Predicting stochastic community dynamics in grasslands under the assumption of competitive symmetry

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HIGHLIGHTS

- We develop a stochastic biomass-based model of community dynamics.
- We use this model to analyze data from a biodiversity experiment.
- Good predictions of multispecific dynamics assuming competitive symmetry are found.

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ABSTRACT

Community dynamics is influenced by multiple ecological processes such as environmental spatio-temporal variation, competition between individuals and demographic stochasticity. Quantifying the respective influence of these various processes and making predictions on community dynamics require the use of a dynamical framework encompassing these various components. We here demonstrate how to adapt the framework of stochastic community dynamics to the peculiarities of herbaceous communities, by using a short temporal resolution adapted to the time scale of competition between herbaceous plants, and by taking into account the seasonal drops in plant aerial biomass following winter, harvesting or consumption by herbivores. We develop a hybrid inference method for this novel modelling framework that both uses numerical simulations and likelihood computations. Applying this methodology to empirical data from the Jena biodiversity experiment, we find that environmental stochasticity has a larger effect on community dynamics than demographic stochasticity, and that both effects are generally smaller than observation errors at the plot scale. We further evidence that plant intrinsic growth rates and carrying capacities are moderately predictable from plant vegetative height, specific leaf area and leaf dry matter content. We do not find any trade-off between demographical components, since species with larger intrinsic growth rates tend to also have lower demographic and environmental variances. Finally, we find that our model is able to make relatively good predictions of multi-specific community dynamics based on the assumption of competitive symmetry.

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1. Introduction

Plant community dynamics is driven by intra- and interspecific interactions, and by environmental factors such as climatic conditions or soil composition. The way these processes influence community dynamics is of utmost importance for understanding community assembly (Ackerly, 2003; Ejrnaes et al., 2006; Chase, 2010), productivity (Mouquet et al., 2002) and stability (Sprugel, 1991; Hector et al., 2010). Studies based on static descriptors of community structure have provided tests for predictions of ecological theories (Stubbs and Wilson, 2004; Cornwell et al., 2006; Norden et al., 2009; Gonzalez et al., 2010). The next step is to quantitatively relate empirical observations to the underlying dynamical processes (Jabot and Chave, 2011; De Mazancourt et al., 2013). In this vein, a growing number of studies aim at building dynamical models of community dynamics based on explicit ecological processes, and at calibrating these models with field data (Lande et al., 2003; Beaumont, 2010), thereby belonging to

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the more general trend towards a more predictive ecology (Mouquet et al., 2015).

To build models of plant community dynamics, the framework of stochastic population dynamics is particularly appealing (Lande et al., 2003). This approach consists of modelling the joint effects of competitive interactions, demographic and environmental stochasticities on community dynamics. Although the role of environmental stochasticity in community dynamics has been recognized for a long time (Chesson and Warner, 1981), it has been neglected in many recent analyses by community ecologists (Chisholm et al., 2014; Kalyuzhny et al., 2015). There is therefore a renewing interest in better taking into account this component of community dynamics in dynamical models (De Mazancourt et al., 2013; Kalyuzhny et al., 2015).

This general framework has been mainly applied to easily countable organisms, such as animals (Lande et al., 2003) or trees (Chisholm et al., 2014; Kalyuzhny et al., 2015). To be applied to herbaceous plants, it has been proposed to model the dynamics of plant biomass instead of population sizes (De Mazancourt et al., 2013). But two additional specificities of herbaceous plant communities have been mainly overlooked in previous studies. First, the time scale of variation in competition between plants is short, due to the temporal variability of resources and to the rapid modification of vertical community structure following plant growth (Wilson and Tilman, 1993; Silvertown et al., 2015). Second, herbaceous plant communities face frequent major disturbance events leading to sudden aerial biomass drops, such as winter mortality of aerial plant tissues or agricultural harvests by mowing or grazing (Jouven et al., 2006; Jabot and Pottier, 2012). These disturbance events periodically reset aerial biomass to low levels, and therefore need to be taken into account in dynamical models of community dynamics.

The present study aims at developing a model of stochastic dynamics for herbaceous plant communities based on biomass rather than population sizes, and taking into account both the short temporal scale of between plant competition and the frequent biomass drops encountered by herbaceous plant communities. We detail an inference method to calibrate the daily time step model parameters from biomass measurements in the field at seasonal time steps, coming from the Jena biodiversity experiment (Weigelt et al., 2010). This methodological development enables us to answer to four questions on herbaceous plant community dynamics: 1) What is the respective influence of demographic and environmental variabilities on community dynamics? 2) Is there an equalizing trade-off between species intrinsic growth rates and their temporal stability as would be expected for species coexistence (Chesson, 2000)? 3) Are species demographical characteristics predictable from plant functional traits? 4) Are multispecific community dynamics predictable from species individual dynamics?

2. Methods

2.1. A new biomass-based model of plant stochastic community dynamics

The model describes the dynamics of species aboveground biomass within a growing season and the way competition, demographic and environmental stochasticities affect species growth. In the following, we call "season" a temporal period during which plants are growing without experiencing a strong biomass decrease or removal (due to winter, harvests or consumption by herbivores). At the end of each season, the aboveground biomass is assumed to drop and this reduced biomass is used to initialize the species dynamics in the following season (Fig. 1). A community is here defined as a group of plants of the same or of different species growing in the same plot p. The intra-seasonal dynamics of plant growth is modelled with a daily time step. The biomass of species i during season T in plot p after t days of growth, $B_i(t,p,T)$, is modelled with the following difference equation:

$$B_i(t+1, p, T) = B_i(t, p, T) + \left(r_{mi} + \sigma_{ei} u_{ei}(T) + \frac{\sigma_{di} u_{di}(T, p)}{\sqrt{B_i(0, p, T)}} \right)$$
$$\cdot B_i(t, p, T) \cdot \left(1 - \frac{B_i(t, p, T) + \sum_{j \neq i} \alpha_{ij} B_j(t, p, T)}{K_i} \right) \quad (1)$$

where r_{mi} is the intrinsic growth rate of species i, K_i is its carrying capacity and α_{ij} is the inter-specific competition coefficient describing the effect of species j on species i. Environmental stochasticity encompasses the inter-seasonal variability in species growth rates stemming from environmental variability. It is modelled through $\sigma_{ei} u_{ei}(T)$ where σ_{ei}^2 is the environmental variance, and $u_{ei}(T)$ are drawn from a normal distribution with zero mean and unit variance. For each species i, $u_{ei}(T)$ are assumed to be constant across all plots p during season T. Demographic stochasticity encompasses intra-specific variability. It is incorporated through $\sigma_{di} u_{di}(T,p)$ where σ_{di}^2 is the demographic variance, and $u_{di}(T,p)$ are drawn from a normal distribution with zero mean and unit variance, and are thus assumed to vary across the plots p. Consequently, the growth rate of a given species is likely to differ across plots because of demographic stochasticity and across seasons because of both demographic and environmental stochasticities. The last logistic term represents intra- and inter-specific competition for resources which decreases the plant growth rate. This growth reduction due to competition increases as plants grow during the season.

The biomass at the start of the growing season $B_i(0,p,T)$ is used in the scaling of the demographic variance in Eq. (1) as being a proxy of the number of growing individuals in season T. $B_i(0,p,T)$ is assumed to be constant across seasons and equal to $B_0 = 2\ \text{g}^{-2}$ for monocultures. This simplifying assumption is justified by the fact that the establishment of monoculture plots was generally well-advanced when biomass monitoring started (Roscher et al., 2004), so that biomass at
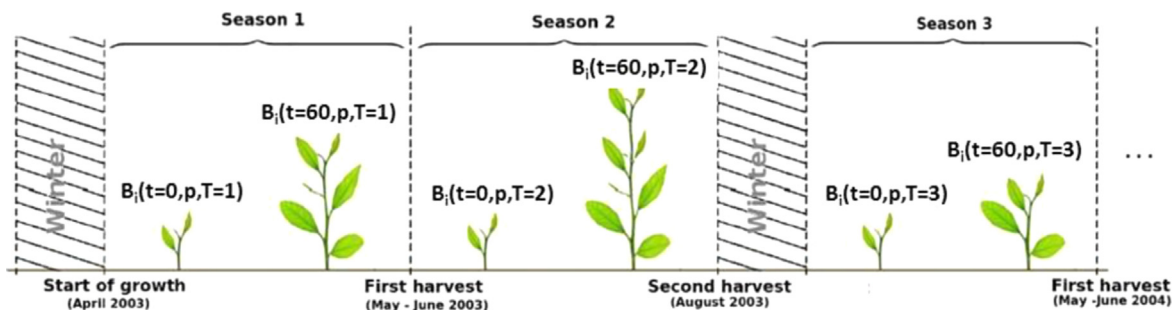

Fig. 1. Model description and relationships with data used for calibration. Only end of season biomass $B_i(t=60,T)$ is known.