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Local population dynamics of an invasive tree species with a complex life-history cycle: A stochastic matrix model

Emmanuelle Sebert-Cuvillier^{a,b}, Frédéric Paccaut^b, Olivier Chabrierie^a,
Patrick Endels^a, Olivier Goubet^b, Guillaume Decocq^{a,*}

^a Département de Botanique, Université de Picardie Jules Verne, F-80037 Amiens Cedex, France

^b Laboratoire Amiénois de Mathématiques Fondamentales et Appliquées (UMR 6140 CNRS), Université de Picardie Jules Verne, F-80037 Amiens Cedex, France

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ABSTRACT

Biological invasions are widely accepted as having a major impact on ecosystem functioning worldwide, giving urgency to a better understanding of the factors that control their spread. Modelling tools have been developed for this purpose but are often discrete-space, discrete-time spatial-mechanistic models that adopt a computer simulation approach and resist mathematical analysis. We constructed a simple demographic matrix model to explore the local population dynamics of an invasive species with a complex life history and whose invasive success depends on resource availability, which occurs stochastically. As a case study we focused on the American black cherry (*Prunus serotina* Ehrh.), a gap-dependent tree able both to constitute a long-living seedling bank under unfavourable light conditions and to resprout vigorously once cut-down, which is invading European temperate forests. The model used was a stage-classified matrix population model (i.e., Lefkovich matrix), integrating environmental stochasticity. Stochastic matrix projection analysis was combined with elasticity analysis and stochastic simulations to search for the species' 'Achille heel'. As expected, the population growth rate (i.e., Lyapunov exponent), which measures the risk of *P. serotina* invasion at the stand scale, increased with light frequency. There was a critical value above which the population of *P. serotina* explodes and below which it locally goes extinct. The resprouting capacity usually speed up the invasion but appeared to play a minor role. The mean duration of stand invasion was measured and important life stage transitions that mostly contribute to the local stochastic growth rate were identified. Some relevant management implications are discussed and the interest of such models for the understanding of demographic characteristics of invasive species is stressed.

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1. Introduction

The invasion of native plant communities by introduced exotics has become one of the most serious threats to biodiversity and ecosystem functioning worldwide (Vitousek et al., 1996; Lonsdale, 1999; Williamson, 1999). To date, the attributes

that make a species an invader are poorly understood (Kolar and Lodge, 2001), as well as the characteristics that predispose an ecosystem to invasion (Cronk and Fuller, 1995). One leading idea considers that the spread of an invasive exotic plant in a given ecosystem depends on the interaction between life history and demographic traits of the alien (i.e., 'invasiveness'),

* Corresponding author. Tel.: +33 322 827 761; fax: +33 322 827 469.

E-mail address: guillaume.decocq@u-picardie.fr (G. Decocq).

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and habitat quality and resource availability of the recipient ecosystem (i.e., ‘invasibility’) (Lonsdale, 1999; Alpert et al., 2000). Despite a number of empirical and theoretical studies, no general theory has yet emerged and generalizations are still lacking (Lonsdale, 1999; Williamson, 1999). It is even unlikely that, given their diversity, any single theory may be able to account for all plant species in all ecosystem types. For example, it is difficult to compare the invasive process of annual weeds spreading on river banks or in urban areas (e.g., *Impatiens glandulifera* and *Ambrosia artemisiifolia*, respectively, see Pysek and Prach, 1993) with long-living trees invading relatively undisturbed forests (e.g., *Acer platanoides*, see Webster et al., 2005). However, understanding population attributes which make a specific species invasive is a prerequisite to manage plant invasions efficiently. This also requires the development of appropriate modelling tools (see reviews in Higgins and Richardson, 1996; Hastings, 1996). Because of the lack of general demographic profile of successful invaders, the choice of a model is a matter of methodological preference and depends both on the given objectives and the life history of the studied species.

Most invasive plant species establish and spread following a resource release or habitat freeing, that usually occurs stochastically (e.g., Davis et al., 2000; Shea and Chesson, 2002). Hence, a model cannot be deterministic, since it has to take into account the environmental heterogeneity and random variations over time, i.e., environmental stochasticity. Two kinds of models can describe stochasticity and heterogeneity: metapopulation models and individual-based cellular automata models (Higgins and Richardson, 1996). They are spatial-mechanistic models, which are discrete-space, discrete-time modelling approaches. By adopting a simulation approach, they are extremely flexible and allow the incorporation of complex extensive biological details for particular ecosystems. While answering specific questions about population growth and providing the basis for simplifying complex ecological systems into an analytical framework, these all-inclusive models typically resist mathematical analysis and can only be understood by statistical and graphical examination of computer simulations (Shreiber and Gutierrez, 1998). In this context, matrix models appear to be a powerful and useful tool for simple demographic modelling as well as for spatially-explicit approaches. Simple demographic matrix models investigate the distribution of a population over different stages. The latter can be age classes, size classes or physiological stages (Caswell, 2001). Spatially explicit matrix models describe the distribution of a population in space (Westerberg and Wennergren, 2003; Lebreton and Gonzalez-Davila, 1993). The greatest advantage of using such a spatially and temporally discrete matrix formulation is that several analytical methods and theories from linear algebra are available (Caswell, 2001). Regarding stage-classified matrix models, the analysis of long-term and transient population dynamics is studied in terms of eigenvalues and eigenvectors of the projection matrix (see Lefkovich, 1965; Usher, 1966). All individuals within a class are treated as identical by these matrix models which are easy to construct from a life cycle graph. Environmental stochasticity can be easily incorporated into matrix population models (Caswell, 2001). In a constant environment, the asymptotic growth rate is given by the dominant eigen-

value of the projection matrix, and so the invasibility criterion is based on this dominant eigenvalue. For stochastic environments, population trajectories are described by random matrix products and the corresponding measure of population growth is given by the dominant Lyapunov exponent, which is also called the stochastic growth rate (Caswell, 2001). The ecological interest of the Lyapunov exponent lies in extending the eigenvalue criterion to more general cases of complex population dynamics such as random fluctuations arising from a stochastic environment (Tuljapurkar, 1986; Ferrière and Gatto, 1995). The concept of Lyapunov exponent hence provides a valuable tool for investigating processes of invasion. Surprisingly, matrix models have not been applied to plant invasions (Higgins and Richardson, 1996), with the notable exception of Parker (2000) who studied the invasion dynamics of the shrub *Cytisus scoparius* in northern USA. However, the study was conducted on a species with a quite simple life-history cycle under constant environmental conditions and thus, the model did not incorporate environmental stochasticity. Our main objective is to apply a stochastic matrix modelling approach to the invasive spread of an alien plant species with a complex life-history cycle under fluctuating environmental conditions.

As a case study, we focus on the American black cherry (*Prunus serotina* Ehrh.), which is spreading throughout European temperate forests (Starfinger, 1997). This is an invasive tree species exhibiting a complex life-history cycle, since (1) it is able to constitute a long-living seedling bank, (2) suppressed saplings may be released once a gap is created, (3) individuals can actively resprout at all life stages (Closset-Kopp et al., in press). As it is a gap-dependent species, light availability is a major control of its spread and changes therein may occur both periodically (i.e., clearcuts in the silvicultural cycle) and catastrophically (i.e., windstorms).

To better understand and predict the spread of this alien tree, we aim at developing a stage-classified matrix population model describing its population dynamics at the local scale, i.e., within a forest stand, integrating environmental stochasticity. Stochastic matrix projection analysis is combined with elasticity analysis and simulations to (1) assess the effects of disturbance frequency (light availability) on the invasion process at a single spatial location and evaluate the time to completion of the invasion process under different scenarios, (2) test the flexible demographic response of *P. serotina* through the production of resprouts, and (3) identify important life stage transitions that contribute most to the local stochastic growth rate. It is expected that disturbance will largely favour the invasion process so that stands most exposed to perturbations will be invaded quite quickly. On the other hand, it may be possible that stands under shaded conditions will not be invaded, or that invasion will be significantly slower. Hence, the population growth rate would increase with increasing light availability and there would be a critical perturbation frequency beyond which the population of *P. serotina* would explode and below which the population would go locally extinct. While yearly production of seed may be relatively high, one could expect that capacity of this species to produce resprouts would add to the speed of the invasion process.

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