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Relaxing the zero-sum assumption in neutral biodiversity theory

Bart Haegeman[a,b], Rampal S. Etienne[c,*]

[a]*INRA, UR50, Laboratory of Environmental Biotechnology, Avenue des Etangs, F-11100 Narbonne, France*
[b]*INRA-INRIA Research Team MERE, UMR Systems Analysis and Biometrics, 2 place Pierre Viala, F-34060 Montpellier, France*
[c]*Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands*

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Abstract

The zero-sum assumption is one of the ingredients of the standard neutral model of biodiversity by Hubbell. It states that the community is saturated all the time, which in this model means that the total number of individuals in the community is constant over time, and therefore introduces a coupling between species abundances. It was shown recently that a neutral model with independent species, and thus without any coupling between species abundances, has the same sampling formula (given a fixed number of individuals in the sample) as the standard model [Etienne, R.S., Alonso, D., McKane, A.J., 2007. The zero-sum assumption in neutral biodiversity theory. J. Theor. Biol. 248, 522–536]. The equilibria of both models are therefore equivalent from a practical point of view. Here we show that this equivalence can be extended to a class of neutral models with density-dependence on the community-level. This result can be interpreted as robustness of the model, i.e. insensitivity of the model to the precise interaction of the species in a neutral community. It can also be interpreted as a lack of resolution, as different mechanisms of interactions between neutral species cannot be distinguished using only a single snapshot of species abundance data.

Keywords: Density-dependence; Neutral model; Detailed balance; Abundance vector

1. Introduction

Neutral biodiversity theory has received much attention since it was revived by Hubbell (2001) and major theoretical advances have been made (reviewed, for instance, in Etienne and Alonso, 2007). Most authors have focused on its most essential assumption, the neutrality assumption, which states that all individuals, regardless of species, behave identically under identical circumstances. Although this assumption seems unrealistic for most ecological communities, neutral theory has been recognized as providing useful null models for comparison with alternative models incorporating species differences and has sharpened our tests to detect deviations from neutrality (Alonso et al., 2006; McGill et al., 2006). We need to be aware, however, that rejection of neutral models failing such tests may not be (completely) due to the neutrality assumption; it may be due to other assumptions in the model, which is, after all, only a single, particular implementation of neutral theory (Etienne, 2007).

In the standard neutral model of biodiversity (Hubbell, 2001), such an assumption is the zero-sum assumption. It states that the individuals in an ecological community play a zero-sum game: each death or emigration event is immediately followed by a birth or immigration event, such that the community remains saturated and therefore introduces a coupling between species abundances. If the resources (e.g. space, light) are constant over time, the zero-sum assumption implies that the total number of individuals in the community is also constant over time. In the standard neutral model it is indeed assumed that community size is fixed. In this paper we will refer to this model as the fixed-community-size (fcs) model.

It was shown recently that a neutral model with independent species—hereafter called the independent-species model (ind)—and thus without any coupling

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[*] Corresponding author. Tel.: +31 503632230.
E-mail addresses: bart.haegeman@inria.fr (B. Haegeman), r.s.etienne@rug.nl (R.S. Etienne).

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between species abundances has the same sampling formula (given a fixed number of individuals in the sample) as the fixed-community-size model (Etienne et al., 2007). The equilibrium of both models are therefore equivalent from a practical point of view. In this paper we will show that this equivalence can be extended to a class of neutral models with density-dependence on the community-level. This class includes the fixed-community-size model and the independent-species model as special cases.

We start by giving an alternative proof for the sampling formula of the independent-species model in equilibrium, because it provides a nice and simple introduction to our extension to community-level density-dependent (cdd) neutral models. This alternative proof is based on the fact that the equilibrium state of the independent-species model can be written as a combination of the equilibrium states of fixed-community-size models for different community sizes. Next, we introduce the novel neutral models with community-level density-dependence, and show that their equilibrium state satisfies the same property. This means that the density-dependent neutral models all have the same sampling formula as the fixed-community-size model and the independent-species model.

2. Independent species

We formulate the independent species model as in Etienne et al. (2007), so it only differs from the fixed-community-size model in that there is no coupling between the population sizes (abundances) of the different species. To briefly summarize, the local community receives immigrants from the metacommunity. This metacommunity consists of S_M species, and is assumed to be so large that only relative abundances have to be taken into account. We denote the relative abundance of species k in the metacommunity by p_k (see Table 1 for an overview of our notation). Because the local community is smaller than the metacommunity and because it is dispersal-limited, it contains usually (much) fewer species than the metacommunity, but potentially it can contain all S_M species, so we will keep track of the abundances of all S_M species, even if they are (temporarily) zero. We denote the abundance of species k in the local community by N_k and define the local community abundance vector, $\vec{N} = (N_1, \ldots, N_{S_M})$. We denote the total abundance of the local community by J_L, that is,

$$J_L = \sum_k N_k.$$

The local community dynamics are determined by the repetitive occurrence of birth, death and immigration events. Due to the neutrality assumption, the birth rate per individual (denoted by β), the death rate per individual (denoted by δ), and the immigration rate from meta- to local community (denoted by λ) do not depend on the identity of the involved species. For species k with abundance N_k, the rate of abundance increase g_{N_k} and the rate of abundance decrease r_{N_k} are given by

$$g_{N_k} = \beta N_k + \lambda p_k,$$

$$r_{N_k} = \delta N_k.$$

We can then write down the corresponding master equation (Van Kampen, 1992). This is a differential equation for the probability $P(N_k, t)$ that at time t the abundance of species k in the local community is N_k:

$$\frac{\mathrm{d}}{\mathrm{d}t} P(N_k, t) = g_{N_k-1} P(N_k - 1, t) + r_{N_k+1} P(N_k + 1, t) - g_{N_k} P(N_k, t) - r_{N_k} P(N_k, t). \quad (1)$$

All species $k = 1, \ldots, S_M$ satisfy such an equation, without any coupling between them. Because the species are independent, the probability $P(\vec{N}, t)$ that at time t the abundance vector is $\vec{N}$ can be written simply as a product of the probabilities $P(N_k, t)$ for all the species $k = 1, \ldots, S_M$:

$$P(\vec{N}, t) = \prod_{k=1}^{S_M} P(N_k, t). \quad (2)$$

Table 1
Explanation of mathematical symbols

Symbol	Explanation
S_M	Number of species in metacommunity
$\vec{p} = (p_1, \ldots, p_{S_M})$	Relative abundance vector of metacommunity
$\vec{N} = (N_1, \ldots, N_{S_M})$	Abundance vector of local community
$J_L = \sum_k N_k$	Local community size
$\vec{n} = (n_1, \ldots, n_{S_M})$	Abundance vector of sample
$J = \sum_k n_k$	Sample size
$P_{fcs}, P_{ind}, P_{cdd}$	Equilibrium probability distribution for the fixed-community-size model, the independent-species model, and the community-level density-dependent model, respectively. Thus, $P_{cdd}(\vec{N} \mid \ldots)$ denotes the probability of abundance vector $\vec{N}$, $P_{cdd}(J_L \mid \ldots)$ denotes the probability of local community size J_L, etc.
$P_{fcs,hyp}, P_{ind,hyp}, P_{cdd,hyp}$	Equilibrium probability distribution of the sample composition (i.e. the abundance vector $\vec{n}$) under sampling without replacement, described by the hypergeometric distribution
β, δ, λ	Birth, death, and immigration rate; constant for the independent-species model, and a function of the local community size J_L for the density-dependent model
g_{N_k}, r_{N_k}	Rate of abundance increase (by birth and immigration) and decrease (by death) of species k with abundance N_k; constant for the independent-species model, and a function of the local community size J_L for the density-dependent model
I	Fundamental dispersal number, or ratio of immigration rate λ and birth rate β for the independent-species and density-dependent model
R	Ratio of birth rate β and death rate δ for the independent-species and density-dependent model