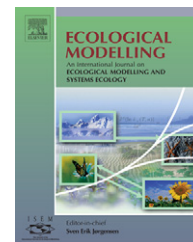


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Symmetric competition causes population oscillations in an individual-based model of forest dynamics

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ABSTRACT

Individual-based modelling is a promising tool for scaling from the individual to the population and community levels that allows a wide range of applied and theoretical approaches. Here, we explore how intra-specific competition affects population dynamics using FORSITE, an individual-based model describing tree–tree interactions in a spatial and stochastic context. We first describe FORSITE design and submodels following the ODD (Overview, Design concepts and Details) guideline for individual-based models. We then use simulation to study how competition symmetry (i.e., the way individual size affects resource partitioning) changes temporal and spatial population dynamics. We compare our results to those of an earlier deterministic (analytical) model of annual plants which found that (i) under asymmetric competition (i.e., advantaging tall individuals), population dynamics converge quickly to a stable equilibrium and (ii) under symmetric competition, some values of competition strength and population growth rate make population dynamics exhibit long-term oscillations. We find generally similar results, despite the existence of overlapping generations in trees. A thorough analysis of stage structures in the model allows us to explain this behaviour. We also show that decreasing tree dispersal distances, in the case of symmetric competition, results in a wave-like spatial pattern, caused by desynchronized sub-populations. Finally, we link the results obtained with FORSITE to different types of resource limitation observed in northern temperate and sub-boreal forests, emphasizing the implications of such difference on long-term biome dynamics. We note that FORSITE is a flexible platform that can be easily adapted for other ecological modelling studies.

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1. Introduction

Scaling up processes from individual to community and landscape levels has long been a critical issue in ecology (Levin, 1992; Wiens et al., 1993). Individual-based modelling (IBM) (DeAngelis and Mooij, 2005; Grimm and Railsback, 2005) is a promising tool for scaling that allows a wide range of applied and theoretical approaches. Recent studies use individual-based models to generate results that could probably not have

been obtained through analytical models alone (Uchmanski, 1999, 2000). The proliferation of IBMs, however, has not yielded substantial advances in ecological theory (Berger and Hildenbrandt, 2000) and Grimm et al. (2006) call for a generalized approach to IBM description.

Recent individual-based plant models have found that taking into account dispersal mechanisms (e.g., Higgins and Cain, 2002), and the effects of environmental heterogeneity (Yu and Wilson, 2001; Snyder and Chesson, 2003) at the individual level

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are critical for understanding community dynamics. Competition is obviously also critical in understanding community dynamics and has been carefully detailed in spatially explicit models of vegetation dynamics (e.g. SORTIE model, Pacala et al., 1996; Berger and Hildenbrandt, 2003). How competition between individuals plays a role in population dynamics, however, is less clear. Intra-specific competition has been extensively studied in community ecology (see Calcagno et al., 2006 for a review) but within this field the mechanism underlying the individual relationships has rarely been explicitly taken into account (Adler and Mosquera, 2000).

In forest ecosystems, competition for light explains a large part of the community structure (Pacala et al., 1996) and for that reason many models have tried to incorporate, explicitly, competition for light at the individual level (Moravie and Robert, 2003; Bauer et al., 2004). However, nutrients like nitrogen, or water supply, can also be limiting factors in forests (Pacala et al., 1996; Wilson, personal communication, 2007). This is particularly true in boreal forests, where tree density and the angle of light incidence make competition for light almost negligible (Pham et al., 2005). In that context, below-ground competition may become relatively more important. Competition for light between large and small trees can be defined as asymmetric, because competition for light favours tall, wide-crowned trees rather than short ones (Bauer et al., 2004). However, root competition is often symmetric (i.e., the resource is equally partitioned between individuals independently of their size; Berntson and Wayne, 2000) or inversely asymmetric (i.e., smaller individuals consume a larger portion of resource than taller ones; Schenk, 2006). The issue of asymmetric vs. symmetric competition is thus, relevant when dealing with forest populations, communities and landscapes.

The importance of competition type (asymmetric vs. symmetric) for plant community structure has been recognized through simulation studies (Weiner, 1990; Pacala and Weiner, 1991; Bauer et al., 2004). Most studies have focussed on how variability in individual growth rates affects size hierarchy formation (Freckleton and Watkinson, 2001). In particular, it has been shown that in populations characterized by symmetric competition, size hierarchy (i.e., the distinct density of different size classes) increases with increasing competition. By comparison, when asymmetric competition occurs size hierarchy does not respond to differences in densities. In his review on asymmetric competition in plant populations, Weiner (1990) recognized that the effect of competition on size hierarchy should have deep implications for population dynamics. Indeed, Pacala and Weiner (1991) showed how adding an asymmetric competition term in an analytical model of plant population dynamics produces convergence to a stable equilibrium, whereas symmetric competition produces sustained oscillations in population sizes under certain conditions.

We are not aware of any individual-based model explicitly focusing on the effect of competition type on long-term dynamics of plant populations. To address this issue, we built FORSITE, a generic individual-, rule-based model that details how dispersal and competition modes affect tree spatial and temporal population dynamics. The aim of this paper is two-fold: (1) to present FORSITE following the ODD (Overview, Design concepts and Details) guideline for

individual-based models suggested by Grimm et al. (2006) and (2) to show how the type of competition can dramatically affect the long-term behaviour of a single-species tree population.

We were particularly interested in Pacala and Weiner's (1991) analytical demonstration of sustained oscillations occurring under symmetric competition and specific conditions. As shown by Uchmanski (1999, 2000), introducing stochastic interactions between individuals can dramatically change the results obtained by an analytical model. Inspired by Pacala and Weiner's study, we expect FORSITE to reveal (i) that under asymmetric competition, population dynamics converge quickly to a stable equilibrium and (ii) that under symmetric competition, when growth rate decays exponentially and when competition increase, population dynamics exhibit long-term oscillations. However, we experiment with various additional parameters to establish the range of this behaviour. Particularly, FORSITE aims to simulate forest dynamics, while Pacala and Weiner's model simulated annual plants. It seems, therefore, interesting to see how the difference in life cycle assumptions, among other things, can influence the model outputs.

Consequently, we adopt a sequential simulation plan that allows testing of these hypotheses and deconstructs the model behaviour by increasing its complexity step by step. This approach allows us to explain thoroughly the relationships between spatial and temporal dynamics that underlie the simulated dynamics.

2. Model description

2.1. Purpose

The aim of FORSITE is to simulate the effects of different types and degrees of competition on tree interactions without incorporating details of the underlying physiological mechanisms, in order to model large scale phenomena. The acronym emphasizes that it is a Forest model with Random, Spatial, Individual and Temporal effects, acknowledging RITES (Random Individual and Temporal effects) that Clark et al. (2004) show to be key in ecological dynamics by focusing explicitly on the scale and timing of individual interaction. Unlike most theoretical plant simulation approaches, in which species are simply ranked as "inferior" and "superior" competitors (as in the widely used lottery model; see Snyder and Chesson, 2003), we simulate competition as the outcome of several mechanisms operating at the individual level. However, competition is designed to allow flexibility in theory testing, and thus, does not include empirically linked physiological details that can be found in classical "gap" models (see Kobe et al., 1995; Pacala et al., 1996) or detailed neighbourhood models (Bauer et al., 2004).

2.2. Implementation

FORSITE is based on the modelling platform CORMAS (Bousquet et al., 1998) using the VisualWorks® environment. This platform allows flexible designs, and allows implementation of individual-based stochastic dynamics in a spatial,

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