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A sampling formula for ecological communities with multiple dispersal syndromes

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HIGHLIGHTS

- We introduce a sampling formula that takes into account dispersal syndromes.
- Using simulated data we validate our sampling formula.
- We apply our sampling formula on tropical tree data from BCI, Panama.
- We show that including dispersal syndrome information improves the fit to the data.

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ABSTRACT

Over the past decade, the neutral theory of biodiversity has stirred up community assembly theory considerably by suggesting that stochasticity in the form of ecological drift is an important factor determining community composition and community turnover. The neutral theory assumes that all species within a community are functionally equivalent (the neutrality assumption), and therefore applies best to communities of trophically similar species. Evidently, trophically similar species may still differ in dispersal ability, and therefore may not be completely functionally equivalent. Here we present a new sampling formula that takes into account the partitioning of a community into two guilds that differ in immigration rate. We show that, using this sampling formula, we can accurately detect a subdivision into guilds from species abundance distributions, given ecological data about dispersal ability. We apply our sampling formula to tropical tree data from Barro Colorado Island, Panama. Tropical trees are divided depending on their dispersal mode, where biotically dispersed trees are grouped as one guild, and abiotically dispersed trees represent another guild. We find that breaking neutrality by adding guild structure to the neutral model significantly improves the fit to data and provides a better understanding of community assembly on BCI. Our findings are thus an important step towards an integration of neutral and niche theory.

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1. Introduction

The astonishing biodiversity around the globe, especially in the tropics, makes one wonder how this biodiversity has originated and how it can be maintained. Traditionally, species composition in an ecological community is explained by species-specific traits and species requirements. By contrast, the more recent neutral theory (Hubbell, 2001; Etienne and Olff, 2004; Rosindell et al., 2011) explains species composition in an ecological community by stochastic demography and dispersal. This theory deliberately neglects species-specific differences (the neutrality assumption). It oversimplifies ecology in order to emphasize that ecological drift is an important factor in community assembly (Rosindell et al., 2011; Wennekes et al., 2012). Despite this simplification the model can convincingly explain various biodiversity patterns, suggesting that indeed ecological drift is an important factor in community assembly (Etienne and Olff, 2004; Alonso et al., 2006).

The neutrality assumption states that all the individuals within an ecological community have the same birth rates, death rates, dispersal rates and speciation rates, irrespective of the species the individuals belong to (Hubbell, 2001). The ecological community is assumed to consist of individuals of functionally equivalent species that compete with each other for space in the community. As a result, patterns in abundance predicted by the theory are purely

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the result of drift, speciation and immigration, and not the result of competitive asymmetries between the species in the local community. The neutrality assumption is the most debated assumption of the Neutral Theory of Biodiversity (McGill et al., 2006; Purves and Pacala, 2008; Turnbull et al., 2008; Gotelli et al., 2009). Most importantly, the neutrality assumption refutes the idea of the unique correspondence between a species and its niche (interpreted here as the set of conditions and requirements for a species to survive (Hutchinson, 1958), although the exact meaning of the niche concept is unclear (Chase and Leibold, 2003; McInerny and Etienne, 2012)). More specifically, the neutrality assumption ignores specific interactions between species and species-specific adaptations, such as habitat specialization; furthermore it ignores the effects of density dependence, ecological succession and the impact of trait differences (Purves and Turnbull, 2010).

Several models explore the continuum between niche and neutral models by looking at the effect of differences in birth and death rates, which might arise through differences in intraspecific and interspecific competition (Jabot and Chave, 2011). In the fully neutral case, intraspecific and interspecific competition are identical, whereas classic coexistence theory predicts that coexistence is promoted when intraspecific competition is stronger than interspecific competition (Adler et al., 2007). Combining community assembly with classic coexistence modelling, Noble and Fagan (2011) showed that when intraspecific competition exceeds interspecific competition, patterns similar to a fully neutral model emerge. Along similar lines, Haegeman and Loreau (2011) investigated how altering the difference between intraspecific and interspecific competition affects the species abundance distribution. They focused on the parameter space where intraspecific competition exceeds interspecific competition, i.e. where classical theory predicts coexistence. They found that with increasing interspecific competition, fluctuations in local community size increase, and the local community becomes more prone to extinction. More importantly they found that altering the difference between intraspecific and interspecific competition only influenced the species abundance distribution marginally, and concluded that from species abundance data alone it might be difficult to assess the degree of intraspecific versus interspecific competition. Proceeding even further, Pigolotti and Cencini (2013) found an analytical expression for the expected species abundance distribution where the degree of intraspecific and interspecific competition can be tuned by a single parameter. Their results suggest a profound impact of the degree of intraspecific versus interspecific competition not only on the species abundance distribution, but also on the average species lifetime and on the total variation in species lifetimes in the local community.

Competitive asymmetry could also result in differences in birth rate irrespective of competition. Du and colleagues found that introducing competitive asymmetry breaks down neutral patterns (Du et al., 2011), but also that these effects can be counteracted by negative density dependence: communities with intermediate competitive asymmetry and intermediate levels of negative density dependence show species abundance distributions that are indistinguishable from neutral distributions, suggesting that neutral patterns can emerge from non-neutral assumptions.

Breaking neutrality through the introduction of differences in dispersal rather than birth and death rates has been less well studied. Turnbull et al. (2008) investigated the effect of an equalizing trade-off between seed mass and seed number on neutrality. They found that after including such a trade-off, neutral patterns break down as soon as seed arrival becomes stochastic. Liu and Zhou (2011) relaxed the neutrality assumption by introducing stochastic differences in dispersal ability between species. As the standard deviation of the Gaussian distribution governing these differences increases, the neutral patterns break down and community assembly becomes deterministic, where species with a high dispersal ability tend to dominate the local community. Liu and colleagues compared the effect of differences in dispersal ability to data generated with the neutral model without these differences, but did not confront their model with empirical data.

Trophically similar species may come close to fitting the neutrality assumption, but differences in dispersal may prevent them from being functionally equivalent. Differences in dispersal might arise through differences in seed size (Muller-Landau and Hardesty, 2005), differences in fruit size (Seidler and Plotkin, 2006) but might also manifest themselves as differences in flight prowess (Valtonen et al., 2013) or differences in pelagic larval duration in coral reef fish (Victor and Wellington, 2000; Almany et al., 2007). In this paper we will study such differences in dispersal, focusing on tropical trees. The majority of tropical tree species (73%) disperse through animal means (Muller-Landau and Hardesty, 2005), such as bats, birds, mammals, ants and sometimes even fish. The other 27% of tree species relies on abiotic factors to disperse their seeds, such as wind, water or ballistics.

By definition, neutral models fail to include differences in dispersal between species that share the same local community and metacommunity. Here we present a model where we classify species according to their dispersal syndrome, We will call the resulting classes guilds. This is a simple, but important step towards incorporating differences between species without needing to explicitly quantify these differences for every species in the community. Instead we only need to quantify the differences between guilds, and assess the importance of these differences for community assembly. Our model breaks the neutrality assumption of the standard neutral model (Hubbell, 2001; Etienne and Alonso, 2005) by subdividing the community into two guilds, where each guild is a group of species that have the same dispersal rate. Between guilds, dispersal rates may differ, but the speciation rate, birth and death rates are identical. We show that our model can accurately distinguish between datasets including a guild structure, and datasets that do not have any guild structure. Our model is able to detect signatures of guild structure from the species abundance distribution when combined with ecological data regarding dispersal, refuting the idea that the species abundance distribution does not contain sufficient information to draw conclusions about underlying community assembly mechanisms. Secondly, we show that parameter estimates obtained with our model are accurate and differ considerably from estimates obtained using the standard neutral model without guild structure. Lastly we illustrate the model by applying it to the tropical tree dataset of Barro Colorado Island (BCI).

2. Model

We assume that there are two guilds X and Y that differ in their immigration parameter m_i ($i = X, Y$); all species *within* each guild share the same migration parameter m_i. All species, regardless of the guild they belong to, have the same fundamental biodiversity number θ, as in the standard neutral model. In the metacommunity, every time step one individual dies and is replaced by an individual from either guild X or guild Y. With probability ν_X a speciation event occurs resulting in a new species that belongs to guild X and to guild Y with probability ν_Y. With probability $1-\nu_X-\nu_Y$ no speciation event occurs; then the new individual belongs to guild X or Y depending on the relative abundance of guilds X and Y in the metacommunity. Over time the relative abundances of both guilds reach a dynamical equilibrium. The equations we derive in Appendix A are applicable to the general case where $\nu_X \neq \nu_Y$. However, we found that the statistical power in such cases is much reduced. Furthermore, we focus here on

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