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Modelling invasibility in endogenously oscillating tree populations: timing of invasion matters

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Abstract The timing of introduction of a new species into an ecosystem can be critical in determining the invasibility (i.e. the sensitivity to invasion) of a resident population. Here, we use an individual-based model to test how (1) the type of competition (symmetric versus asymmetric) and (2) seed masting influence the success of invasion by producing oscillatory dynamics in resident tree populations. We focus on a case where two species (one resident, one invader introduced at low density) do not differ in terms of competitive abilities. By varying the time of introduction of the invader, we show that oscillations in the resident population favour invasion, by creating "invasibility windows" during which resource is available for the invader due to transiently depressed resident population density. We discuss this result in the context of current knowledge on forest dynamics and invasions, emphasizing the importance of variability in population dynamics.

Keywords Forest model · Invasion criteria · Species coexistence · Oscillations · Exploitation competition · Stochasticity · Individual-based model

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Introduction

Two major concepts have been used to understand biological invasions (Lonsdale 1999): invasibility (the sensitivity of a community or landscape to invasion) and invasiveness (a species' ability to invade new habitats). Numerous hypotheses have been suggested to explain how different ecological features affect both invasibility and invasiveness, and have been tested through retrospective (e.g. Mack et al. 2000; Richardson and Pysek 2006), empirical (e.g. Veltman et al. 1996; Reinhart et al. 2006) or modelling approaches (e.g. Schoolmaster and Snyder 2007). Modelling studies have shown that invasiveness is affected by species traits like dispersal, growth rate, or environmental tolerance (Higgins and Richardson 1996; Eppstein and Molofsky 2007). On the other hand, invasibility can be viewed as an emergent property of the environment (through species richness, environmental heterogeneity, or disturbance regime) (Mack et al. 2000). Davis et al. (2000) generalized this view through the theory of "fluctuating resources" that create vacant spots (or "windows of opportunity"—(Myster 1993) that can be colonized by a non-native species (Richardson and Pysek 2006). Such increases in available resource benefiting a potential invader can be created either directly through an increase in resource (in which case the invasibility is caused by a change in the environment) or by a decrease in the resident species' density (in which case the invasibility can be caused by endogenous mechanisms Vandermeer 2006). For instance, in a modified Lotka–Volterra competition system with fluctuating population density and with strength of competition varying exogenously with time, Namba and Takahashi (1993) showed how the timing of invasion interacts with population dynamics, invasions occurring when the strength of competition is out of phase with population density. The phenomenon through which a newcomer's is able to establish on sites where the resident population is transiently at low density is similar in some respects to the winning-by-default or winning-by-forfeit hypothesis advanced by Hurtt and Pacala (1995). The idea of environmental fluctuation and resource availability has been the focus of several studies (Barlow and Kean 2004; Kinezaki et al. 2006; Schoolmaster and Snyder 2007). On the other hand, to our knowledge no study has explicitly focussed on the potential relationships between endogenous fluctuation and invasibility windows.

In the present paper, we study how endogenous oscillation of population density can affect the success of invasion. In a previous study (Caplat et al. 2008), we introduced FORSITE, an individual-, rule-based model that details how dispersal and competition modes affect spatial and temporal tree dynamics. We found that pure symmetric competition (i.e. when the competition strength an individual exerts on other members of the population does not depend on the individual's size Pacala and Weiner 1991) creates strong oscillations in a tree population, while asymmetric competition (when larger trees exert greater competitive pressures on smaller trees than vice versa) lead to a durable steady state in population size. In forest ecosystems, competition for light, which explains a large part of the community structure, causes asymmetric competition (i.e. taller trees get more light than shorter trees). However, nutrients like nitrogen, or water supply, can also be limiting factors, particularly 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 can make competition more symmetric between large and small individuals (Berntson and Wayne 2000). The issue of type of competition is thus relevant when dealing with forest populations, communities and landscapes. Here we are interested in seeing how symmetric competition can increase the risk of invasion by producing cycles in the resident population.

Competitive symmetry is but one of many mechanisms which has been shown to lead to oscillatory population dynamics in models (Caplat et al. 2008). Population oscillation is in fact a relatively frequently documented pattern in many different kinds of populations (Greenman et al. 2005). As a consequence, one can ask if all mechanisms leading to population oscillation are equal in their contribution to invasibility. For that reason we include in our study another mechanism that causes populations to oscillate: mast seeding. Mast seeding is the phenomenon of massive production of seeds at intermittent intervals that is synchronized within a species across large areas (Schnurr et al. 2002; Lamontagne and Boutin 2007). Many tree species exhibit this phenomenon, from the well known bamboo to northern temperate forest species (Frey et al. 2007). In its broad definition, masting can be viewed as any fluctuation in seed production caused by endogenous and exogenous factors (e.g. climate). However, it is more specifically defined as an endogenous synchronization, operating at the species level as a result of selection (Keeley and Bond 1999; Schnurr et al. 2002); this is the definition we adopt here, in order to avoid confusion with fecundity oscillations caused by the environment, which has been well studied elsewhere. Masting synchrony can have important consequences on forest dynamics through increased or decreased seed predation (Keeley and Bond 1999; Schnurr et al. 2002). Another potential effect of fecundity oscillation is an increase of a population's sensitivity to invasion (Takenaka 2006; Frey et al. 2007), which, as far as we know, has not been studied explicitly. A population experiencing mast seeding should exhibit important variation of seedling and adult density over time, favouring the establishment of a newcomer through the fluctuation of available resource (Davis et al. 2000; Schoolmaster and Snyder 2007).

In the present paper, we use a two-species version of the FORSITE model (FORSITE-INV) to test (1) whether competition symmetry affects the fate of an invasion, (2) how the oscillation of the resident population reacts to the invasion as dependent on the timing of the arrival of the invader, and (3) whether another source of endogenous fluctuation (seed masting) leads to qualitatively the same results as competition symmetry. Although approaching these questions from a clear theoretical angle, we design the system to enhance the applicability of real cases of invasions (accidental introduction of propagules, plantation of ornamental trees).

Model description

Purpose

FORSITE-INV simulates the effects of tree–tree interactions in a "resident–invader" two-species system. Unlike most theoretical plant simulation models of interspecific competition (Cosner and Lazer 1984; Namba and Takahashi 1993; Chesson 2000; Laird and Schamp 2006), in which competition strength is governed by synthetic parameters defined at the species level, we simulate competition as the outcome of several mechanisms operating at the individual level. An important feature is that FORSITE-INV does not differentiate between intra- and interspecific competition (that is, both species are symmetric in their interactions), yet species can dominate due to better growth or dispersal (that is, the interactions between individual trees can have a symmetric or asymmetric competitive relationship to their neighbours through resource use, as can be found in forest models such as BEFORE, Rademacher et al. 2004). However, FORSITE-INV 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).

Implementation

FORSITE-INV is implemented on the modelling platform CORMAS 2008 (Bousquet et al. 1998) using the VisualWorks environment (VW7.4nc, Cincom Smalltalk®). This platform allows flexible designs, and allows implementation of individual-based stochastic dynamics in a spatial, dynamic context. The code is available upon request by contacting the corresponding author.

State variables and scales

The model includes two hierarchical levels: individual trees and habitat cells. Both tree species are simulated the same way, with different parameter values (defined at the species level, see Table 1). Individuals are defined by the following state variables: species, identity number, age, and height. They are distributed on a homogeneous, torroidal grid of 20 × 20 hexagonal habitat cells. The choice of cell diameter depends in the modelled system and was set to the scale of the competitive neighbourhood, which we fixed at 20 m (i.e. the size of a large canopy tree crown, Table 1).

Process overview and scheduling

The model proceeds in annual time steps. Within each year every tree consumes a theoretical resource from its habitat, grows, reproduces (if it has reached sexual maturity), and may die. Resource uptake is a function of the density of competing individuals within the habitat cell; growth is a function of resource uptake, and affects reproduction ability through fecundity and dispersal distance. Death may occur due to stresses from slow growth, caused by competition, or death may also occur at some constant rate (Table 1) due to other causes.

Submodels

A tree is affected by competition with its neighbours (individuals present in the same cell) for limited resources. The resource available r (ranging between 0 and 1) for a given tree is affected by the density of taller individuals within the same habitat cell $(N_{H>Hi})$ through the parameter h, and by the density of individuals smaller or of the same size within the same habitat cell $(N_{H\leq Hi})$ through the parameter s:

$$r = e^{-C} \tag{1}$$

with

$$C = \frac{N_{H>Hi}}{h} + \frac{N_{H\leq Hi}}{s} \tag{2}$$

Parameters h and s allow us to vary the strength and type of competition. The case $s = h$ defines pure symmetrical competition (Weiner 1990) in which the resource is equally partitioned among individuals irrespective of their size, whereas the cases $s > h$ defines asymmetrical competition where an individual is less affected by smaller individuals than by larger individuals.

Table 1 Overview of the model parameters and values used in the present analysis

Level	Parameter	Description	Range of values
Model	x	Cell diameter	20
	N_c	Number of habitat cells	400
Species	R	Growth rate (m yr^{-1})	0.1–0.15
	$H_{\max}$	Maximum height (m)	25
	$f_{\max}$	Species maximum fecundity (seedlings yr^{-1})	5
	T_{m}	Masting time	10–50
	ϕ	Phase shift (for masting synchrony)	0–25
Individual tree	h	Strength of taller tree competition	30
	s	Strength of shorter tree competition	30
	M_0	Probability of mortality at zero growth	0.7
	M_d	Decay of growth-dependent mortality	0.8
	M_c	Intrinsic mortality	0.01
	H_{rep}	Height threshold for reproduction (m)	2
	f	Species maximum fecundity (seedlings yr^{-1})	1–9
	p	Probability of short distance dispersal	0.95
	α	Mode of the short dispersal kernel (m)	10
	c	Exponent in the height/dispersal function	1.5
	β	Mode of the long dispersal kernel. Defined by D and c	(500)
	D	Distance increment (m) by height increment for the height/dispersal function	2.5

Growth follows a Gompertz function (Moravie and Robert 2003; Zeide 2004) defining the annual height increment g as:

$$g = RH\ln\left(\frac{H_{\max}}{H}\right)r \tag{3}$$

where H is the tree height, $H_{\max}$ the tree maximum height, r the available resource and R the tree growth rate at maximum resource.

A tree becomes adult if it reaches a threshold height fixed at 2 m. An adult tree produces f seeds (Table 1). An adult tree produces f seeds depending on $f_{\max}$, its species' average fecundity, and its mast seeding behaviour. To simulate mast seeding, we introduce a sine function in the definition of $f_{\max}$. We define f_t the annual average fecundity of the species by:

$$f_t = f_{\max} + \lambda\sin(2\pi t/Tm + \phi) \tag{4}$$

where λ defines the amplitude of the fecundity cycle, ϕ the phase shift (expressed as a fraction of Pi), and T_m the length of the cycle (defined at the species level). This formulation allows considering cases in which two species have the same cycles but are out of phase (by fixing one species' ϕ to 0, and varying the other's), or cases in which the two species have different cycles. Note that the resulting f_t is defined at the species level, "forcing" fecundity oscillation at the individual level through synchrony, but can be seen as a biologically endogenous mechanism (as opposed to environmental variability). The individual fecundity f is defined for a given step t as:

$$f = f_t\frac{H}{H_{\max}} \tag{5}$$

where $f_{\max}$ is the species maximum fecundity. Dispersal is defined for both species as a double exponential (mixed) kernel, with a typical fat-tailed shape that allows us to take account of the rare but important long distance events (Clark et al. 1998; Higgins et al. 2000; Debain et al. 2007). The density of probability for a single seed is given for d (distance from the seed source) by the following:

$$P(d) = \frac{p}{2\pi\alpha}e^{\left(-\frac{d}{\alpha}\right)} + \frac{(1-p)}{2\pi\beta}e^{\left(-\frac{d}{\beta}\right)} \tag{6}$$

The first term gives the probability of seeds being dispersed at short distance (proportion p of the seeds, p being defined at the species level), while the second represents long distance dispersal (proportion $(1 - p)$). This function was shown by Higgins and Cain (2002) to allow great flexibility in dispersal modelling: with $p = 1$ one can simulate a local dispersal case, whereas with $p = 0$ and b bigger than the size of the grid one can simulate a global dispersal case. Parameters α and β (modes of respectively short distance and long distance dispersal kernel, Table 1) are constant that we define following Debain et al. (2007). Seeds germinate (with a 100% rate) the year following dispersal and start to grow from an initial height of 2 cm following (3). For the sake of simplicity, growth parameters for seedlings are assumed to follow the same rules as adults (which should not affect growth trajectories as the growth curve at young age is almost linear).

Trees die according to two processes: (1) intrinsic mortality representing all causes of mortality which are not related to growth (senescence, disturbances occurring at the individual level; Keane et al. 2001). Each individual dies with a constant probability Mi per year; (2) growth dependent mortality affecting trees that grow too slowly. This effect has been found in forest ecosystems due to limits in the individual ability to cope with suppressed growth (Keane et al. 2001):

$$m = M_0 e^{-M_d g} \tag{7}$$

where M_0 is the probability of mortality at zero growth, M_d the decay of growth dependent mortality, I_h the annual height increment, and m the probability of death per year. Complementary information about the model can be found in Caplat et al. (2008).

Simulations

Our aim is to test the effects of population size oscillations of the resident species on invasibility. We thus study cases in which the invader and resident are identical with respect to traits that should affect competitive ability. This approach is similar to the classical lottery model in which species success is related to local seedling density (Chesson 2000; Snyder and Chesson 2003), although it does not include any a priori spatial or temporal variation in resource distribution. This "perfect similarity" case can thus be described as a null hypothesis since any competitive advantage added to the invader could only increase its chances of successful establishment. Indeed, according to the standard invasion criterion (Chesson 2000), in such a case (similar species with homogenous resource) a species with initial low density should not invade. To check the qualitative behaviour of the model we also run simulations corresponding to a "classical case" of invasion, in which the invader is characterized by a higher growth rate than the resident (i.e. individual tree annual height increment is larger; see Table 1). This case can be seen as a translation of Tilman's R* rule (Tilman 1994) in which the invader is advantaged by an ability to exploit the resource more efficiently than the resident.

Simulations all follow the same basic design: seeds of the resident species are uniformly distributed over the grid, and the model runs until the population oscillates about a constant average value, or simply reaches an approximately constant equilibrium population size. Then, for 50 steps after a "time of first introduction" t_{init}, seeds of the invader species are distributed uniformly over the grid, with an average density (number of seeds per cell) N_{init} (Table 1). This operates a constant propagule pressure which can mimic two realistic scenarios: accidental introduction of seeds by animals (e.g. via livestock) over several years, or plantation of trees (e.g. via restoration), which effectively disperses seeds during their adult life. A simulation is considered finished when one of the two species goes extinct, or at $t = 8{,}000$ years if neither species has gone extinct by then. Thus we define three potential "fates" for each simulation: successful invasion, in which the invader completely excludes the resident (leading to extinction of the resident); extinction of the invader, i.e. failed invasion in which the invader population crashes before the end of the simulation; coexistence, when both populations are still present at $t = 8{,}000$ years. We run 200 simulations for each set of parameter values (limited due to computational restrictions), which allows us to determine the relative frequency of the three invasion outcome types as a function of the simulation parameters. We record the time to extinction for one or the other species (thereafter "extinction time"), and we analyse with an analysis of variance ("aov" function under R "stats" package) including as covariates the model parameters under focus (see below). Individual effect of parameters is tested with a chi-square test (chisq-test function under R "stats" package) run on the 200 replicates for each simulation.

Effects of competition symmetry

We define two sub-cases: runs with symmetric competition (a tree growth's rate is affected by its neighbours but with no dependence on their height) and runs with asymmetric competition (a tree's growth rate is affected only by taller neighbours). We test the effects of time of introduction (t_{init}, three values) and initial density of invader (N_{init}, three values) for each of the sub-cases (Table 2).

Effects of seed masting

Here we define three sub-cases representing different possibilities of masting synchrony. "Out of phase" masting occurs when the phase-shift ϕ (see Eq. 4 above) is Pi; "In phase" masting occurs when the phase-shift ϕ is equal to 0, and for the "resident only" sub-case only the resident species exhibit masting synchrony. For each of these three sub-cases we test the effects of time of introduction (Fig. 1; $t_{\mathrm{init}} = 80, 130$), initial density of invader ($N_{\mathrm{init}} = 5, 10, 50$), and masting time ($T_m = 10, 20, 50$).

Results

At very low initial density of invaders N_{init} (lower than two, not shown), invasion always fails due to stochastic fade-out (i.e. the invader population crashes after several decades). This is true for all the simulations. The following results are only for cases where N_{init} is sufficiently high to prevent these early extinctions.

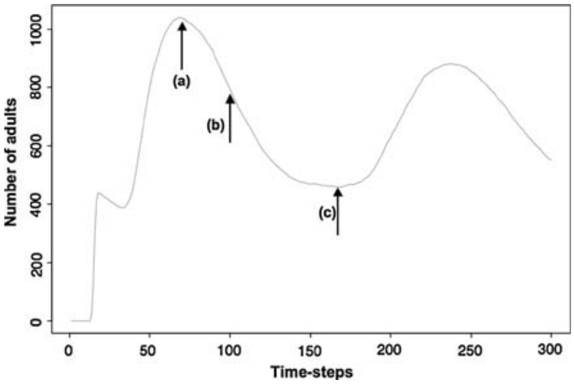


Fig. 1 Timing of the different introductions relative to the resident population dynamics. a "peak" $T_{\mathrm{init}} = 80$, b "intermediate" $T_{\mathrm{init}} = 110$, c "valley" $T_{\mathrm{init}} = 140$

Classical case with increased invasiveness

When the invader species is advantaged by a higher growth rate (Fig. 2), it always invades the landscape grid, irrespective of timing of introduction or type of competition, leading eventually to the exclusion of the resident species. However, the time needed to exclude the resident is on average shorter with symmetric competition (Fig. 2, bottom) than with asymmetric competition (Fig. 2, top).

Effect of competition symmetry

In the "perfect similarity case" where the two species have identical parameter values, initial densities that are sufficiently high to avoid early stochastic fade-out do not necessarily ensure invasion success. Indeed, for the same set of parameters, presumably due to

Table 2 Effect of time of introduction, density of invader, and competition type on the frequency of invader extinction (top value), successful invasion (with exclusion of the resident species; middle value) and long-term coexistence (bottom value), in the case of "perfect similarity"

Competition	Symmetric			Asymmetric		
	$t_{\mathrm{init}} = 80$	$t_{\mathrm{init}} = 110$	$t_{\mathrm{init}} = 130$	$t_{\mathrm{init}} = 80$	$t_{\mathrm{init}} = 110$	$t_{\mathrm{init}} = 130$
N_{init}						
5	0.39	0.27	0.80	0.79	0.70	0.78
	0.52	0.50	0.14	0.00	0.00	0.00
	0.09	0.23	0.06	0.21	0.30	0.22
10	0.27	0.70	0.95	0.63	0.65	0.62
	0.63	0.00	0.04	0.00	0.00	0.00
	0.10	0.30	0.01	0.37	0.35	0.38
20	0.15	0.48	0.94	0.44	0.48	0.45
	0.80	0.42	0.05	0.00	0.42	0.00
	0.05	0.10	0.01	0.56	0.10	0.55

stochastic effects, three invasion outcome types can be observed (Fig. 3): (a) extinction of the invader, (b) successful invasion (leading to extinction of the resident species); and (c) long term-coexistence characterized by phase shifted oscillations. It is important to note that, in cases where outcome (c) is reported, one or the other species may actually go extinct at some point well beyond the cutoff time of $t = 8{,}000$ years.

The relative frequency of the three different outcomes with different parameter values (Table 2) show an effect of competition type, t_{init} and N_{init} on the invasion dynamics. When competition is asymmetric, invasions are never successful (Table 2; Fig. 4). However, when competition is symmetric, all three behaviours are observed and an effect of both N_{init} and t_{init} becomes apparent (Table 2; Fig. 5). Figure 5 shows how the relative effects of N_{init} and t_{init} are contrasted between the cases with symmetric competition, and the cases with asymmetric competition. When competition is symmetric, there is a strong effect of the time of introduction. When introduced at a peak in the resident dynamics ($t_{\text{init}} = 130$) the invader almost never drives the resident species to extinction. On the other hand, the frequency of successful invasion is higher than 0.5 for introductions that occur in a valley in the resident dynamics ($t_{\text{init}} = 80$, Table 2; Fig. 5). When competition is asymmetric (Fig. 5, bottom), no effect of t_{init} can

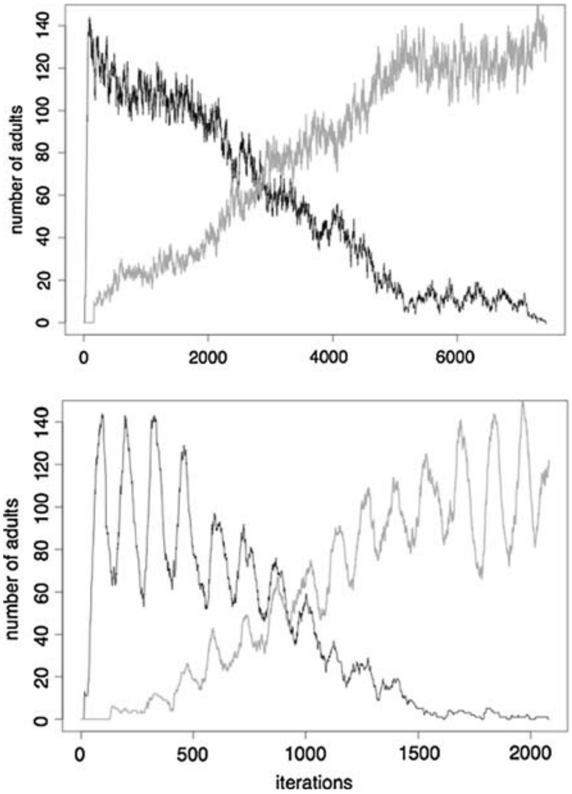
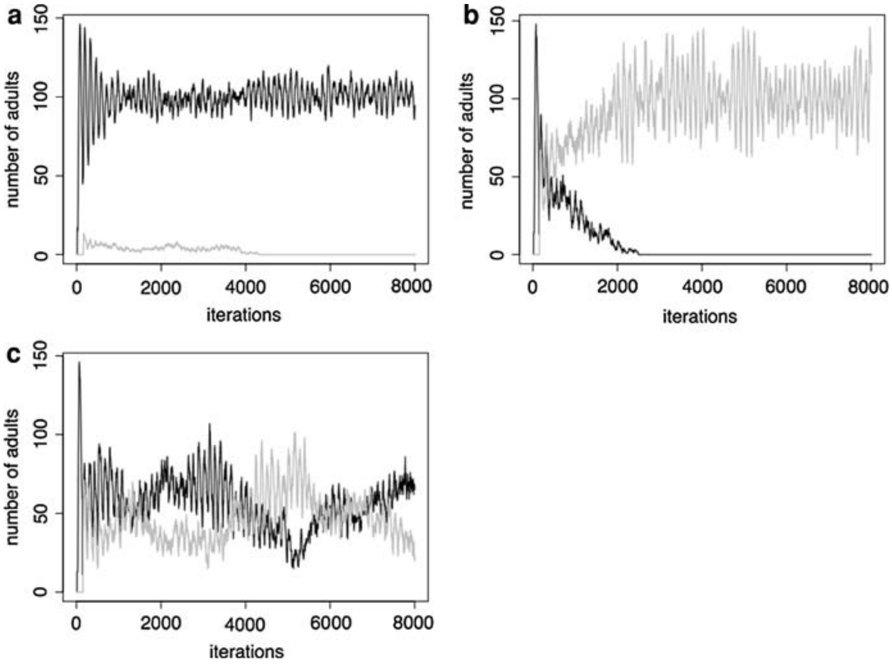


Fig. 2 Two-species dynamics when the invader (*in grey*) has a competitive advantage (higher growth rate) over the resident (*in black*). (*Top*) asymmetric competition ($a = 30$, $s = 40{,}000$); (*bottom*) symmetric competition ($a = 100$, $s = 100$)

Fig. 3 Different model outcomes obtained with the same parameters (symmetric competition, $t_{\text{init}} = 130$, and $N_{\text{init}} = 20$). **a** Extinction of the invader, **b** successful invasion and **c** stable coexistence. *In black*, the resident species, in *grey* the invader



be observed, but despite the absence of successful invasions, there is a strong effect of density N_{init} on the frequency of coexistence.

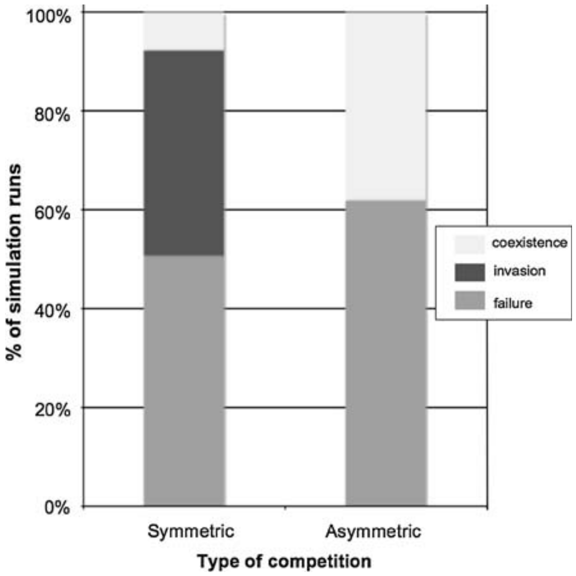


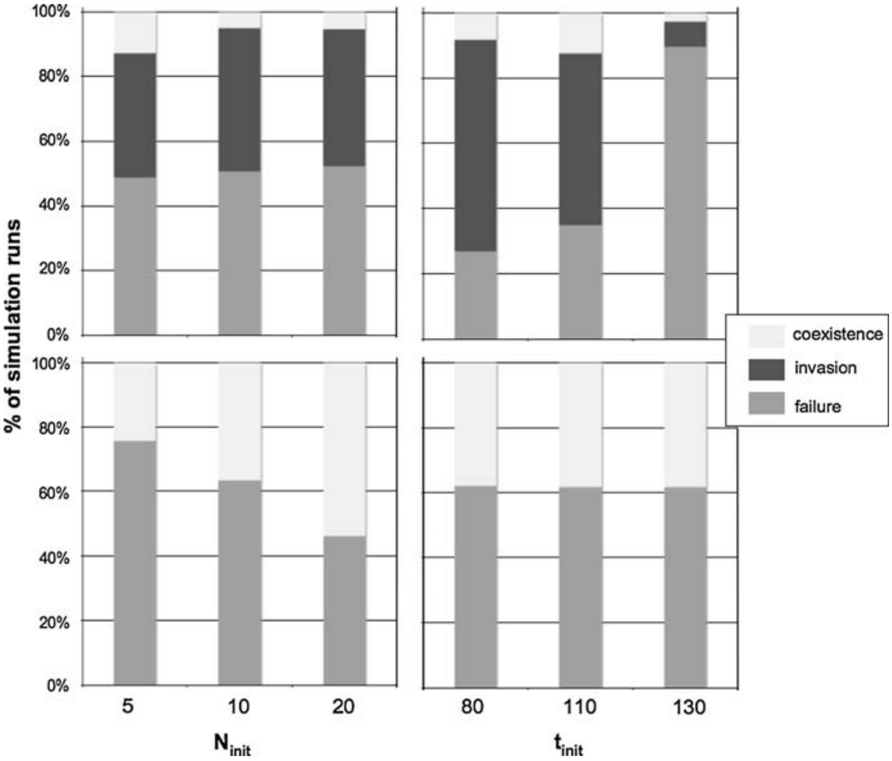
Fig. 4 Effect of competition type on the frequency of different invasion dynamics. Synthesis from all simulations (different parameter settings)

Time to extinction of both species is highly variable (ranging from 10 years after introduction of the invader to 8,000), with a coefficient of variation within replicates of 0.36. The ANOVA run on species' extinction times with competition type, t_{init} and N_{init} as covariates confirms a significant global effect ($P < 0.001$) of the three variables on mean time to extinction of one or the other species. Individual effects of the three variables on the invader's mean time to extinction confirm the results obtained with the frequency of model outcomes. Particularly, density N_{init} and the invader's time to extinction exhibit a positive relationship when competition is asymmetric, and negative when competition is symmetric (Fig. 6).

Effects of seed masting

When oscillation in fecundity is introduced, the synchronicity of seed masting between the two species (defined by the phase shift ϕ) determines the outcome of invasion. If the species are perfectly out-of-phase ($\phi = Pi$) the invader always establishes (Fig. 7), and the two species exhibit a double-phase oscillation

Fig. 5 Effect of time of introduction t_{init} and initial density of invader N_{init} on the frequency of model outcomes, with symmetric (*top panels*) and asymmetric (*bottom panels*) competition



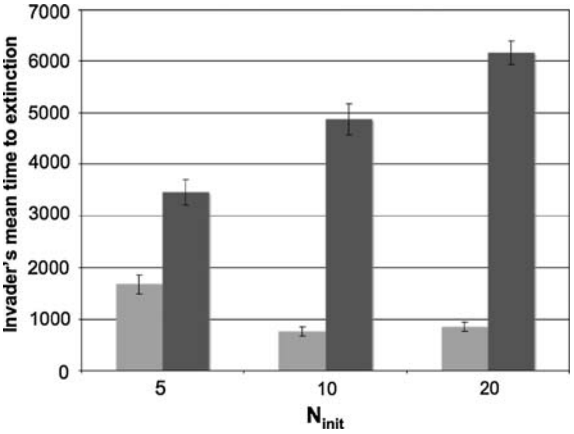


Fig. 6 Effect of competition type (symmetric competition: *left columns*, asymmetric competition: *right columns*) and initial density of invader N_{init} on the invader's mean time to extinction. *Error bars* indicate the standard error for each value. Effects of competition type and N_{init} are all significant ($P < 0.001$) with a chi-square test on 200 replicates

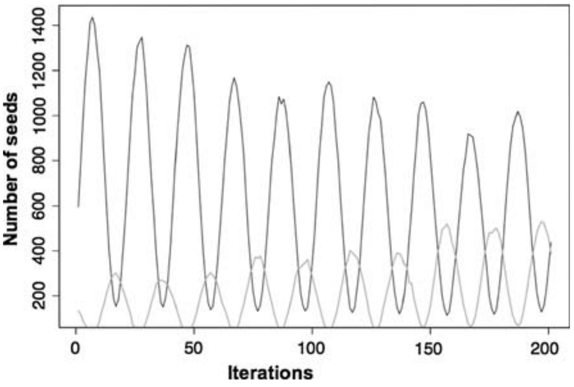


Fig. 7 Dynamics of tree seed production over time showing the establishment of the invader (*grey*) when its masting is out of phase with the resident (*black*). ($t_{\text{init}} = 80$, $N_{\text{init}} = 10$, $T_{\text{m}} = 20$, and $\phi = 10$)

(Fig. 3c), both reaching the end of the simulation regardless of the simulation settings (Fig. 8, left column). If the species are in phase ($\phi = 0$), both outcomes of failed invasion or coexistence are observed (Fig. 8, middle column). When only the invader exhibits seed masting, the invader always takes the landscape over (Fig. 8, right column). The ANOVA run on species' extinction times with $T_m\phi$, t_{init} and N_{init} and their interactions as covariables confirms these results as a significant effect ($P < 0.001$) is found only for the interaction between phase shift ϕ and masting period T_m.

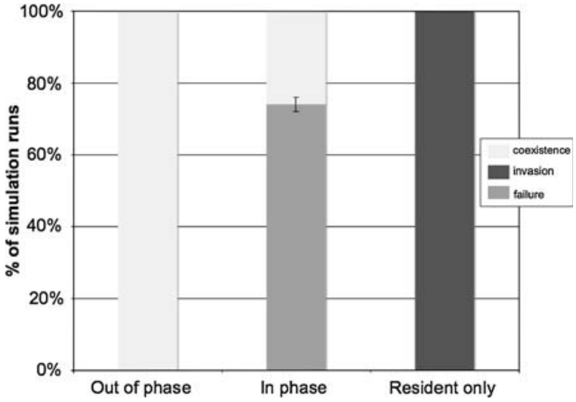


Fig. 8 Effect of masting synchrony on the frequency of invasion outcomes, regrouped from different simulations settings. The *error bar* indicates the dispersion of values between simulations

Discussion

Resource fluctuation theory, advanced by Davis et al. (2000), stipulates "a plant community becomes more susceptible to invasion whenever there is an increase in unused resources" (Davis et al. 2000, p. 2). While several studies have demonstrated the plausibility of this theory when dealing with environmental heterogeneity, we chose to study the effect of population-based (endogenous) fluctuations, by comparing two mechanisms (symmetric competition and mast seeding) that lead populations to oscillate. Our approach follows from the idea of Davis et al. (2000), but focuses on the mechanisms that lead to unused resources, creating invasibility windows (Drake et al. 2006).

A neutral model for invasion

Coexistence models (Pacala and Tilman 1994; Hurtt and Pacala 1995; Durrett and Levin 1998; Bolker and Pacala 1999) define how different strategies can allow an invader (a species introduced at low densities) to coexist with a resident species (already present at high density). The description of what "competition" is in these models is often extremely simple (Adler and Mosquera 2000): species are often ranked as phenomenologically "inferior" or "superior" competitors, depending on their probability to recruit when present at the same seedling density. While this lends considerable transparency to the models, this approach does not leave the meaning of "competitive" very clear: Grime (1977) defined as "competitive" a species growing fast enough to exploit local resources before other species, whereas for (Bolker et al. 2003) this characterizes an inferior competitor exhibiting a spatial successional niche strategy. Is a good competitor a species that can take over when another species is already present, grow faster than other species or reduce the resource more efficiently? The individual-based approach avoids defining competition phenomenologically, and instead focus on a range of mechanisms that can lead to higher or lower chance of establishment in the presence of other individuals. In this particular case, we explore a case in which two species are identical with respect to key parameters known to influence invasibility (in a way similar to the study of evolutionary branching and phenotypic diversity when there is no variation in fitness, Geritz et al. (1998), but initial differences in invader density or time of introduction (in relation to the cyclic dynamic of the resident) affects the fate of the system. The interest of exploring invasions with perfect similarity is double: (1) it can be seen as a "null" assumption, as any competitive advantage added to the invader could only increase its chances of successful establishment, (2) in numerous cases of alien species invasion (Sax et al. 2007), or shifted-niche caused by environmental changes, it is impossible to assess the invasiveness of a species, and an invader can be in many aspects similar to a resident species, at least in terms of the traits usually considered as related to competitiveness (Richardson and Pysek 2006). This approach provides a "best case" scenario to assess the risk of invasion, knowing that the range of conditions that lead to successful invasion can be only widened by a difference in species' traits.

Invasibility versus invasiveness

FORSITE-INV simulations confirm that oscillating resident populations (caused by competition symmetry) are susceptible to invasion under conditions that would be harmless if the resident population size was stable over time. Indeed, not only do invasions spread more quickly when an "aggressive" competitor is introduced, but they can also occur even if the invader is identical to the resident species in all traits relevant for the dynamics. Successful invasions not related to competitive advantage can happen due to temporal population oscillations in the resident population that create windows of opportunity for the invader species by creating a surplus of limiting resource. Indeed, our analysis show that, when resident population oscillates due to symmetric competition, introduction of an invader is more likely to succeed when it occurs with a "valley" in the resident's dynamics, and is overall variable over time. This phenomenon is made possible by very difficult conditions for the invader in our system, as it is introduced only at the stage of seeds and for a short time. When oscillations are caused by a mechanism working at the species level (masting synchrony), their effect on invasion outcome is even stronger than with symmetric competition: the phase-shift of the two species' oscillations completely determines invasion success. And if only the resident exhibit masting synchrony, the invader has full advantage and always takes over the landscape. Coexistence is thus highly constrained by the dynamics of the resident. By fixing a null invasiveness (of the introduced species), we show the importance of invasibility (of the resident community) in biological invasions. Numerous theoretical and empirical studies have shown the potential of traits as dispersal, fecundity or short life-span to promote invasiveness (Sakai et al. 2001; Richardson and Pysek 2006), but because only a few traits have consistently been identified as predictors of invasion success (Küster et al. 2008) for conservation purpose it might be easier to assess a given community's invasibility (Charret et al. 2007). For that reason, it seems crucial to understand how invasibility works, even in the absence of environmental variation, and our results confirm the multiplicity of mechanisms underlying this notion.

Individual-based approach and mechanisms

When cycles are caused by competition symmetry, the key phase for the invader is establishment. When introduced in a "peak" of resident density, the competition exerted by resident individuals is very high, and prevents seedlings from growing (Caplat et al. 2008). The introduced seedlings die out after a few years. When introduced in a "valley", on the other hand, the invader is able to establish as the competition exerted by the resident population is at its lowest. However, if the initial density of the invader is not high enough, the invader cannot take over and may die out. Once established, the invader follows the same dynamics as the resident, since inter-specific and intra-specific competition are of equivalent strength. Because oscillations emerge from individual interactions, the invader cycles in phase with the resident, and the success of one or the other is highly stochastic, as indicated by the three possible model outcomes (Fig. 2). Due to slight differences in both species' density or age structure, after the establishment phase one species can dominate and exclude the other. At this stage, it is interesting to note that because of strong competitive interactions in the model a high density of invader can negatively affect its success (as expressed through the mean time to extinction, Fig. 6). In many cases though, a double-phased oscillation ensues, with the two species exhibiting a perfect negative synchronicity (Vandermeer 2006). This behaviour, particularly within a model that showed its robustness in other contexts (Caplat et al. 2008), opens exciting perspectives for theoretical as well as applied studies. Because of stochasticity in individual interactions, the invader has the possibility to expand to some extent with most of the settings, however, its chance of success depends highly on the simulation settings. Invader's survival also likely benefits from the storage effect (Chesson 2000; Higgins et al. 2000) due to its iteroparous adults. Consequently different outcomes appear with different frequencies. A thorough analysis of the influence of parameters on population dynamics (for instance using the survival analysis presented in Grimm and Wissel 2004), or a comparison between FORSITE and a mathematical (analytical) population dynamics model should shed light on this behaviour, but is beyond the scope of the present work.

On the other hand, seed masting is an intrinsic characteristic of the species, and does not change with species interactions (viewed from a modeller's point of view, it is "forced"). Therefore, oscillations of the resident population are not affected by the increase of competition when the invader is introduced, and then provide recurrent opportunities for the invader that can establish regardless of the time of introduction. An out-of-phase oscillation of the two populations provides the ideal condition for stable coexistence, since one population is at its maximum of resource consumption while the other is at its minimum. However, when the cycles are in phase, the dynamics are comparable to the case with competition-based oscillations: the two species compete with each other and the outcome is stochastic. If only the resident species exhibit seed masting (and thus cycles), the invader can establish when competition is low, but then will not "recede" to let the resident species increase in density, leading to a successful invasion.

These findings can have strong implications for real cases of species invasion or reintroduction, especially since many reintroduction plans attempt to take advantage of ecological succession or resident species dynamics (Maunder 1992). When planning an introduction or trying to prevent an invasion, one may check for the presence of cycles in the densities of the species that compose the resident community. For instance, recurring introduction of seeds over a cycle length might enhance the success of invasions/restoration strategies. Cycles linked to the presence of symmetric competition might be rare, as this phenomenon is likely highly context-dependent (since competition asymmetry dominates most forests interactions). Seed-masting, on the other hand, is a common phenomenon (Frey et al. 2007; Lamontagne and Boutin 2007) and appears in our study as an important mechanism that can increase invasibility. In the Mediterranean mountains of Southern France, black pine (*Pinus nigra*) is considered an invader and out-competes the native Scots pine (*P. sylvestris*) (Boulant et al. 2008); both black pine superior invasiveness (high fecundity and growth rate) and the tendency of Scots pine to exhibit seed masting may contribute to the dynamics (J. Lepart, personal communication). In other contexts, simple succession processes favouring the establishment of large cohorts can create synchrony in reproduction (since all trees reach the age of first reproduction about the same age). Unfortunately, in most ecosystems oscillations of fecundity might be difficult to detect due to the lack of long-term studies (Muko and Iwasa 2008). Furthermore, regular oscillations as described in our model are likely to be hidden by other types of fluctuation (e.g. caused by climatic variability, environmental variation). The authors hope that continued work on using theoretical approaches, including individual-based simulations, to inform the planning of empirical studies may mitigate some of the issues associated with the need for very long timeframes in empirical ecological research.

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References

Adler FR, Mosquera J (2000) Is space necessary? Interference competition and limits to biodiversity. Ecology 81:3226–3232

Barlow ND, Kean JM (2004) Resource abundance and invasiveness: a simple model. Biol Invasions 6:261–268. doi:10.1023/B:BINV.0000034590.77961.6e

Bauer S, Wyszomirski T, Berger U, Hildenbrandt H, Grimm V (2004) Asymmetric competition as a natural outcome of neighbour interactions among plants: results from the field-of-neighbourhood modelling approach. Plant Ecol 170:135–145

Berntson GM, Wayne PM (2000) Characterizing the size dependence of resource acquisition within crowded plant populations. Ecology 81:1072–1085

Bolker BM, Pacala SW (1999) Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. Am Nat 153:575–602. doi:10.1086/303199

Bolker BM, Pacala SW, Neuhauser C (2003) Spatial dynamics in model plant communities: what do we really know? Am Nat 162:135–148. doi:10.1086/376575

Boulant N, Kunstler G, Rambal S, Lepart J (2008) Seed supply, drought, and grazing determine spatio-temporal patterns of recruitment for native and introduced invasive pines in grasslands. Divers Distrib 14:862–874. doi:10.1111/j.1472-4642.2008.00494.x

Bousquet F, Bakam I, Proton H, Le Page C (1998) Cormas: common-pool resources and multi-agent systems. Lect Notes Artif Intell 1416:826–838

Caplat P, Anand M, Bauch C (2008) Symmetric competition causes population oscillations in an individual-based model of forest dynamics. Ecol Model 211:491–500. doi:10.1016/j.ecolmodel.2007.10.002

Charret IC, Louzada JNC, Costa AT (2007) Individual-based model for coevolving competing populations. Phys Stat Mech Appl 385:249–254

Chesson P (2000) General theory of competitive coexistence in spatially-varying environments. Theor Popul Biol 58:211–237. doi:10.1006/tpbi.2000.1486

Cosner C, Lazer AC (1984) Stable coexistence states in the Volterra–Lotka competition model with diffusion. SIAM J Appl Math 44:1112–1132. doi:10.1137/0144080

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534. doi:10.1046/j.1365-2745.2000.00473.x

Debain S, Chadoeuf J, Curt T, Kunstler G, Lepart J (2007) Comparing effective dispersal in expanding population of *Pinus sylvestris* and *Pinus nigra* in calcareous grassland. Can J For Res 37:103–115. doi:10.1139/X06-265

Drake JM, Drury KLS, Lodge DM, Blukacz A, Yan ND, Dwyer G (2006) Demographic stochasticity, environmental variability, and windows of invasion risk for *Bythotrephes longimanus* in North America. Biol Invasions 8:843–861. doi:10.1007/s10530-005-4205-2

Durrett R, Levin S (1998) Spatial aspects of interspecific competition. Theor Popul Biol 53:30–43. doi:10.1006/tpbi.1997.1338

Eppstein MJ, Molofsky J (2007) Invasiveness in plant communities with feedbacks. Ecol Lett 10:253–263. doi:10.1111/j.1461-0248.2007.01017.x

Frey BR, Ashton MS, McKenna JJ, Ellum D, Finkral A (2007) Topographic and temporal patterns in tree seedling establishment, growth, and survival among masting species of southern New England mixed-deciduous forests. For Ecol Manag 245:54–63. doi:10.1016/j.foreco.2007.03.069

Geritz SAH, Kisdi E, Meszena G, Metz JAJ (1998) Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evol Ecol 12:35–57. doi:10.1023/A:1006554906681

Greenman JV, Benton TG, Boots M, White AR (2005) The evolution of oscillatory behavior in age-structured species. Am Nat 166:68–78. doi:10.1086/430640

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194. doi:10.1086/283244

Grimm V, Wissel C (2004) The intrinsic mean time to extinction: a unifying approach to analysing persistence and viability of populations. Oikos 105:501–511. doi:10.1111/j.0030-1299.2004.12606.x

Higgins SI, Richardson DM (1996) A review of models of alien plant spread. Ecol Model 87:249–265. doi:10.1016/0304-3800(95)00022-4

Higgins SI, Pickett STA, Bond WJ (2000) Predicting extinction risks for plants: environmental stochasticity can save declining populations. Trends Ecol Evol 15:516–520. doi:10.1016/S0169-5347(00)01993-5

Higgins SI, Cain ML (2002) Spatially realistic plant metapopulation models and the colonization-competition trade-off. J Ecol 90:616–626

Hurtt GC, Pacala SW (1995) The consequences of recruitment limitation—reconciling chance, history and competitive differences between plants. J Theor Biol 176:1–12. doi:10.1006/jtbi.1995.0170

Keane RE, Austin M, Field C, Huth A, Lexer MJ, Peters D, Solomon A, Wyckoff P (2001) Tree mortality in gap models: application to climate change. Clim Change 51:509–540. doi:10.1023/A:1012539409854

Keeley JE, Bond WJ (1999) Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. Am Nat 154:383–391. doi:10.1086/303243

Kinezaki N, Kawasaki K, Shigesada N (2006) Spatial dynamics of invasion in sinusoidally varying environments. Popul Ecol 48:263–270. doi:10.1007/s10144-006-0263-2

Kobe RK, Pacala SW, Silander JA, Canham CD (1995) Juvenile tree survivorship as a component of shade tolerance. Ecol Appl 5:517–532. doi:10.2307/1942040

Küster EC, Kuhn I, Bruelheide H, Klotz S (2008) Trait interactions help explain plant invasion success in the German flora. J Ecol 96:860–868. doi:10.1111/j.1365-2745.2008.01406.x

Laird RA, Schamp BS (2006) Competitive intransitivity promotes species coexistence. Am Nat 168:182–193. doi:10.1086/506259

Lamontagne JM, Boutin S (2007) Local-scale synchrony and variability in mast seed production patterns of *Picea glauca*. J Ecol 95:991–1000. doi:10.1111/j.1365-2745.2007.01266.x

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710. doi:10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2

Maunder M (1992) Plant reintroduction—an overview. Biodivers Conserv 1:51–61. doi:10.1007/BF00700250

Moravie MA, Robert A (2003) A model to assess relationships between forest dynamics and spatial structure. J Veg Sci 14:823–834. doi:10.1658/1100-9233(2003)014[0823:AMTARB]2.0.CO;2

Muko S, Iwasa Y (2008) Spatial heterogeneity of mortality and temporal fluctuation in fertility promote coexistence but not vice versa: a random-community approach. J Theor Biol 253:593–600. doi:10.1016/j.jtbi.2008.04.008

Myster RW (1993) Tree invasion and establishment in old fields at Hutcheson-memorial-forest. Bot Rev 59:251–272. doi:10.1007/BF02857418

Namba T, Takahashi S (1993) Competitive coexistence in a seasonally fluctuating environment II. Multiple stable states and invasion success. Theor Popul Biol 44:374–402. doi:10.1006/tpbi.1993.1033

Pacala SW, Tilman D (1994) Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. Am Nat 143:222–257. doi:10.1086/285602

Pacala SW, Weiner J (1991) Effects of competitive asymmetry on a local density model of plant interference. J Theor Biol 149:165–179. doi:10.1016/S0022-5193(05)80275-9

Pacala SW, Canham CD, Saponara J, Silander JA, Kobe RK, Ribbens E (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol Monogr 66:1–43. doi:10.2307/2963479

Pham AT, De Grandpré L, Gauthier S, Bergeron Y (2005) Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. Can J For Res 34:353–364. doi:10.1139/x03-265

Rademacher C, Neuert C, Grundmann V, Wissel C, Grimm V (2004) Reconstructing spatiotemporal dynamics of Central European natural beech forests: the rule-based forest model BEFORE. For Ecol Manag 194:349–368. doi:10.1016/j.foreco.2004.02.022

Reinhart KO, Maestre FT, Callaway RG (2006) Facilitation and inhibition of seedlings of an invasive tree (*Acer platanoides*) by different tree species in a mountain ecosystem. Biol Inv 8:231–240. doi:10.1007/s10530-004-5163-9

Richardson DM, Pysek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog Phys Geogr 30:409–431. doi:10.1191/0309133306pp490pr

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annu Rev Ecol Syst 32:305–332. doi:10.1146/annurev.ecolsys.32.081501.114037

Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hasting SA, Holt RD, Mayfield MM, O'Connor MI, Rice WR (2007) Ecological and evolutionary insights from species invasions. Trends Ecol Evol 22:465–471. doi:10.1016/j.tree.2007.06.009

Schnurr JL, Ostfeld RS, Canham CD (2002) Direct and indirect effects of masting on rodent populations and tree seed survival. Oikos 96:402–410. doi:10.1034/j.1600-0706.2002.960302.x

Schoolmaster DRJ, Snyder RE (2007) Invasibility in a spatiotemporally fluctuating environment is determined by the periodicity of fluctuations and resident turnover rates. Proc R Soc Lond B Biol Sci 274:1429–1435. doi:10.1098/rspb.2007.0118

Snyder RE, Chesson P (2003) Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. Ecol Lett 6:301–309. doi:10.1046/j.1461-0248.2003.00434.x

Takenaka A (2006) Dynamics of seedling populations and tree species coexistence in a forest: a simulation study. Ecol Res 21:356–363. doi:10.1007/s11284-006-0165-y

Tilman D (1994) Competition and biodiversity in spatially structured habitats. Ecology 75:2–16. doi:10.2307/1939377

Vandermeer J (2006) Oscillating populations and biodiversity maintenance. Bioscience 56:967–975. doi:10.1641/0006-3568(2006)56[967:OPABM]2.0.CO;2

Veltman CJ, Nee S, Crawley MJ (1996) Correlates of introduction success in exotic New Zealand birds. Am Nat 147:542–557. doi:10.1086/285865

Weiner J (1990) Asymmetric competition in plant-populations. Trends Ecol Evol 5:360–364. doi:10.1016/0169-5347(90)90095-U

Zeide B (2004) Intrinsic units in growth modelling. Ecol Model 175:249–259. doi:10.1016/j.ecolmodel.2003.10.017