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

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HIGHLIGHTS

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

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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.

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

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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 community maintains certain diversity via a balance between local extinction and successive immigration from the larger and relatively static outer metacommunity. Spatially discrete communities 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 community 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). Some field studies also concluded that neutral patterns do not necessarily verify the neutral theory in real communities (Harpole and Tilman, 2006; Wootton, 2005). Many other studies have demonstrated the co-existence of niche differentiation and neutral mechanisms which are irrelevant to species labels in real communities (Chu et al., 2007; Dumbrell et al., 2009; Leibold and 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 generated 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 discrete 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 communities, 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 are $b_n = b(n+\gamma)$ and $d_n = dn$ respectively, where b and d denote the per-capita density-independent birth and death rates and γ is a parameter for immigration, which is assumed to be species-independent corresponding to immigration from a time-averaged metacommunity in a species-symmetric manner. To do so, they essentially ignored any immigration between local communities within the metacommunity and the rates of immigration considered were small. Then they solved the master equation that regulates the dynamics of a species and obtained the probability that a species has n individuals, which follows a negative binomial distribution:

$$p(n) = \frac{(1-x)^{\gamma}}{\Gamma(\gamma)} \frac{x^n}{n!} \Gamma(n+\gamma), \tag{1}$$

where x is the ratio of the per capita birth to death rate (b/d, the lifetime reproductive success), and $\Gamma(z) = \int_0^{\infty} t^{z-1} e^{-t} dt$, which is equal to $(z-1)!$ for integer z. Further, they obtained the mean number of species with abundance n:

$$<\varphi_n> = \theta \frac{x^n}{n!} \Gamma(n+\gamma), \tag{2}$$

where $\theta = S_{<obs>} / ((1-x)^{-\gamma} - 1)\Gamma(\gamma)$ is the fundamental biodiversity parameter, and $S_{<obs>}$ is the number of observed species. The above multiple discrete communities' neutral model has an implicit assumption of high diversity limit (Volkov et al., 2007), because the model neglects inter-species interactions and only works as a proper approximation for high-diversity communities (Alonso and McKane, 2004; Chave, 2004; Zhang et al., 2012).

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:

$$<\varphi_{n,i}> = \theta_i \frac{x_i^n}{n!} \Gamma(n+\gamma_i), \tag{3}$$

where $\theta_i = S_{<obs>,i} / \left((1-x_i)^{-\gamma_i} - 1\right)\Gamma(\gamma_i)$ is the biodiversity parameter for niche i, x_i is the ratio of per capita birth to death rates of each species in niche i, and γ_i is a parameter for immigration of niche i. According to Eq. (3), we can obtain the expression of J_i:

$$J_i = \sum_{n=1}^{\infty} n <\varphi_{n,i}> = \sum_{n=1}^{\infty} n\theta_i \frac{x_i^n}{n!} \Gamma(n+\gamma_i) = \theta_i \frac{\Gamma(\gamma_i)}{(1-x_i)^{\gamma_i}} \sum_{n=0}^{\infty} np(n) = \theta_i \frac{x_i \Gamma(1+\gamma_i)}{(1-x_i)^{1+\gamma_i}} \tag{4}$$

The total expected number of species with abundance n in the community consisting of K niches is:

$$<\varphi_n; K> = \sum_{i=1}^{K} <\varphi_{n,i}> \tag{5}$$

We consider two scenarios for niche differentiation. The first one is analogous to the one adopted by Chisholm and Pacala (2010), in which individuals of species from different niche classes share equivalent lifetime reproductive success, i.e. the same ratio of per capita birth to death rates (x), and the same immigration parameter (γ). In this case, the only possible difference between different niches is niche size. The second one is that the per capita birth to death rates (x) and immigration parameter (γ) vary among species of different niches. For instance, different corals dominate along the environmental gradients of light intensity or water flow and exhibit different growth rates,