

**IDEA AND  
PERSPECTIVE****Invasiveness in plant communities with feedbacks**

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**Abstract**

The detrimental effects of invasive plant species on ecosystems are well documented. While much research has focused on discovering ecological influences associated with invasiveness, it remains unclear how these influences interact, causing some introduced exotic species to become invasive threats. Here we develop a framework that incorporates the influences of propagule pressure, frequency independent growth rates, feedback relationships, resource competition and spatial scale of interactions. Our results show that these ecological influences interact in complex ways, resulting in expected outcomes ranging from inability to establish, to naturalization, to conditional invasion dependent on quantity and spatial distribution of propagules, to unconditional takeover. We propose a way to predict the likelihood of these four possible outcomes, for a species recently introduced into a given target community. Such information could enable conservation biologists to craft strategies and target remediation efforts more efficiently and effectively in order to help maintain biodiversity in ecological communities.

**Keywords**

Cellular automata, enemy release hypotheses, feedbacks, frequency dependence, Lotka–Volterra competition, predicting invasiveness, propagule pressure, spatially explicit models.

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**INTRODUCTION**

Introductions of non-native species can result in the replacement of native species by invasive non-native species within a community, resulting in significant detrimental ecological and economic impacts (Vitousek *et al.* 1997; Wilcove *et al.* 1998; Pimentel *et al.* 2005). Not all introduced species establish into new communities (Williamson & Fitter 1996) and moreover, of those that successfully establish, a large fraction becomes naturalized into the resident community rather than invasive (Richardson *et al.* 2000). There have been several attempts to determine statistical associations between invasiveness and various life history traits (e.g. Scott & Panetta 1993; Reichard & Hamilton 1997; Kolar & Lodge 2001) or taxonomic relationships (e.g. Daehler 1998; Pyšek 1998). While such correlative approaches can suggest plausible hypothesis for further testing, they are not sufficiently mechanistic to predict whether any particular introduced species will become invasive. Furthermore, there is often no clear distinction made between those plants that completely displace native communities and those that establish and encroach but ultimately become naturalized and coexist at some equilibrium frequency (Richardson *et al.* 2000).

In contrast to retrospective analyses, empirical studies have focused on the ecological mechanisms behind invasiveness. For example, the enemy release hypothesis of invasiveness (Keane & Crawley 2002) posits that introduced plants leave their native pests behind when they are introduced into a new community, thereby permitting a reallocation of resources away from enemy defence and towards growth of the introduced species (compensatory release) and/or a direct increase in growth or survivorship (regulatory release) (Colautti *et al.* 2004). Release from native enemies may also permit evolution towards capacity for higher growth at the expense of defence (Blossey & Notzold 1995). There is a growing body of evidence that the magnitude and direction of feedbacks that plants experience with soil biota in the target community can impact the ability of an introduced species to invade successfully (e.g. Klironomos 2002; Bever 2003; Reinhart *et al.* 2003; Callaway *et al.* 2004a,b; Knevel *et al.* 2004; Reinhart & Callaway 2004). For recent reviews, see Wolfe & Klironomos 2005; Reinhart & Callaway 2006). Other types of frequency dependent feedback mechanisms may also affect invasiveness, including abiotic soil changes caused by alterations in rates of accumulation or decomposition of leaf litter (Kourtev *et al.* 1999; Gould & Gorchov 2000; Ashton *et al.* 2005),

attraction of pollinators (Smithson & McNair 1996; Ågren 1996), or even mechanical benefits from clustering of seedlings (Molofsky *et al.* 2000). To make the situation more complicated, changes in feedbacks from native to introduced ranges are not necessarily consistent for different types of feedback mechanisms. Agrawal *et al.* (2005) studied 30 native and introduced plant species and found that the degree of enemy release in introduced plants varied between enemy guilds, as well as in space and time. Along with these feedback mechanisms, propagule pressure (comprising both temporal frequency and size of introductions) can also be important for early establishment of introduced species, and thus ultimately for invasion (Kolar & Lodge 2001; Lockwood *et al.* 2005; Von Holle & Simberloff 2005).

As many competing influences may be involved in determining invasiveness, theoretical models are needed for exploring the complex nature of the interaction of these ecological influences (Hastings *et al.* 2005). Recently, Levine *et al.* (2006) developed a one-dimensional, discrete-in-time, single-species integrodifference model to examine the likelihood that local intraspecific feedbacks between an invading species and the soil environment affect the rate of spread of the invasion, assuming a one-generation time lag for feedback effects. They conclude that while intraspecific feedbacks do affect the density of the invaders, they are not likely to affect the rate of invasive spread, based on the assumption that colonizers at the front of the invasion grow in soils not yet modified by feedback effects. However, short range dispersal mechanisms could mean that spreading invasive colonizers may land close enough to the invasion front so that their local interaction neighbourhoods overlap the boundary of species' clusters and affect the dynamics of cluster growth (e.g. Silander & Klepeis 1999), as modelled in Eppstein *et al.* (2006). Furthermore, interspecific feedback interactions between the invader and resident community, not included in the previous models of Levine *et al.* (2006) or Eppstein *et al.* (2006), could also affect the rate of invasive spread. Von Holle & Simberloff (2005) showed that success of propagules in the forest understory was, in fact, positively affected by density of the resident community, possibly due to increased soil moisture retention at higher plant densities during a period of drought. It may also be the case that local changes to the environment caused by the invading species (e.g. to the soil, light availability, litter cover, etc.) have a more negative effect on the resident species than on colonizing invaders near the front, thereby providing a net positive benefit for colonizing invaders ahead of the front (Silander & Klepeis 1999).

Despite the many important advances in understanding the potential causes of invasiveness, it remains unclear how the various ecological influences interact, and there is little theory to guide ecologists in predicting whether a particular introduced plant species is likely to become an invasive

threat that may warrant costly intervention. In this contribution, we develop a model for investigating the complex interactions between five critical ecological variables: (1) frequency independent suitability of the target habitat for individuals in both introduced and native resident species; (2) intra- and interspecific frequency dependent feedback relationships of introduced and native species in the target community; (3) competition for resources; (4) propagule number and spatial distribution; and (5) the spatially explicit nature of ecological interactions. This new model provides a framework for ecologists to examine the potential importance of various ecological influences, to validate model predictions against field and laboratory data (and determine where the model needs refinement), and to help gain a better understanding of how complex interactions in ecological influences can result in the emergence of invasiveness. The results also suggest a phenomenological approach for making specific predictions about which one of four possible scenarios will occur following an introduction: (1) extirpation of the introduced species from the new range; (2) establishment with subsequent naturalization (i.e. coexistence of native and introduced species); (3) conditional extirpation or invasion, dependent upon propagule number and spatial distribution, and (4) unconditional invasion (i.e. replacement of native with introduced species).

## MODEL DEVELOPMENT

We first develop a deterministic model in which we assume that the fitness of each species  $i$  in an  $s$ -species target community has a frequency independent component ( $\beta_i$ ) (species' differences in  $\beta$  correspond to inherent 'fitness inequalities', as defined by Chesson (2000), as well as frequency dependent species interaction feedback components ( $\alpha_{ij}$ ) [which can be 'stabilizing' (Chesson 2000) or 'destabilizing', depending on their relative signs and magnitudes]. For example, in plant communities with linear frequency dependence, where  $\alpha_{ij}$  is a (positive or negative) frequency dependence coefficient that represents the influence of the time-varying frequency of species  $j$  ( $F_j^t$ ) on the suitability of the environment for growth by species  $i$ , the quality of the habitat for colonization by species  $i$  at time  $t$  is as follows:

$$H_i^t = \beta_i + \sum_{j=1 \dots s} \alpha_{ij} F_j^t. \quad (1)$$

For brevity, we refer to  $H$  as 'fitness'. In previous work (Eppstein *et al.* 2006), we examined a simpler model that assumed identical maximum fitness for all species in the community (but different average fitnesses, when averaged over all frequencies). The reformulation in eqn (1) allows us

to examine the much broader parameter space described by the combined impacts of both frequency independent and frequency dependent terms. Assuming  $D_i^t$  is the population density of species  $i$  at time  $t$ , we define the quantity  $F_i^{t+1}$  as follows:

$$F_i^{t+1} = \frac{H_i^t D_i^t}{\sum_{j=1 \dots s} H_j^t D_j^t} \tag{2}$$

Note that since species frequencies at time  $t$  affect the probabilities of occupancy at time  $t + 1$ , there is effectively a one-generation lag in the frequency dependent feedback effects, consistent with the model of Levine *et al.* (2006). In an infinite population mean field model,  $F_i^{t+1}$  can be interpreted as a deterministic, discrete-in-time approximation of the expected frequency of species  $i$  at time  $t + 1$ . The predicted population growth rate  $r$  of species  $i$  from time step  $t$  to  $t + 1$  is then given by:

$$r_i^t = \frac{F_i^{t+1}}{F_i^t} \tag{3}$$

In a more general sense, a frequency dependent growth rate can be combined with resource-based competitive interactions in an  $s$ -species plant community. For example, with linear frequency dependence the equation for each species  $i$  is

$$\frac{dN_i}{dt} = \frac{\left( \beta_i + \sum_{j=1 \dots s} \alpha_{ij} \gamma_{ij} \frac{N_j}{K_j} \right) K_i}{\left( \beta_i + \sum_{j=1 \dots s} \alpha_{ij} \gamma_{ij} \frac{N_j}{K_j} \right) N_i + \sum_{j \neq i} \left[ \left( \beta_i + \sum_{j=1 \dots s} \alpha_{ij} \gamma_{ij} \frac{N_j}{K_j} \right) \gamma_{ij} N_j \right]} N_i \left[ 1 - \sum_{j=1 \dots s} \gamma_{ij} (1 - d_j) \frac{N_j}{K_j} \right] - d_i N_i, \tag{4}$$

where  $N_i$  is the number of individuals,  $d_i$  the probability of dying after propagules have been created (which may itself be a function of species' densities),  $\gamma_{ij}$  the competition coefficients [which may also be functions of species' density (Chesson 2000)] and  $K_j$  the carrying capacity. Note that, in eqn (4), frequencies are computed relative to the species-specific resource requirements. If there are no frequency dependent components to growth rate, eqn (4) reverts to the familiar Lotka–Volterra two-species competition model. Alternatively, in a community of annual plants ( $d_i = 1$ ) where competition is for space ( $K_i = K_j = \sum N_k, \forall k$ ) and all species require the same amount of space per individual ( $\gamma_{ij} = 1$ ), eqn (4) reduces to

$$\frac{dN_i}{dt} = \frac{H_i^t D_i^t}{\sum_{j=1 \dots s} H_j^t D_j^t} \frac{N_i}{F_i^t} \tag{5}$$

which is equivalent to eqns (1)–(3). For simplicity, we illustrate the implications of these equations for a two-species community, where species 1 (S1) represents the native species (or an amalgam of the native community), and species 2 (S2) is the introduced non-native species.

In a mean field model, the interaction neighbourhood is the entire community. However, in order to understand the effects of stochasticity, propagule pressure, and local vs. global spatial interaction neighbourhoods, we also implemented eqns (1)–(3) using a stochastic cellular automata. In this spatially explicit model, these equations are applied locally at all discrete spatial locations in the model, where  $F_i^t$  is computed within some local interaction neighbourhood, and  $D_i^t$  is computed within some local dispersal neighbourhood. For simplicity, we herein assume that interaction and dispersal neighbourhoods are equivalent, and that frequency and density are equal; i.e.  $D_i^t \equiv F_i^t$ . In the spatially explicit model, occupancy of a given location at time  $t + 1$  is determined stochastically with probability  $F_i^{t+1}$ , for each discrete location in the model. The expected number of individuals of species  $i$  in the spatially explicit population at time  $t + 1$  is simply the sum of the  $F_i^{t+1}$  over all discrete locations in the domain. In the spatially explicit model, eqn (3) is also computed for a given location, and  $r_i^t$  thus represents the expected increase in the population of species  $i$  in the local neighbourhood. Spatially explicit models were implemented in Matlab using  $100 \times 100$  cell stochastic

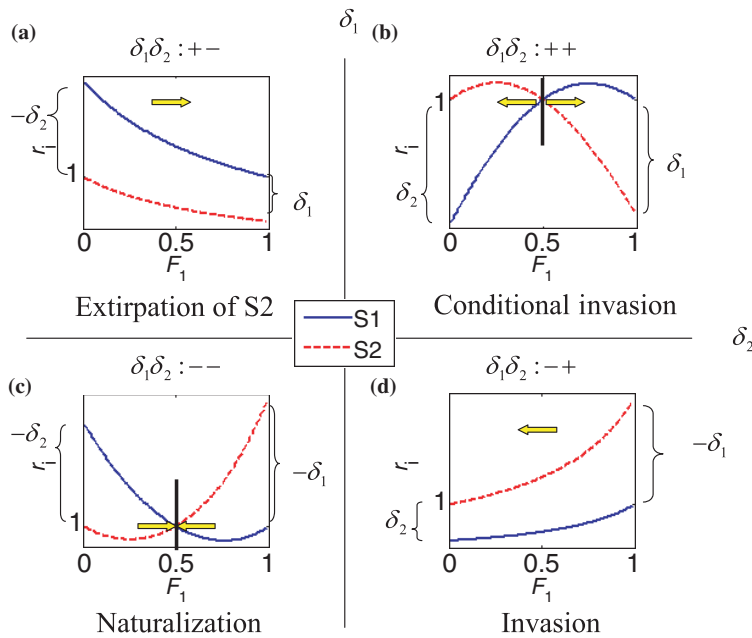
cellular automata with absorbing boundaries and either 9-cell ( $3 \times 3$ ) local neighbourhoods or 10 000-cell (mean field) neighbourhoods.

**RESULTS**

**Distinguishing different classes of outcomes**

In a two-species community, there are four classes of invasiveness (Fig. 1). These four classes are associated with the four possible combinations of signs of the differences  $\delta$  in the species' population growth rates  $r_i$  at two frequency extremes (e.g. at 99% S1 and at 1% S1), where frequencies are calculated at the spatial scale of neighbourhood interactions. Specifically, we calculate

$$\delta_1 = r_1|_{F_1=0.99} - r_2|_{F_1=0.99} \tag{6}$$



**Figure 1** Representative growth curves for the four classes of invasiveness corresponding to the four  $\delta_1\delta_2$  quadrants, defined by the signs of the differences in the predicted growth rates at the two frequency extremes. Arrows show expected directional changes in frequencies.

and

$$\delta_2 = r_2|_{F_1=0.01} - r_1|_{F_1=0.01}. \tag{7}$$

The outcomes predicted in the four  $\delta_1\delta_2$  quadrants are as follows:

*Extirpation quadrant*

When  $\delta_1$  is positive and  $\delta_2$  is negative (Fig. 1a), S2 cannot invade and is rapidly extirpated from the community, as the expected growth rate of S1 is higher than that of S2 at all frequencies. In the other three quadrants, S2 is also vulnerable to early extirpation due to stochastic effects when it is at low frequency, but in the event that S2 does become established the following outcomes are predicted.

*Conditional invasion quadrant*

When both  $\delta_1$  and  $\delta_2$  are positive (Fig. 1b), there exists an unstable equilibrium frequency at the intersection of the two growth curves, so one species or the other will dominate depending on initial frequencies (founder control), as indicated by the yellow arrows. In this quadrant, S2 may be able to invade and take over if propagule pressure is high enough such that the number of introduced individuals that survive to reproduce at the end of the first generation results in an  $F_1$  to the left of the unstable equilibrium point, but S2 is otherwise extirpated from the community.

*Naturalization quadrant*

When both  $\delta_1$  and  $\delta_2$  are negative (Fig. 1c), there exists a stable equilibrium frequency at the intersection point; thus,

the two species are predicted to coexist at the equilibrium frequency. Introduced species in this quadrant may still be considered problematic, if the stable equilibrium is far to the left.

*Unconditional invasion quadrant*

When  $\delta_1$  is negative and  $\delta_2$  is positive (Fig. 1d), S2 is predicted to invade and fully replace S1, as the growth rate of S2 is higher than that of S1 at all frequencies.

The four  $\delta_1\delta_2$  outcome quadrants occur regardless of the exact form of the model; for example, whether interactions are local or global (Bolker *et al.* 2003), whether growth rates are frequency independent (Bolker *et al.* 2003) or frequency dependence is linear (as in this paper) or nonlinear [e.g. through incorporation of an Allee affect (Taylor & Hastings 2005)], whether plants are annuals or perennials, or whether competition coefficients are equal to 1. However, the parametric conditions determining those quadrants will vary.

The well-known result for the classic Lotka–Volterra two-species competition equations is that the four  $\delta_1\delta_2$  outcomes are determined by the relative strengths of the (positive) intra- and interspecific competition coefficients  $\gamma$ . Specifically, in the mean field case

$$\text{sign}(\delta_i) = \text{sign}(\gamma_{ij} - \gamma_{ii}). \tag{8}$$

Spatially localized Lotka–Volterra competition interactions reduce the regions of co-existence and founder control, relative to those defined by eqn (8) (Neuhauser & Pacala 1999; Bolker *et al.* 2003).

With linear frequency dependence, net feedback effects in a two-species model represent the slopes of the lines defined by eqn (1), and are defined as follows

$$\alpha_1 = \alpha_{11} - \alpha_{12}, \tag{9}$$

$$\alpha_2 = \alpha_{22} - \alpha_{21}. \tag{10}$$

When the growth rates are identical ( $\beta_1 = \beta_2$ ) and all competition coefficients equal ( $\gamma_{ij} = 1$ ), the four possible outcomes in the mean field case are determined by the four  $\alpha_1\alpha_2$  quadrants, defined by the four combinations of signs of net frequency dependence coefficients ( $\alpha_i$ ) that are possible in two-species model (Eppstein *et al.* 2006). As with spatially explicit competition models, smaller spatial scales of interactions reduce the range of parametric conditions in which coexistence can occur in the frequency dependence model (Eppstein *et al.* 2006).

However, when species specific frequency independent terms ( $\beta_j$ ) are also taken into account, as in eqn (5), the net frequency dependent  $\alpha_1\alpha_2$  quadrants are not sufficient for predicting outcomes. In this case, the following parametric conditions define the quadrants for the mean field case:

$$\text{sign}(\delta_i) = \text{sign}(\beta_j + \alpha_{ji} - \beta_i - \alpha_{ij}). \tag{11}$$

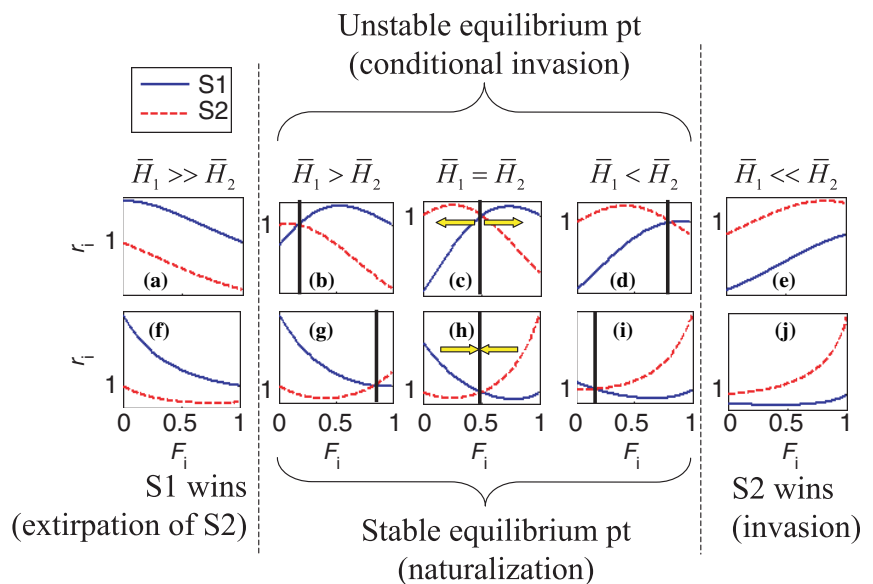
Given almost any of the four possible combinations of signs of net frequency dependence (the  $\alpha_1\alpha_2$  quadrants), it is possible to end up in almost any of the possible invasiveness classes (the  $\delta_1\delta_2$  quadrants). The only exceptions are that (a) if both  $\alpha_1$  and  $\alpha_2$  are negative (i.e., the ecologically feasible case where both species experience net negative feedbacks), it is not possible to end up in the conditional invasion quadrant, and (b) if both  $\alpha_1$  and  $\alpha_2$  are positive (i.e. both species experience net positive feedback, which is less ecologically likely), it is not possible to end up in the

naturalization quadrant. It is worth noting that, even in the ecologically feasible case where the introduced species experiences net positive feedback and the resident community experiences net negative feedback, all four possible invasiveness outcomes are possible.

If the two species have equal average fitness  $\bar{H}_i$  (averaged over all frequencies), then the predicted growth curves will intersect at  $F_1 = 0.5$ , as shown in Fig. 2c,h. However, as the average relative fitnesses of the two species change, the intersection point is moved either to the right (higher frequency of S1) or to the left (lower frequency of S1) (Fig. 2). Of particular interest are the cases illustrated in Fig. 2g,d. In Fig. 2g, S2 is able to establish and coexist at low frequency, even though it has a substantially lower average fitness in the target community than S1. On the other hand, when an unstable equilibrium point has been pushed far enough to the right, as in Fig. 2d, the predicted invasion outcome is rendered very sensitive to propagule pressure, propagule distribution, and the spatial scale of neighbourhood interactions, as described in the next section. As the average fitnesses of S1 and S2 become sufficiently different so that the curves no longer intersect, the invasion class switches to the invasion or extirpation quadrants (Fig. 2).

**Conditional invasion/extirpation, based on perceived propagule pressure**

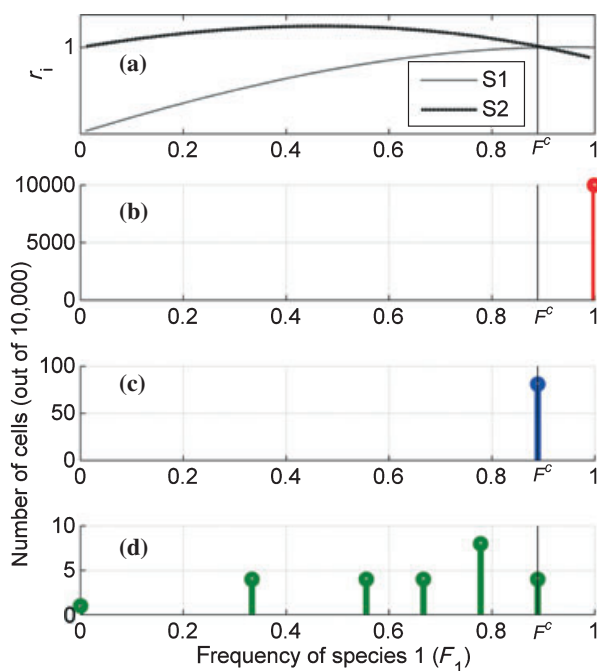
Propagule pressure can play an important role in the invasion process for outcomes in the conditional invasion quadrant, where an unstable equilibrium exists. In this quadrant, the unstable equilibrium becomes a critical frequency ( $F^c$ ) and the introduced species is predicted to be either extirpated or become invasive, depending on



**Figure 2** Representative changes in equilibrium frequencies (thick black vertical lines) and predicted outcomes as a function of relative fitnesses of the two species, averaged over all frequencies ( $\bar{H}_i$ ). The fitness of S2 relative to that of S1 is shown increasing left to right, from (a)–(e) and from (f)–(j). When average fitnesses are equal, equilibrium frequencies are at 0.5, as shown in (c) and (h).

whether the propagule pressure results in a minimum *perceived*  $F_1$  to the right or left of  $F^c$ , respectively. Note that the maximum *perceived* propagule pressure of S2 is, in this two species case, equivalent to the minimum perceived  $F_1$ . In a mean field model, minimum perceived  $F_1$  is simply computed from the number of propagules of S2 in the entire field. However, when interactions are localized, invasion success will depend on both  $F^c$  and the minimum perceived  $F_1$  in any of the overlapping local interaction neighbourhoods in the field.

To illustrate the effect of the interaction neighbourhood size on perceived propagule pressure, we consider three scenarios into which nine propagules of the introduced species displace nine residents in a 10 000 member community initially fully populated by 100% of the resident species, for a representative case in the conditional invasion quadrant, where the critical frequency  $F^c$  is 8/9 (Fig. 3a). In the mean field scenario (M), nine propagules of S2 are



**Figure 3** (a) A representative case of conditional invasion, (b) histogram of the apparent frequency of S1 in a mean field with 9 propagules (scenario M), (c) histogram of the apparent frequency of S1 within all neighbourhoods containing a single propagule, with  $3 \times 3$  cell interaction neighbourhoods and nine scattered propagules (scenario S), and (d) histogram of the apparent frequency of S1 within all neighbourhoods containing at least one propagule, with  $3 \times 3$  cell interaction neighbourhoods and nine clumped propagules (scenario C); the average perceived  $F_1$  (over all local neighbourhoods overlapping the clump) is 0.64. In all panels, the unstable equilibrium frequency at  $F_1 = 8/9$  is labelled as the critical point  $F^c$ .

introduced into a 10 000 member community with a single global interaction neighbourhood, and initially fully populated by 100% of the resident species S1. In the scattered scenario (S), the nine propagules of S2 are positioned uniformly across a 10 000 member community and interactions are localized within  $3 \times 3$  cell overlapping interaction neighbourhoods. In the clumped scenario (C), the nine propagules of S2 are introduced into adjacent locations in the centre of the 10 000 member community, also with spatially local  $3 \times 3$  cell overlapping interaction neighbourhoods. For simplicity, we only consider a single introduction event at a time.

In the mean field scenario M, spatial frequencies are calculated on a community-wide basis. Thus, all locations in the community experience a very low perceived propagule pressure and the minimum perceived  $F_1$  of 9991/10 000 remains to the right of the critical point  $F^c$  (Fig. 3b), with the effect that the introduced species cannot become established and is rapidly extirpated from the community. In the scattered scenario S, the perceived  $F_1$  in any local neighbourhoods containing a single propagule is reduced, in this example, to exactly the critical point  $F^c$  (Fig. 3c). Consequently, invasion may be possible depending on stochastic events; the more propagules, the greater the chance that the introduced species will become established in at least one local neighbourhood, from where it can spread and ultimately dominate the community. In the clumped scenario C this effect is even more pronounced because the perceived  $F_1$ , averaged over all local neighbourhoods overlapping the clump, is now only 0.64, which is considerably to the left of the critical point  $F^c$  (Fig. 3d), and invasion is now likely. It is interesting to note that naturalization, which would intuitively seem to be an outcome intermediate to extirpation of, or invasion by, S2, is not an option predicted for the conditional invasion quadrant.

### Perceived propagule pressure and early extirpation

Regardless of the deterministic predictive quadrant, stochastic effects put introduced individuals of S2 at high risk of early extirpation while their numbers are still low (Tilman 2004). Furthermore, the chance of early extirpation is also influenced by the perceived propagule pressure, which takes into account both the spatial scale of the interaction neighbourhoods and the spatial distribution of propagules. In our spatially explicit model, the probability that species 2 will disappear from all cells  $c$  in the community at time  $t + 1$  is computed as

$$\rho_2^{t+1} = \prod_{V_c} (1 - F_2^{t+1}|_c), \quad (12)$$

where the spatial frequencies  $F_i$  are computed within interaction neighbourhoods. As expected, this extirpation

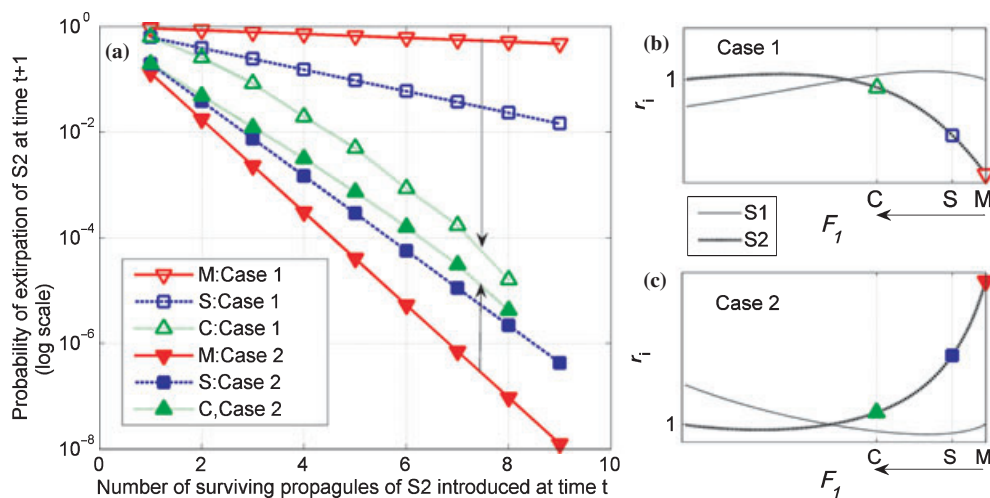
probability decreases exponentially with the number of propagules of S2 remaining in the community during a given generation  $t$  (Fig. 4a). We examine how extirpation probability is influenced for the three scenarios (M, S, and C) described in the previous section, and for two representative cases. Case 1: in which the introduced species experiences an increasing population growth rate as it increases in frequency, as occurs in the conditional invasion quadrant (Fig. 4b), and case 2: in which the introduced species experiences a decreasing population growth rate as it increases in frequency, as occurs in both the naturalization quadrant (as selected here, in Fig. 4c) and in the invasion quadrant. Note that the perceived propagule pressure (in those neighbourhoods containing propagules) increases with smaller neighbourhood sizes and greater clumping of propagules, i.e. from M to S to C, as indicated by the direction of the black arrows in Fig. 4. Not surprisingly, the chance of extirpation is much higher when the growth rate of the introduced species is less than that of the resident species than when the opposite is true (Fig. 4a, case 1 vs. case 2). However, the probability of extirpation is also very sensitive to the perceived neighbourhood size and spatial distribution of introduced propagules, and cases 1 and 2 are affected in opposite ways by perceived propagule pressure. In case 1, higher perceived propagule pressure dramatically *decreases* the probability of extirpation of the introduced species (Fig. 4a, upper black arrow), as expected growth rates of S2 *increase* as perceived propagule pressure increases (Fig. 4b, black arrow). Thus, in case 1 the likelihood of establishment is increased by greater perceived propagule pressure. On the other hand, in case 2, higher perceived

propagule pressure has the counter-intuitive opposite effect and actually *increases* the probability of extirpation of S2 (Fig. 4a, lower black arrow), because expected growth rates of S2 *decrease* as the perceived propagule pressure increases (Fig. 4c, black arrow). In other words, in case 2 the likelihood of early establishment is actually increased by lower perceived propagule pressure. These probabilities are only shown for a single given time step in a single introduction event. As shown by Von Holle & Simberloff (2005), repeated propagule introduction events will increase the likelihood of establishment.

**MODEL CALIBRATION, VALIDATION AND USAGE**

The model presented may be used in a variety of ways, including in computational studies of simulated multi-species communities, for making model predictions based on direct estimation of model parameters, for indirectly estimating model parameters using direct measurements of growth rates, and for predicting invasiveness based on relative growth rates at different species' frequencies. These approaches are outlined below.

Computational studies that systematically vary the values of the different parameters in eqn (4) can help ecologists understand how the various ecological parameters interact to influence invasiveness. For example, varying  $d_i$  in eqn (4) indicates that outcomes are not qualitatively different for two-species perennial communities (where both species have identical death rates) vs. annual plant communities, although the processes occur more slowly. However, higher



**Figure 4** (a) The probability of extirpation of S2 at the next time step as a function of the number of and distribution of surviving propagules introduced and the interaction neighbourhood size, shown for (b) case 1: representative growth curves in conditional invasion quadrant, and (c) case 2: representative growth curves in the naturalization quadrant. In all panels, the direction of increasing perceived propagule pressure, averaged over all neighbourhoods containing propagules, is shown by the black arrow.

probabilities of survivorship can offset frequency dependent disadvantages. Equation (4) could be used to study the interacting effects of frequency dependent and competitive interactions in randomly constructed or evolving simulated multi-species plant communities.

Direct estimates of model parameters may be possible for specific ecological communities. In addition to coefficients such as  $\alpha$ ,  $\beta$  and  $\gamma$ , the spatial and temporal scales of interactions and the form of the possibly nonlinear frequency dependence functions could also be estimated. For example, soil feedbacks could be estimated by measuring growth rates in soils from the target community that are either sterilized or previously occupied by the introduced or resident species (e.g. as in Klironomos 2002; Bever 2003; Callaway *et al.* 2004b). Similar controlled experiments could examine differential feedback effects through mechanisms other than soil biota (pollinators, shading, etc.). Although such studies would be difficult and labour intensive, by comparing the resulting predicted growth rates against measured growth rates the model may be validated and/or improved. In this way, the model can generate testable hypotheses regarding mechanisms of invasiveness, which can then guide future experiments that help refine the model, and so on.

Model parameters could also be indirectly calibrated based on measured species' growth rates, using nonlinear parameter estimation techniques such as the approximate extended Kalman filter (Eppstein & Dougherty 1996). Even in spatially heterogeneous domains with noisy data, tomographic approaches have proven effective in estimating spatially variant model parameters in other application areas (Eppstein & Dougherty 1998; Eppstein *et al.* 2002). In the context of plant communities, spatially distributed parameter values could be optimally adjusted in order to minimize discrepancies between predicted and observed population growth rates. Of course, real communities are far too complex and heterogeneous to be simulated exactly. Attempts to identify or calibrate model parameters from real community growth data must be approached with care, as such inverse problems are inherently non-unique, unless they are appropriately constrained and regularized (Eppstein *et al.* 2002).

Our results indicate that a precise mechanistic understanding of the causes of invasiveness may not be required for predicting to what degree a recently introduced species is expected to replace native residents in a given target community. We propose that such a prediction could be based on measurements of the relative population growth rates  $r_i$  measured as the change in the number of stems or tillers or the increase in the amount of area occupied per unit area of a recently introduced species compared with the growth rate of the resident species (in aggregate) in a given target community. Differences between  $r_1$  and  $r_2$  at

two or more different local frequencies of the species could then provide an estimate of the invasiveness class. It is important to note that the different frequencies are defined at the spatial scale of the interaction neighbourhoods, which may be quite small if the majority of feedback interactions are localized. Thus, even small patches of new potential invaders can be used for 'high' frequency growth measurements. In the case of outcomes where the introduced species is predicted to be either conditionally invasive or naturalized, additional studies at intermediate frequencies could be used to estimate the location of the unstable and stable equilibrium frequencies, respectively. In the case of an unstable equilibrium point, this could indicate to what degree an invasion outcome is likely to be influenced by clumping of propagules. In the case of a stable equilibrium point, this could be used to estimate how much of the native community is likely to be displaced. While not appropriate as a screening tool for making policy decisions about importation of new species, such studies could help to identify which recently introduced species may become potentially disruptive to the local communities and warrant aggressive management and possibly help conservationists design effective management strategies.

As an initial test of the model, we have recently commenced studies using the invasive grass *Phalaris arundinacea* (Poacea). Data collection is currently underway for estimating species' population growth rates in both the native (naturalized) range of *P. arundinacea* in Europe and in introduced (invasive) ranges of *P. arundinacea* in the USA [see Lavergne & Molofsky (2004), Lavergne & Molofsky (2007) for a description of the species and sites]. Specifically, we are measuring the change in number of tillers per m<sup>2</sup> for *P. arundinacea* and the resident community at several sites that differ in their relative local frequencies of *P. arundinacea*. Expectations are that relative growth rates in the European communities will predict the naturalization of *P. arundinacea*, while measurements of relative growth rates in the US ranges will predict invasion or conditional invasion. Davies *et al.* (2000) proposed that alterations in resource levels can change the degree of invasiveness, and Blumenthal (2005, 2006) suggested that this effect could differentially benefit those introduced species that experience the greatest benefits from enemy release. We have begun transplant studies in which *P. arundinacea* was introduced at different planting densities into an experimental field in Vermont (within the invasive range of *P. arundinacea*). Controlled manipulation of resources within the context of these experimental introductions may allow us to determine to what degree changes in ecological conditions can differentially influence frequency independent growth rates ( $\beta$ ) in *P. arundinacea* relative to resident species. Such

information could help in understanding under what conditions *P. arundinacea* is likely to be invasive, and predicting how human alteration of resources (whether intentional or unintentional) could influence the invasion potential of *P. arundinacea*.

## DISCUSSION

Our results demonstrate that any of the four classes of invasiveness (invasion, conditional invasion, naturalization, or inability to establish) can occur for most possible combinations of positive and negative intra- and interspecific frequency dependent feedback coefficients in residents and introduced species. Thus, while a switch from net negative feedback in the home range to net positive feedback in the new range may help to explain why some introduced species are not invasive at home but become invasive when transported elsewhere (Hierro *et al.* 2005; Mitchell *et al.* 2006), our model suggests that the existence of such a switch alone is not sufficient to predict which non-native species are likely to become invasive threats and require management in a target community to which they have been introduced. Rather than comparing changes in feedbacks of the introduced species between native and target communities, our results imply that comparisons of relative frequency dependent population growth rates in the target community in question are necessary for predicting to what degree recently established species may become invasive threats.

Propagule pressure, defined as a combination of the number of individuals introduced in a single event and the temporal frequency of such events, is known to be a significant factor in determining the likelihood of establishment of an introduced species (Kolar & Lodge 2001; Tilman 2004; Von Holle & Simberloff 2005), regardless of the expected invasiveness outcome. However, spatial distribution of propagules can also influence invasiveness, such as when there is an Allee effect (Taylor & Hastings 2005; Johnson *et al.* 2006). Our model shows that clumping of propagules can either increase or decrease the likelihood of establishment of an introduced species, depending on whether population growth rates are positively or negatively correlated with perceived frequencies within interaction neighbourhoods. In some cases the degree of clumping of propagules can actually change the expected outcome from extirpation to invasion. This finding is particularly relevant when we consider that clumped propagule distributions are highly likely from human mediated introductions.

Most ecological models, including ours and that of Levine *et al.* (2006), employ numerous simplifications, such as (a) treating the native community as a single lumped species or by simply modelling only the dynamics of the invasive species, respectively, (b) ignoring environmental heterogeneity, (c) assuming that feedback relationships remain

constant over time, (d) simulating annual vs. perennial plants, and (e) using simplified models of frequency dependence. Nonetheless, these simplified models can still provide useful insights and testable hypotheses regarding, in this case, the likelihood of invasiveness (this paper) and the spread of invasive species (Eppstein *et al.* 2006; Levine *et al.* 2006), which can help guide effective and efficient management practices. Our results, along with those of Levine *et al.* (2006), underscore the importance of obtaining a clearer understanding of spatial and temporal scales of feedback interactions in order to use predictive models effectively. The key is creating as simple a model as possible that still captures the fundamental dynamics of interest. Field studies, such as those described here for *P. arundinacea*, will provide a means of determining when the correct balance of model simplicity and descriptive power has been achieved.

In summary, we develop a new theoretical model that enables ecologists to explore the complex influences of spatially localized frequency dependent and competitive interactions. We also propose a method for estimating to what degree a recently introduced exotic species is likely to become a problem species that warrants intervention. This new ecological framework may allow us to understand and predict better which few newly established species are likely to become invasive, and to devise efficient and effective conservation management strategies.

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