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Characteristics of temporal changes in communities where dynamics differ between species

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ABSTRACT

Communities with different phenotypic variation among species can have identical species abundance distributions, although their temporal dynamics may be very different. By using stochastic species abundance models, both the lognormal and beta prime abundance distributions can be obtained with either homogeneous or heterogeneous dynamics among species. Assuming that anthropogenic activity disturbs the communities such that species' carrying capacities are decreasing deterministically, the structure of the communities are studied using simulations. In order to construct homogeneous communities with reasonable variation in abundance, the parameter values describing the dynamics of the species can be unrealistic in terms of long return times to equilibrium. Species in heterogeneous communities can have stronger density regulation, while maintaining the same variation in abundance, by assuming heterogeneity in one of the dynamical parameters. The heterogeneity generates variation in carrying capacity among species, while reducing the temporal stochasticity. If carrying capacity decreases, changes in community structure occur at a much slower rate for the homogeneous compared to the heterogeneous communities. Even over short time periods, the difference in response to deterministic changes in carrying capacity between homogeneous and heterogeneous community models can be substantial, making the heterogeneous model a recommended starting point for community analysis.

1. Introduction

In community ecology, biologists try to understand how species persists in concert with each other over time, in space or both. The initial studies of species communities were concerned with fitting probability distributions to abundances (counts) of butterflies (Fisher et al., 1943). Several different distributions have been applied to describe the composition of species communities in a wide variety of taxa, possibly where the data have been transformed to a log scale. The probability distributions fitted to abundance data are known as species abundance distributions in community ecology and can be used to compare the structure of communities at different spatio-temporal locations and assess the durability of communities based on the number of common and rare species present (McGill, 2011). Additionally, numerous indices have been constructed to describe the diversity and similarity of communities (Gotelli and Colwell, 2011; Maurer and McGill, 2011). How communities may develop over time is a particularly important issue in conservation biology (Buckland et al., 2005; Magurran et al., 2010; McGill, 2011).

While species abundance distributions can be fitted to data and compared at different points in time, the distributions themselves give no important information about how the community will develop in the future. It is, however, possible to describe a community of species assuming that each single species can be characterized by a dynamic population model and still obtain well-known abundance distributions. The population model used to describe single species dynamics contains the information needed to simulate each species' temporal fluctuations and can accordingly be used to study how the whole community progresses over time. Single species dynamics are determined by different biological attributes, for instance growth rate, carrying capacity and environmental stochasticity. Using single species dynamics to obtain species abundance distributions were introduced by Engen and Lande (1996a,b) and some of the main results are reiterated in Section 2, but the focus in this article is on temporal dynamics of communities.

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When characterizing communities using single species dynamics, a common simplifying assumption is that all the species have the same vital rates, i.e. the same growth rate and carrying capacity. However, it has been shown that dynamics of species can vary considerably among species within the same taxa (Engen et al., 2011). Such variation in dynamics among species will be described as heterogeneity in different vital rates in this article, while homogeneous communities have no variation in vital rates among species. The main topic of this article is to analyse how variation among species influence the structure of communities over time. Our comparison of communities is restricted to constructing species abundance distributions with different magnitudes of heterogeneity, starting with a homogeneous community, but identical abundance distributions.

Communities are often studied under the assumption that the environment of the different species are constant, meaning that vital rates and the magnitude of the variation in annual fluctuations are constant over the whole time frame considered. Anthropogenic activities, however, such as habitat destruction, over-exploitation, introduced species and pollution, are currently causing the sixth major mass extinction of species (Lande et al., 2003) and will generate changes in species community composition, structure and diversity (Kneitel and Pages, 2010). For instance, a reduction or fragmentation of habitat can reduce the carrying capacity of the species present in a community. Despite recent attempts by the international community to stop the reduction of biological diversity, the majority of indices measuring biodiversity show declining trends, while anthropogenic pressure on ecosystems have increased (Butchart et al., 2010). This study will emphasize on how anthropogenic activities can change species communities, by analysing how communities with different degrees of heterogeneity in the dynamics will vary in their response to permanent changes in the environment, using simulations.

This article has the following structure: first, the main theory of Engen and Lande (1996a,b) on stochastic species abundance models and heterogeneous communities is described. Second, the simulation procedure used to study the temporal dynamics of the communities is explained, and the different community indices applied are presented. The first case study of community dynamics considered shows species with a Gompertz type of density regulation. Communities with the same abundance distribution when observed at a single point of time, but with completely different temporal dynamics, are compared, both when the carrying capacities of the species' are either constant or when the carrying capacities are gradually declining. In the second case study, we first consider species following a homogeneous Beverton–Holt model of density regulation, meaning that all the species in the community have the same vital rates. This Beverton–Holt dynamics is compared to heterogeneous communities with logistic type of density regulation, i.e. the vital rates vary between species in the community. Here also, the different communities show different temporal dynamics, but maintain the same instantaneous abundance distribution. Finally, the effect of a declining trend in carrying capacity is studied for the second case. Considerable differences between simulated homogeneous and heterogeneous communities are illustrated, emphasizing the importance of allowing for variation in the vital rates between species in a community.

2. Methods

2.1. General theory

The stochastic species abundance models introduced by Engen and Lande (1996a,b) obtained the lognormal and gamma distribution, respectively, by modelling the individual species' dynamics using multivariate diffusion processes. The models assume that the temporal variation in population abundance in a community is caused by environmental fluctuations in the growth rate of each individual species independently. The dynamical approach by Engen and Lande (1996a) generated abundances following an inhomogeneous Poisson process with rate $\lambda(x)$, where x is the abundance, meaning that the number of species with abundances in some region Ω is Poisson distributed with mean $\int_\Omega \lambda(x)dx$ at any time. The species abundance distribution is then the Poisson rate scaled as a proper distribution, that is, $f(x) = \lambda(x)/\int \lambda(u)du$, where the integration runs over all possible abundances. Such dynamical abundance models provide means to study the community dynamics over time, whereas the abundance distributions only provide snapshots of the community compositions at specified time points. Note that the abundance x could be measured on a different scale, e.g. the log scale for a Gompertz model, without invalidating the theory described here.

Using the diffusion approximation for the single species dynamics with infinitesimal mean $\mu(x;\theta)$ and variance $\nu(x;\theta)$, Engen and Lande (1996a) derived a general expression for the Poisson rate of species abundances

$$\lambda(x;\theta) = \frac{2\beta}{\nu(x;\theta)} e^{2\int_a^x \mu(u;\theta)/\nu(u;\theta)du}, \tag{1}$$

where a is the extinction barrier and β the speciation rate. However, speciations are not included in the following analysis which deals with time intervals so small that speciations are unlikely. An advantage of the approach of Engen and Lande (1996a) is that it, in a simple way, allows for heterogeneity among species. Species entering the community are described by a set of parameters $\theta \in \Theta$, corresponding to abundance model $\lambda(x;\theta)$, thereby introducing heterogeneity by assuming that θ vary among species. If θ at speciation or colonization can be considered a realization of a stochastic variable with distribution $\pi(\theta)$, then the abundance model is given by the inhomogeneous Poisson rate (Engen and Lande, 1996a)

$$\lambda(x) = \int_{\theta\in\Theta} \lambda(x;\theta)\pi(\theta)d\theta. \tag{2}$$

This result shows the possibility of obtaining the same abundance model $\lambda(x)$ from different combinations of its components $\lambda(x;\theta)$ and $\pi(\theta)$. An observation of a community at a given time will only give information about the rate $\lambda(x)$ and the corresponding species abundance distribution while containing no information about its components $\lambda(x;\theta)$ and $\pi(\theta)$. Knowledge of species heterogeneity is likely to be crucial when it comes to permanent environmental changes and management of ecosystems. Fluctuations in population abundance are assumed to be caused by environmental stochasticity, described by environmental variance in the infinitesimal variance of the diffusion process. Demographic stochasticity is only relevant in small populations and will not be considered in the following analysis. Although demographic variance increases the probability of extinction at small abundances, it will not change the general results presented here. Note also that the dynamics of the species within a community is assumed to be independent.

The non-uniqueness in temporal characteristics of abundance models with the same abundance distribution is the starting point of this analysis. Heterogeneity can be defined by considering variability among species in different parameters describing the population dynamics. If one parameter vary among species, one or more of the other population parameters have to be adjusted in order to obtain the same abundance distribution as