wAIC_c$).

3.2. Fitting hybrid niche-neutral model with different $x$ and $\gamma$ for different niches

When $x$ and $\gamma$ vary across different niches, Eq. (5) cannot be simplified analytically. We fit the multiple discrete communities' neutral model (M1) and the hybrid niche-neutral model M1 consisting of different niches ($i=2, 4, 8, and 16$) using the least squares method to the SADs of Indo-Pacific coral reefs in three habitats, namely slope, crest and flat, within each there are 60 sampled local communities (Connolly et al., 2005; Dornelas and Connolly, 2008). It should be noted that the hybrid niche-neutral model with multiple niches is constrained within each habitat rather than across different habitats. In order to further compare the goodness of fit of different models, we also fit the models of different number of niches to individual-abundance distributions (IADs), which differ from the SADs only in that the vertical values of bars are the number of individuals rather than the number of species in each abundance category. Since the binning method may also affect the goodness of fit of different models (Gray et al., 2006), we fit the models to both binned SADs and IADs according to log 2 abundance categories (BSADs and BIADs, respectively), and to unbinned SADs and IADs (USADs and UIADs, respectively) with abundance categories of 1, 2, 3, ..., and so on. It should be noted that once the fitting method is based on maximizing the probability of observing abundance distribution $D=(n_1, n_2, ..., n_3)$ where $n_i$ is the abundance of species $i$, the goodness of fit to SAD and IAD are identical and the difference between the SAD and IAD will be less meaningful (Etienne, 2005).

Chi-Square goodness-of-fit test and the values of $R^2$ are used to compare the goodness of fit of different models. Moreover, because nested models with more parameters often fit the observed data better than those with less freedom, we rank the models using Akaike's information criterion corrected for small sample sizes ($AIC_c$) (Burnham and Anderson, 2002) by calculating the difference between the model's $AIC$ and that of the top-ranked model ($AAIC_c$), and the relative model weights ($wAIC_c$).

3.2.1. Comparing the goodness of fit of different models to BSADs and BIADs in Indo-Pacific coral reefs

For BSADs and BIADs of Indo-Pacific coral reefs, only up to two niches can be considered in the fitting process because of the limit on the freedom determined by the limited number of bins of the dataset. The average BSAD is a log-series-like in the three habitats. Hybrid niche-neutral model significantly improve the goodness of fit to the observed BSADs (Fig. 1). Although the values of $R^2$ of the two-niche hybrid model are only slightly higher than that of M1, the Chi-Square goodness-of-fit test generally rejects the M1 but favours the two-niche hybrid model (Table S1).

Fig. 1 suggests that the poor fit of M1 to coral reefs is mainly due to its failure in being fit to common species. Because a small deviation of the number of species in the very abundant categories of BSADs can result in very large differences in the number of individuals between those predicted and observed, the neutral model significantly underestimated the number of individuals in especially those categories for common species (Fig. 2). The hybrid

![Image](https://example.com/image.jpg)  
Fig. 1. The binned species abundance distribution of coral-reef communities. We plot the fits of M1 and M2 to the coral-reef BSADs in slope (a), crest (b), and flat (c). The bars are the observed numbers of species binned into log 2 abundance categories. The first histogram bar represents $<\varphi(1)>$, the second $<\varphi(2)>+<\varphi(3)>$, the third $<\varphi(4)>+<\varphi(5)>+<\varphi(6)>+<\varphi(7)>$, and so on. Subplots a–c show the average species abundance of 60 local communities in slope, crest and flat, respectively. The y-axis is logarithmic. Parameter values predicted by different models are shown in Table S5.
niche-neutral model of two niches fit much better to the BIADs of coral reefs than M1 (Fig. 2). Both the Chi-Square goodness-of-fit test and the values of $R^2$ support the hybrid niche-neutral models rather than the multiple discrete communities’ neutral model in the coral-reefs in the slope and crest, while both models were rejected by Chi-Square goodness-of-fit test in the flat habitat (Table S2). Even after accounting for the extra parameters of the hybrid model, M2 still outperforms the neutral model in these communities because the values of AICc of M2 are generally lower than that of the neutral model (Tables S1 and S2).

3.2.2. Comparing the goodness of fit of different models to USADs and UIADs in Indo-Pacific coral reefs

Hybrid niche-neutral models significantly improve the goodness of fit to both the observed USADs (Fig. 3 and Table S3) and UIADs (Fig. 4 and Table S4). Again, there is no significant difference between $R^2$’s when fitting different models to USADs, but both $R^2$ and Chi-Square goodness-of-fit test favour the hybrid niche-neutral models rather than the neutral model M1 (Table S3). According to AICc, the hybrid models with more parameters are still better than the neutral model. Unfortunately, all the models are rejected by Chi-square goodness-of-fit test when fitting to the observed UIADs, but the values of $R^2$ suggest that the hybrid models outperform the neutral model (Table S4). In this case, the values of AICc of hybrid models, except M16, are smaller than those of the neutral model. Overall, M2 and M4 perform better than other hybrid niche-neutral models of more niches according to AICc.

According to the fitting results of hybrid models of more than two niches, there is a negative relationship between the predicted values of $x$ and $g$ for different niches (Fig. 5), which confirm our hypothesis that species from different niches possess different positions on the manifold of trade-offs between these two vital demographic parameters of $x$ and $g$. However, the general pattern of the trade-off manifold varies among different habitats, suggesting possible effects of habitat heterogeneity on the relationship between $x$ and $g$. The size of the niche ($J$) generally increases with $x$ (Fig. 5), but there is no consistent relationship between the niche size and $g$ (results not shown).

4. Discussion

Currently, one research focus in community ecology is to integrate the niche theory and neutral theory to explain the observed biodiversity patterns (Mutshinda and O’Hara, 2011;
In this respect, it is important to distinguish whether the two theories produce similar patterns via different mechanisms, or interact to jointly produce observed diversity patterns, or whether the patterns generated by the neutral model are robust to niche structure. Herein we show that although the multiple discrete communities’ neutral model proposed by Volkov et al. (2007) for spatially discrete communities remains robust to a strong niche structure, the introduction of more realistic niche differentiation modes can greatly improve the goodness of fit to Indo-Pacific coral reefs. Actually, the multiple discrete communities’ neutral model fails to predict the number of the common species. By incorporating niche differentiation into the neutral model, the hybrid niche-neutral models can generally reproduce both the SADs and IADs observed in Indo-Pacific coral reefs. We suggest that niche mechanisms may play important roles in regulating the communities we have studied.

The SADs predicted by the multiple discrete communities’ neutral model remain exactly the same when a strong niche structure was introduced. In this respect, our conclusions are similar to but also stronger than those reached by Chisholm and Pacala (2010) for spatially continuous communities like BCI rainforests, in which they showed that the niche and neutral model predicted similar SADs in the case of a large community size and very high diversity. Note that there is a common limit in Chisholm and Pacala’s model that the hybrid niche-neutral models can generally reproduce both the SADs and IADs observed in Indo-Pacific coral reefs. We suggest that niche mechanisms may play important roles in regulating the communities we have studied.

An interesting result in our paper is that hybrid niche-neutral models with more realistic niche differentiation modes can greatly improve the goodness of fit to Indo-Pacific coral reefs. Actually, the multiple discrete communities’ neutral model fails to capture the combination of many rare species and a few highly abundant species that characterize the Indo-Pacific coral reef communities; it especially underestimates the number of common species. The shape of SAD predicted by the neutral model varies according to the vital parameters (Fig. S1). Hence, the hybrid niche-neutral model can capture both the abundance of rare and common species by introducing two or more niches with different parameter values. We showed that niche differentiation and neutral drift can interact to regulate species distributions in coral-reef communities. Our results also suggest a possible trade-off between species lifetime reproductive success and immigration among different niche classes. Both theoretical and field studies have demonstrated the niche differentiation of corals along gradients of light and turbidity (Ebersole, 1985; Anthony and Connolly, 2004; Hoogenboom and Connolly, 2009), providing theoretical and experimental supports for our hybrid niche-neutral models. For instance, Hoogenboom and Connolly (2009) have defined the fundamental niche dimensions of corals and shown that there existed a specific niche differentiation along gradients of light and flow for different coral species according to theoretical analysis and field observations. Though their study was based on species distribution ranges and they did not take into account the explicit effects of the niche differentiation on species abundance, they clearly demonstrated the existence of niche differentiation in reef corals. However, direct studies on recruitment and migration rates of corals are difficult and scarce. Further elaborately designed experiments are helpful for testing the existence of trade-offs between lifetime reproductive success and migration and for better understanding the community assembly of corals.

An interesting result in our paper is that hybrid niche-neutral models greatly improve the goodness of fit to common species. O’Hara (2005) showed that the most common species can give rise to a very large likelihood ratio and that, by removing the most common species, the likelihood ratio drops to a very small value. We argue that we can obtain a reasonable goodness of fit by adding the number of niches rather than by removing the common species. The fits to SADs give rise to a high per capita birth to death ratio for common species which can greatly increase the number of common species that is quite consistent with the actual communities, because common species usually have a high lifetime reproductive success compared with rare species (Fischer and Matthies, 1998).
We showed that individual-based IADs provide a more powerful test of model fit than the species-based SADs when the least square methods is used for model fitting. This is somewhat consistent with the conclusion arrived at by Connolly et al. (2009), who used both individual-based and species-based bootstrap simulations to test different models against the species abundance distributions of Indo-Pacific corals and reef fishes. They found that although the goodness of fit is remarkably consistent between these two methods, the goodness-of-fit estimates are approximately twice as precise and lack of model

Fig. 5. The decline with x of γ (left column), and increase with x of J (right column), for parameter values predicted by the hybrid niche-neutral models (M4, M8, M16) in fitting to USADs in coral reefs. Different points illustrate the fitted parameters for the different niches. Different curves are used to fit the data of x and γ for different habitats: $y = a + b/x$ (slope), $y = a \exp(bx)$ (crest), $y = a + bx$ (flat). Exponential growth curve of the form $y = a \exp(bx)$ was fitted to the data of x and J. Different colours are for different models: black for M4, red for M8, and green for M16.
fit is detected more frequently when individual-based rather than species-based sampling is employed. Hence, we propose that both SADs and IADs should be involved in inferring species distribution patterns and the underlying structuring rules of ecological communities, except likelihood based methods are available in comparison of goodness of fit of different models (Etienne, 2005).

In conclusion, the hybrid niche-neutral models outperform the equivalent multiple discrete communities’ neutral model in fitting to Indo-Pacific coral reef data. This suggests that niche differentiation and neutral drift may interact to regulate the structure of these communities. It also gives support to the future efforts to merge the niche theory and neutral theory in developing a unified theory of biodiversity.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtbi.2012.10.019.

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