Examining the colonization process of exotic species varying in competitive abilities using a cellular automaton model

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ARTICLE INFO

ABSTRACT

Current threats of invasive species have significant implications for ecological systems. Given their potential impacts, invasive species have been the subject of extensive empirical and theoretical studies. However, these studies have tended to focus on species that produce highly visible ecological and economic impacts. In our study, we take a step back from focusing on these high-impact invasive species, and examine the general colonization (invasion) process of exotic species that have various "competitive abilities" against the native species. Using a two-species cellular automaton model, we demonstrate that: (1) a threshold level of competitive ability is required for the exotic species to successfully establish in a new landscape and (2) an exotic species with superior competitive ability does not necessarily become dominant in a landscape (alternatively, a species that has inferior competitive ability may successfully colonize a new system). Our findings have significant implications for the study of species invasions and also provide clues to how species assemble in ecological communities.

1. Introduction

Current threats of invasive species have significant implications for ecological, economic and social systems (Vitousek et al., 1996; Dukes and Mooney, 1999; Williamson, 1999; Pimentel et al., 2000; Davis et al., 2000). For ecological systems, invasive species are a serious concern because the spread of invasive alien species is believed to cause species extinctions (Fritts and Rodda, 1998; Wilcove et al., 1998; but see Gurevitch and Padilla, 2004), leading to homogenization of the world's floras and faunas (Elton, 1958; McKinney and Lockwood, 1999). Such changes will consequently affect landscape dynamics (With, 2002) and ecosystem function (Elton, 1958; Drake et al., 1989).

Given the potential impacts on ecological systems, invasive species have been the subject of extensive empirical and theoretical studies. Most of the previous work has examined the traits that make for successful invaders (Rejmánek, 1996; Rejmánek and Richardson, 1996; Williamson and Fitter, 1996a,b; review by Kolar and Lodge, 2001), as well as the determinants of community invasibility (Elton, 1958; Lonsdale, 1999), including factors such as species diversity (Levine and D'Antonio, 1999; Levine, 2000), resources (Sher and Hyatt, 1999; Davis et al., 2000), natural enemies (Keane and Crawley, 2002) and trophic structure (Miller et al., 2002). Various theoretical models of species invasions have also been constructed to simulate and understand the patterns of spatial spread,

the rates of spread and the determinants of spatial spread of invasive species (Higgins et al., 1996; With, 2002; reviews by Andow et al., 1990; Higgins and Richardson, 1996; Hastings et al., 2005). Some studies have used model parameter values obtained empirically in the field in an attempt to predict the outcome of actual species invasions (Bossenbroek et al., 2001; Marco et al., 2002; Cannas et al., 2003). Efforts have also been made to link invasion theory with the practice of biological control (Fagan et al., 2002).

These studies on species invasions have tended to focus on species that are more likely to be successful colonizers than those that quickly disappear from the invaded communities. Additionally, survivors producing highly visible ecological and economic impacts are more likely to be studied than inconspicuous or innocuous species (Simberloff, 1997). Given this tendency, failed or non-visible colonists are underrecorded, and this creates a significant bias in the data on invasive species (Lodge, 1993). Although a comparison of characteristics of established and failed (or non-visible) colonists would be the most powerful test for identifying the traits that allow these species to become successful invaders, such comparative studies are uncommon in the literature given the lack of information available on failed or non-visible colonists; this is particularly true for plants (Kolar and Lodge, 2001; see Goodwin et al., 1999 for a plant example). Therefore, to improve our understanding of species invasion processes, elucidating the factors that allow species to persist (non-visible species) or that lead to unsuccessful colonizations (failed species) is just as important as elucidating the mechanism that permits species to become "invasive" in ecological communities. Broad understanding of species invasions, or colonizations, of local communities will also provide clues to the long-standing issues of community assembly (Lodge, 1993), which has important implications for community structure, composition and dynamics (Ricklefs and Schluter, 1994; Loreau and Mouquet, 1999; Miller et al., 2002), and consequently for ecosystem functioning (Tilman et al., 1997; Chapin et al., 1998).

In the present study, we take a step back from focusing on high-impact invasive species and examine the invasion, or colonization, process more broadly. We do so by investigating invasions in which the invading (colonizing) species has certain "competitive abilities" relative to the native species, but its competitive ability is not necessarily greater than that of the native species. The objective of this study was to investigate the levels of competitive ability at which the invading species become "highly visible invasive species" (they invade and become dominant in the landscape) or "failed species" (they are unable to establish in the landscape). We examine this by developing a two-species cellular automaton (CA) model, in which the individuals are assumed to be plants. Although there are various definitions for the terms used in research on species invasions (Richardson et al., 2000; Heger and Trepl, 2003), we will use the term "exotic species" to represent an "invading" or "colonizing" species, and the term "colonization" to represent "invasion." This is done because we believe that the use of the terms "invading species" and "invasion" tends to put too much emphasis on species that have a significant impact on a system. We will use the terms "invading species" or "invasion" only in referring to species that become dominant in the landscape after a colonization event.

2. Methods

2.1. Description of the cellular automaton model

Our model simulates the dynamics of two species (exotic and native species) on a 50-by-50 lattice (landscape), in which only one individual may occupy a single grid cell at any given time during the simulation. The model goes through two basic processes during one generation (iteration): dispersal and competition. At the beginning of each generation, all individuals that are present in the landscape disperse seeds into their own and/or surrounding cells. The cells where the seeds fall are determined by a bivariate exponential function (Fig. 1). The seeds that fall outside the lattice are considered to be lost from the landscape (i.e. absorbing edges). The reproducing individuals die immediately after seed dispersal, simulating an annual system. The new cohort of individuals that occupy the landscape in the next generation is determined by competition among seeds that have dispersed into the grid cells. Competition is played out separately for each grid cell, and two factors determine the outcome of this interaction: the relative number of seeds that has dispersed into a grid cell (exotic versus native), and a function that uses this relative number to
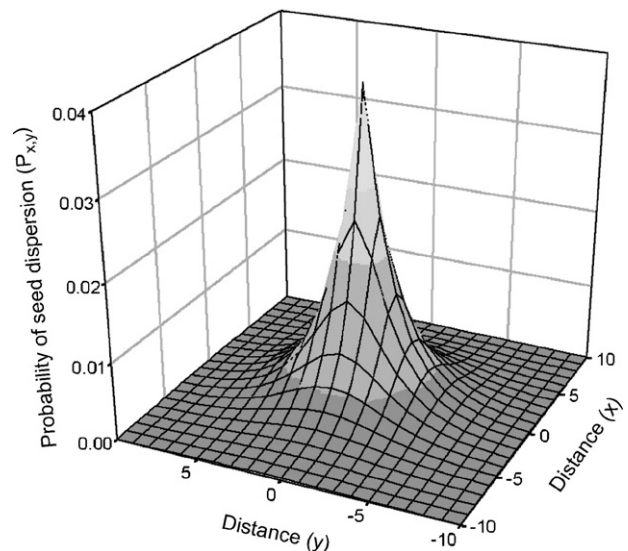
Fig. 1 – Surface plot of the bivariate exponential function used for seed dispersal. The probability ($P_{x,y}$) that a seed will disperse into a grid cell that is x cells in the horizontal direction and y cells in the vertical direction from the origin (0,0) (i.e. seed producing individual) is calculated as: $P_{x,y} = \exp(-(x^2 + y^2)^{-0.5}/\gamma)/(2\pi\gamma^2)$, where γ is the function parameter. γ was set to 2 for both invasive and native species in our simulations. The figure illustrates the surface plot for $\gamma = 2$. When $\gamma = 2$, a seed will fall within its own cell or its surrounding cells (immediate neighbors) approximately 21% of the time (includes cells in the diagonal direction); the seed will fall within a distance of six cells approximately 80% of the time.
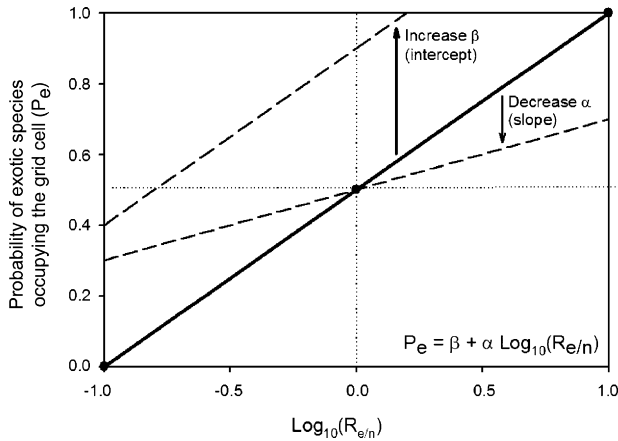
Fig. 2 – Examples of the "competition function." This function is used to determine the species that will occupy the grid cell in the next generation. The function takes the ratio of the number of seeds that has dispersed into a grid cell ($R_{e/n}$, exotic species vs. native species), and uses it to calculate the probability that an exotic species will occupy the grid cell (P_e). Modifying the coefficient values (e.g. decreasing α and increasing β) alters the nature of competitive interactions between the exotic and the native species. See text for details.

calculate the probability of exotic species occupying this cell ("competition function," see next section for details). Once the next cohort of individuals is determined, they disperse seeds once again; this dispersal–competition process is reiterated until it reaches a predefined number of generations, or until one of the species is lost from the landscape.

2.2. Competition function

The "competition function" takes the ratio of the number of seeds (exotic species versus native species) dispersed into a grid cell ($R_{e/n}$), and uses it to calculate the probability that the exotic species will occupy this grid cell (P_e) in the next generation (Fig. 2). If this calculated value of P_e is greater than a uniformly distributed random number (r_n, $0 < r_n < 1$), the grid cell becomes occupied by the exotic species. The competition function simply takes a linear form:

$$P_e = \beta + \alpha \log_{10}(R_{e/n}) \tag{1}$$

where α and β are the function coefficients (i.e. slope (α) and intercept (β) of a linear function). If the calculated value of P_e is greater than 1, P_e is set to 1, and if P_e is less than 0, P_e will be set to 0. For example, if $\alpha = 0.5$ and $\beta = 0.5$ (solid line in Fig. 2), and if the number of seeds of exotic and native species in a grid cell is equal ($R_{e/n} = 1$, $\log_{10}(R_{e/n}) = 0$), the exotic species has a 50% chance of occupying the grid cell in the next generation ($P_e = 0.5$). If the exotic species has 10 times more seeds than the native species ($R_{e/n} = 10$ or $\log_{10}(R_{e/n}) = 1$), the exotic species will always occupy the grid cell ($P_e = 1$), but if the number of seeds of the exotic species is one-tenth of that of the native species ($R_{e/n} = 0.1$ or $\log_{10}(R_{e/n}) = -1$), the native species will always occupy the grid cell ($P_e = 0$). Note that if one species

is absent from the grid cell, the species that is present will occupy the cell by default.

We varied the values of α and β in our simulations, thereby altering the nature of the competitive interactions between the two species. Changing the value of α, or the slope of the linear function (Fig. 2), modifies how the relative number of seeds ($R_{e/n}$) affects the outcome of competitive interactions. Smaller values of α reduce the effects of density; at $\alpha = 0$, the difference in the relative number of seeds ($R_{e/n}$) has no effect on P_e (i.e. the relative number of seeds does not affect the outcome of competition between the exotic and native species). Modification of β (Fig. 2) affects the relative effect of a single individual of one species on another species. If the value of β is increased, a single exotic species will have more "weight" against the native species (similar to the "competition coefficient" in the Lotka–Volterra two-species competition model). The modification of β also has the effect of making the competitive interaction asymmetric.

It should be emphasized that the variation in the value of β is considered to result from a variety of factors that influence the relative success of the exotic species against the native species; these factors may include predation, resource competition, disease or physical environment. The number of seeds, which is explicitly set to be equal in our model parameter, can also be considered to "vary" through the modification of the competition function coefficient (i.e. increasing the value of β can be thought of as exotic species dispersing "seed" that actually represents several seeds). The competition function is not intended to represent any particular plant trait or environmental condition that would change the competitiveness of the exotic species against the native species; rather, it should be considered as representing the "global performance" of an exotic species against the native species. In real systems, the probability of success of colonists will also change with a combination of plant and community characteristics (Heger and Trepl, 2003).

2.3. Simulation set-up

The main objective of the simulations was to test the effects of different parameterizations of the competition function (i.e. differences in the values of α and β) on the colonization process. In the current simulations, values of α ranged from 0 to 0.7, and β ranged from 0.2 to 1.1 (note: β can take on values greater than 1 and less than 0. If the calculated value of P_e is greater than 1, P_e will be given a value of 1). The range of values of α and β were selected based on an examination of preliminary simulations. Simulation results were examined to see if the exotic species was able to (or unable to) establish in the landscape, given specific combinations of α and β. We ran 100 replicate simulations for each selected combination of α and β.

At the start of every simulation run, all grid cells were filled with native species. The exotic species was then substituted in 10 randomly selected cells to mimic a colonization event (for a 50-by-50 lattice, the initial abundance of the native and exotic species is therefore 2490 and 10, respectively). Both the exotic and native species were set up to have identical dispersal and reproductive characteristics: they had identical dispersal function parameter values (Fig. 1) and dispersed five

seeds per generation per individual. Note that random dispersal of seeds creates "gaps" in the landscape; at 5 seeds per individual, there are, on average, 40 empty cells (1.6% of the total number of grid cells) at every generation. These gaps may help the exotic species become established in the landscape in some instances.

Each simulation was set to run for 200 generations, but was halted before reaching the 200th generation if the exotic species failed to establish (i.e. "extinction"), or if the number of exotic species exceeded 1250 (i.e. more than one-half the number of total grid cells). We assumed that if the exotic species reached 1250 individuals, it would not go extinct. We set the generation time to 200 because preliminary test simulations (5000 generations) showed that most simulation results were apparent in less than 50 generations (the abundance of the species reached equilibrium value at about the same time). These settings were made to reduce computation time.

Note that cellular automaton models (interacting particle models), such as the one described here, can be approximated analytically using methods such as pair approximations and moment methods (Durrett and Levin, 1994; Bolker and Pacala, 1997, 1999). As the interaction neighborhood in an interacting particle system increases, a partial differential equation or an integro-differential equation becomes a good approximation (Committee on Mathematical Sciences Research for DOE's Computational Biology, 2005). However, these approximations can produce qualitative and quantitative inconsistencies with the interacting particle models when the landscape under examination is small (finite) and when the seeds disperse over short distances (i.e. when the "interaction neighborhood" is small) (Klausmeier and Tilman, 2002). Given these limitations, the modeling framework we have developed here is not particularly suitable for analytical approximations. Furthermore, interacting particle models allow us to follow the dynamics of the system, and give a sense of the state of the system over time and space. Thus, for our objectives, we believe the cellular automaton model (interacting particle models) will give more detailed information and insight into what is happening during the colonization process.

3. Results

The values of the competition function coefficients, α and β, are important in determining the outcome of colonization events by an exotic species (Fig. 3). For a given value of α, larger values of β result in successful colonizations in all replicate simulations, whereas smaller values of β result in unsuccessful colonizations (Fig. 3a, note: "unsuccessful colonization" means that the exotic species was not able to maintain a sustainable population in the landscape). This pattern is predictable, as an increase in β essentially increases the competitive ability of the exotic species against the native species. Conversely, for a given value of β, smaller values of α result in successful colonizations in every replicate simulation, whereas larger values of α result in unsuccessful colonizations (Fig. 3b). This pattern is observed because exotic species are significantly "outnumbered" by the native species in the initial stages of colonization; if the impact of seed density is strong in determining the competitive interactions (i.e.
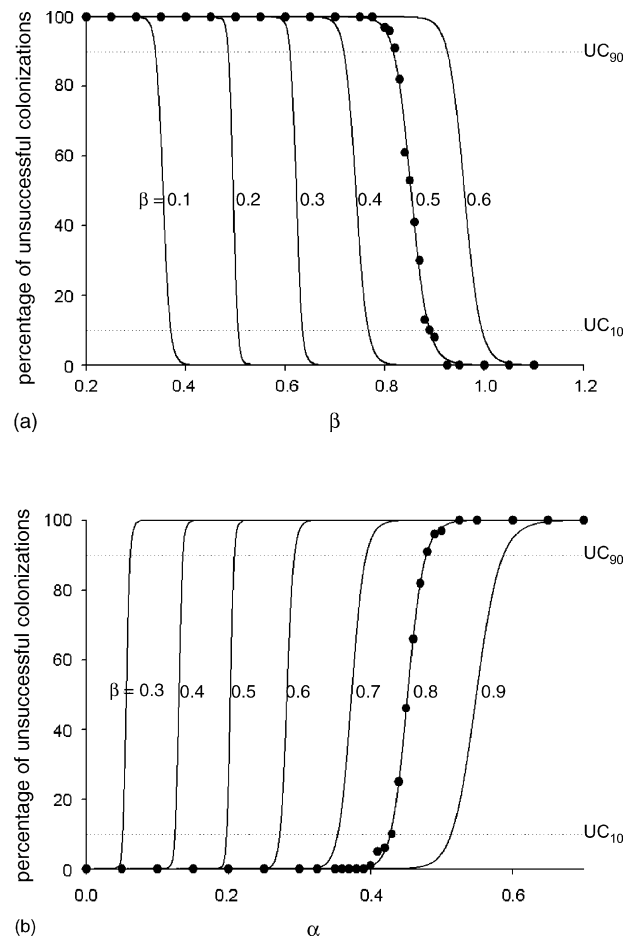
Fig. 3 – Percentage of colonizations that were unsuccessful for various combinations of α and β. The results are shown: (a) by varying the value of β while keeping α constant and (b) by varying the value of α while keeping β constant. The figure shows response functions (Hill equation[*]), which are fitted to the original simulation output data. Examples of the actual simulation data points for the series of simulations are shown as scatter plots in each diagram; each point represents the result of 100 simulations for a specific combination of α and β. The coefficient values of the Hill equation (EC_{50}, HS) and the R^2 values for each regression shown in this figure are given in Table 1. UC_{90} (or UC_{10}) is a reference used to identify the values of α and β at which 90% (or 10%) of the simulations results in unsuccessful colonization. See Table 1 for the actual values of UC_{90} and UC_{10} for each function plot. [*]The Hill equation takes the form $P_{uc} = B + (T - B)/(1 + 10^{(\log_{10}(EC_{50})-\log_{10}(COEFF))HS})$, where P_{uc} is the percentage of unsuccessful colonizations, COEFF the value of α or β and T, B, EC_{50} and HS (Hill slope) are the equation parameters. B and T denote the values of P_{uc} for the minimal and maximal curve asymptote, respectively. EC_{50} denotes the value of COEFF that produces the response halfway between B and T (in our case, $P_{uc} = 50$), and HS denotes the steepness of the curve. In our data, because T = 100 and B = 0, the Hill equation simply becomes $P_{uc} = 100/(1 + 10^{(\log_{10}(EC_{50})-\log_{10}(COEFF))HS})$.

Table 1 – Parameter values of the fitted Hill equation (EC$_{50}$, Hill slope) and their respective R^2 values (see Fig. 3 legend for an explanation of the Hill equation)

α	Coefficient values of the Hill equation		R^2 value of the fitted function	Value of β at which:		Absolute value of the difference $|UC_{10} - UC_{90}|$
	EC$_{50}$	Hill slope		10% of the simulations results in unsuccessful colonization (UC$_{10}$)	90% of the simulations results in unsuccessful colonization (UC$_{90}$)	
0.05	0.29	−94.4	0.99	0.297	0.283	0.014
0.10[a]	0.35	−50.5	0.98	0.370	0.339	0.031
0.15	0.43	−146.5	0.99	0.434	0.421	0.013
0.20[a]	0.50	−111.2	0.98	0.505	0.485	0.020
0.25	0.56	−134.5	0.99	0.569	0.551	0.018
0.30[a]	0.62	−108.0	0.99	0.635	0.609	0.025
0.35	0.68	−83.3	0.99	0.703	0.667	0.036
0.40[a]	0.74	−66.3	0.99	0.767	0.718	0.049
0.45	0.83	−61.9	0.99	0.827	0.771	0.057
0.50[a]	0.85	−51.3	0.99	0.817	0.817	0.073
0.55	0.91	−51.9	0.98	0.944	0.868	0.077
0.60[a]	0.96	−60.6	0.99	0.995	0.926	0.070
0.65	1.00	−45.1	0.99	1.051	0.953	0.098
0.70	1.05	−35.0	0.99	1.121	0.989	0.132

β	Coefficient values of the Hill equation		R^2 value of the fitted function	Value of α at which:		Absolute value of the difference $|UC_{10} - UC_{90}|$
	EC$_{50}$	Hill slope		10% of the simulations results in unsuccessful colonization (UC$_{10}$)	90% of the simulations results in unsuccessful colonization (UC$_{90}$)	
0.30[b]	0.06	23.1	0.97	0.05	0.06	0.011
0.40[b]	0.13	50.6	0.99	0.12	0.14	0.011
0.45	0.17	61.3	0.97	0.16	0.17	0.012
0.50[b]	0.20	82.1	0.98	0.20	0.21	0.011
0.55	0.24	74.4	0.99	0.23	0.25	0.014
0.60[b]	0.28	60.2	0.99	0.27	0.29	0.021
0.65	0.32	65.8	0.99	0.31	0.33	0.021
0.70[b]	0.37	40.9	0.98	0.35	0.39	0.040
0.75	0.41	42.9	0.99	0.39	0.43	0.042
0.80[b]	0.45	39.3	0.99	0.43	0.48	0.051
0.85	0.85	32.5	0.99	0.47	0.54	0.068
0.90[b]	0.55	32.9	0.99	0.51	0.59	0.073
0.95	0.59	35.2	0.99	0.55	0.62	0.073
1.00	0.65	28.5	0.99	0.60	0.71	0.101

Results of regressions that vary the value of β while keeping α constant; corresponds to the response curves shown in Fig. 3a. Results of regressions that vary the value of α while keeping β constant; corresponds to the response curves shown in Fig. 3b. UC$_{90}$ (or UC$_{10}$) is a reference used to identify the values of α or β at which 90% (or 10%) of the simulations results in unsuccessful colonization.

[a] Function plots are shown in Fig. 3a.
[b] Function plots are shown in Fig. 3b.

larger α), it will be extremely difficult for the exotic species to establish and increase its population.

Slight changes in the competition function coefficient values (α or β) do not change the outcome of colonization events over most of their range (Fig. 3). However, there is a striking and abrupt change in going from 100% successful colonization to 100% unsuccessful colonization (or vice versa) within a very narrow range of α or β (Fig. 3). To illustrate this numerically, for each response curve shown in Fig. 3, we have calculated the values of α or β at which 90% (and 10%) of the simulations result in unsuccessful colonizations (Table 1 and Fig. 3). For example, for a response curve where α is kept constant at 0.05,

the value of β at which 10% of the simulations results in unsuccessful colonization (UC$_{10}$) is 0.297, while 90% unsuccessful colonization (UC$_{90}$) is found when the value of β is 0.283. The difference between these two values (UC$_{10}$ and UC$_{90}$) is merely 0.014, which is all that is required to change the outcome of a colonization event (Table 1).

Successful colonization by the exotic species does not necessarily lead to complete replacement of the native species by the exotic species. The exotic species, upon successful colonization, may increase rapidly and reach an equilibrium at which it coexists with the native species. To examine this, we ran another simulation set, with simulations being done at
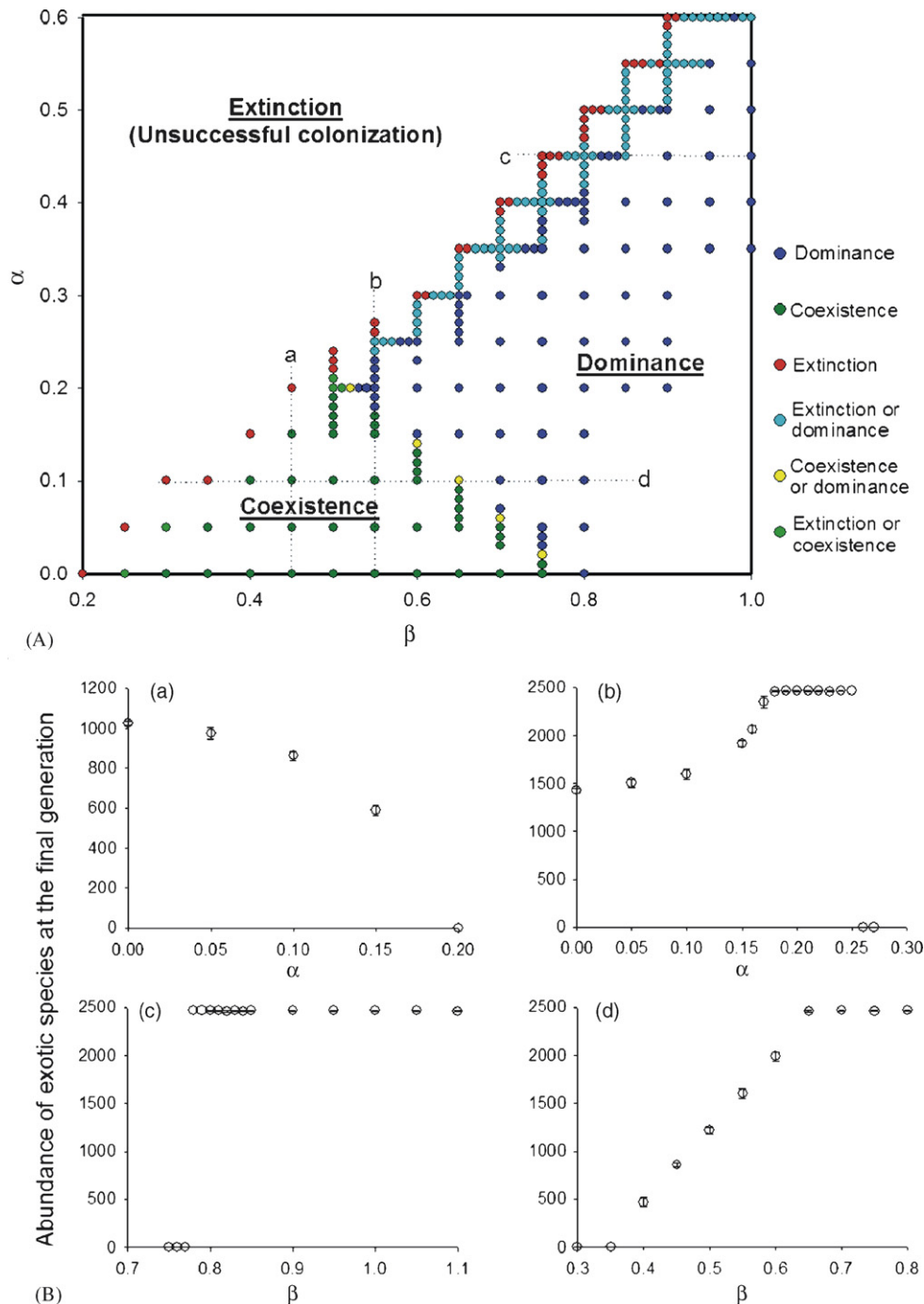
Fig. 4 – (A) Results of simulations examining the coexistence of exotic and native species. Each point represents the results of 10 replicate simulations for a specific combination of α and β; the color of these dots classifies the different outcomes of these simulations. "Extinction" means that all 10 replicate simulations resulted in unsuccessful colonization, and "dominance" means that all 10 resulted in the exotic species taking over the landscape (i.e. extinction of the native species). "Coexistence" means that both native and exotic species persisted in the landscape in all replicate simulations, at least until the 200th iteration (note: if the abundance of the exotic or the native species equilibrated close to zero, then this species may go extinct if the simulations ran for more generations because of temporal fluctuations of abundance. For example, the yellow points in the diagram may in fact be all "dominance" if the simulation ran for longer generations. Thus, "coexistence" should be considered cautiously, particularly at the borders of different simulation outcomes). Combinations of these outcomes (e.g. "extinction or dominance") indicate that some of the 10 replications resulted in one outcome ("extinction") and some in the other ("dominance"). (B) Mean abundance (number of grid cells occupied) of the exotic species at the final generation (iteration). The mean values are shown for four "transects" (a–d) indicated in (A). The error bars indicate 1 standard deviation. Note that simulations that resulted in "extinctions" were not used to calculate the mean value.

finer intervals of α and β within and near the range at which abrupt changes occur in the outcome of the simulations. In this simulation series, we allowed the simulations to run until one of the species went extinct or until it reached the maximum number of iterations (200 generations), whichever came first. This set-up allowed us to examine the abundance of the exotic species at equilibrium, and also see whether or not the native species was completely replaced by the exotic species (note: in the first simulation series, obtaining this information was not possible because the simulation was stopped when the number of exotic species reached 1250—see Section 2). Allowing the simulations to run until one of the species went extinct, and running the simulations at finer intervals in the transitional zone, required significantly more computation time than in the first simulation series. To avoid lengthening the time it took to complete the simulation set, we limited the number of replicates to 10 for each combination of α and β.

The results from this simulation set showed that there is a range of competition function coefficient values (α, β) that allow the two species to coexist in the landscape (Fig. 4A). Within this range, the two species reach equilibrium at specific abundances which are determined by the combination of α and β values (Fig. 4B). One notable finding here is that, even if the colonizing species has a superior competitive ability than the native species on a one-to-one basis ($\beta > 0.5$), it does not necessarily follow that this species will establish in the landscape and completely replace the native species. This argument can also be reversed: even if the colonizing species has an inferior competitive performance against the native species on a one-to-one basis ($\beta < 0.5$), it may still be able to successfully colonize the landscape and maintain a viable population (however, the species will not be able to completely replace the native species). This has important implications for the ecology of invasions, and more generally for species composition and assemblage in ecological communities.

4. Discussion

Our results show that there are ranges of competition function coefficient values (α or β) in which abrupt changes from 100% successful colonization to 100% unsuccessful colonization (or vice versa) are found. Given its narrow range, this transitional zone can be considered a "colonization threshold" for the system studied here. The question then becomes, why do these thresholds emerge? We believe that successful colonization by exotic species largely rests on the ability of the exotic species to develop and maintain a specific spatial distribution pattern ("spatial aggregation") in the landscape, allowing it to form a "patch" that receives a sufficient density of seeds at the end of each generation. The ability of an exotic species to maintain this spatial pattern largely depends on the values of α and β, but random pattern formation is likely to play a key role when the values of α and β fall within the range of the colonization threshold. We are exploring our simulation results in more detail to examine whether the predictions we have made here hold true.

The threshold level of competitive ability found in this study, in which a slight change in the competition function can make the difference between extinction and dominance in
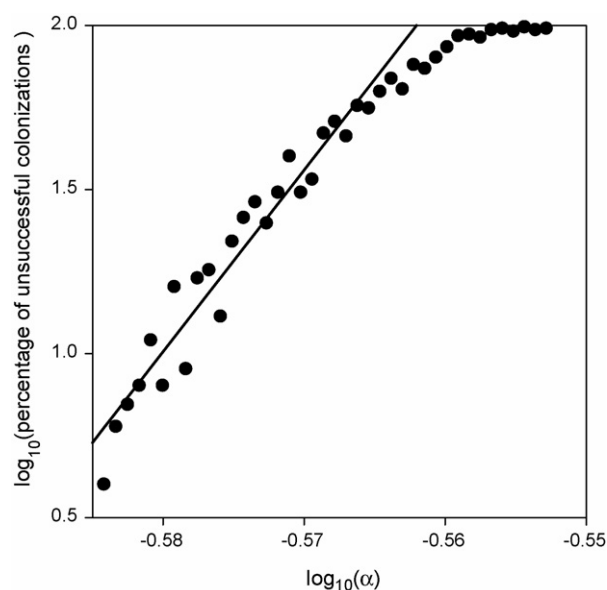
Fig. 5 – **Example of a relationship between α and the percentage of unsuccessful colonizations around the threshold level (note: $\beta = 0.6$). This relationship is also shown in Fig. 3b, but the resolution at which α is examined is much higher in this figure, and it is shown on a log–log scale. As the value of α is decreased, the percentage of unsuccessful colonizations (i.e. order parameter) steadily declines toward zero, and as the value approaches zero, the relationship between the two variables shows a power-law scaling.**

the landscape, is analogous to the phase transitions found in many physical systems. Further investigation of the behavior of the system at one of these threshold points shows evidence of power-law scaling typical of critical states in second-order phase transitions (Fig. 5). It is quite possible that the system is in a self-organized critical (SOC) state at the threshold point, making it highly sensitive to small external perturbations (Bak et al., 1988; Jensen, 1998). This type of behavior has been observed previously in other ecological models of disturbance processes and in some ecological data (Jørgensen et al., 1998). If the colonization process in real ecosystems takes place under conditions equivalent to self-organized criticality, the implications for invasive species biology are significant: a very small change in the initial density of an exotic species could lead to a complete transformation of the landscape. Such threshold behavior may warrant more investigation.

An important finding in this study is the fact that an exotic species with greater competitive ability than the native species ($\beta > 0.5$) does not necessary outcompete it and become dominant in the colonized landscape. Alternatively, an exotic species that has less competitive ability than the native species ($\beta < 0.5$) may still be able to establish itself and maintain a viable population in the landscape. These results suggest that a mere comparison of the traits of exotic and native species may not fully explain why some species are able to colonize or invade a landscape; this could have important implications for the results of empirical studies that have examined the traits that allow exotic species to become suc-

cessful invaders. For example, if a study finds a "statistically significant" difference between an exotic species and a native species in some plant trait that is associated with competitive ability, one might argue that it is possible to make predictions about whether or not this exotic species will become invasive in the new landscape. However, in practice, it will be difficult to demonstrate "how much" of a difference is actually required for the exotic species to become invasive. To be able to predict whether or not a species will be able to establish in the landscape based on studies that examine the traits of exotic and native species, a combined empirical and theoretical (modeling) approach is likely to be necessary (e.g. Bossenbroek et al., 2001; Marco et al., 2002; Cannas et al., 2003).

For simulation runs that resulted in successful colonization, the exotic species' abundance increased very rapidly in the initial stages of the simulation, typically reaching equilibrium abundance in less than 50 generations. One of the main features of invasive species that worries conservation managers is the rate at which they spread and become prevalent in the landscape. This characteristic of invasive species raises concerns about potential extinctions of native species (Fritts and Rodda, 1998; Wilcove et al., 1998) and homogenization of species composition (Elton, 1958; McKinney and Lockwood, 1999). Our simulations show that the rate at which the exotic species increases does not accurately predict whether or not the exotic species will become dominant (i.e. become an invasive species). Thus, not all species with this characteristic (i.e. rapid population growth) pose equal threats to communities, although some authors believe that all invaded communities are threatened equally (Gurevitch and Padilla, 2004).

We have shown that the effects of density on the competition function (i.e. changes in α) strongly influence the outcome of the colonization process (i.e. dominance, coexistence and extinction). Our understanding of the effects of density therefore could be crucial in elucidating the colonization/invasion process of exotic species, particularly since exotic species are usually "outnumbered" by native species in the earlier stages of colonization. In our model, we simulated the effects of density by calculating the ratio of seeds for exotic species versus native species ($R_{e/n}$), and by incorporating this ratio into the competition function (Fig. 2). However, there are two potential problems with this approach. First, the use of the ratio treats $R_{e/n} = 1/1 = 1$ exactly the same as $R_{e/n} = 100/100 = 1$, although these two cases may result in different competitive dynamics. Second, the shape of the function may not correspond to what we have used here (i.e. linear relationship in a log-linear space; Fig. 2). To circumvent these issues, the competition function should ideally be derived based on experimental work that examines the outcome of competitive interactions by varying the densities of two competing species. Although the effects of relative density on the competitive interaction between competing species have been examined extensively in the past, many of these empirical studies have used experimental designs (i.e. substitution and additive designs) whose results cannot easily be incorporated into competition models such as the one used here (see Inouye, 2001). For a competition function such as ours to be built on empirical data, experiments that use a response surface approach, varying the densities of two competing species independently (Goldberg and Scheiner, 1993; Gibson et al., 1999; Inouye, 2001), would

be required. However, this kind of experimental design has rarely been used in ecology (Inouye, 2001), a situation that prevents us from generating a competition function that is more closely based on empirical data. Thus, empirical studies using the response surface design to examine the competitive interactions between exotic and native species may be necessary for increasing our understanding of the process by which exotic species colonize or invade a new environment.

4.1. Comments related to the model

Although various plant or community characteristics can be considered as being "embedded" in the competition function (see Section 2.2), the differences in the parameter values of the seed dispersal function cannot be considered as being incorporated. Hovestadt et al. (2000) have demonstrated, through a model, that differences in dispersal distance cause species to undergo succession, with far-dispersing species dominating the landscape initially, but eventually being replaced by short dispersers (note: all other plant characteristics are identical among the species used in this study). This again is a consequence of the ability of short-dispersing species to maintain spatial aggregation in the landscape. Similarly, in our model, if one species had been assigned a shorter dispersal distance, this species (be it exotic or native) would have been favored in maintaining a population within the landscape. Nonetheless, although using different dispersal distances may have altered the quantitative aspects of our results (e.g. the range of values of α or β that are within the colonization threshold), the general conclusions of our results are not expected to change.

Although our model examines the species colonization process using two species, there are obviously more than two species in real systems. While it is more desirable to examine the colonization process using a multiple-species environment, simulating multi-species competitive interactions would be very difficult with our model, as species-by-species interactions would increase rapidly as the number of species increased. It would also be very difficult to generate a rule to decide the outcome of competitive interactions with several different species competing for the same grid cell. In order to incorporate multiple species into our model, a different approach to modeling competitive interactions would be necessary (e.g. resource-based mechanistic model of competition; Tilman, 1988, pp. 52–97).

5. Conclusions

Using a two-species cellular automaton model, we have demonstrated that: (1) there is a threshold level of competitive ability that is required for an exotic species to successfully establish in a new landscape and (2) an exotic species with superior competitive ability does not necessarily become dominant in a landscape (alternatively, a species that has inferior competitive ability can colonize a new system). The fact that an exotic species with an inferior competitive ability can colonize a new system and persist (i.e. is not competitively excluded by the competitively superior native species) may contribute to increasing the biodiversity of a given ecosystem. Recent large empirical data sets on relative species abun-

dances have shown evidence of a large number of rare species in ecological communities (Hubbell, 2001, pp. 30–47). The fact that these competitively inferior exotic species can colonize and maintain a smaller, but stable population in the landscape may provide clues to the existence of large numbers of rare species in ecological communities. Thus, although our results are based on a two-species theoretical system, they may have some important implications for understanding the assembly and the structure of ecological communities.

Acknowledgements

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