# Intrinsic time dependence in the diversity-invasibility relationship

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Abstract. Contrasting patterns in the diversity-invasibility relationship have intrigued ecologists for many years, and are now known as the "invasion paradox." Experiments usually detect negative relationships, while field surveys find them to be positive. It is widely believed that the paradox is driven by differences in spatial scale, but this is challenged by field surveys that find positive relationships at all spatial scales. If factors that determine invasion dynamics change during the invasion process, the paradox may be partially driven by differences in temporal scale. Here we used simulation (cellular automata) models to explore the generality of temporal change in the diversity-invasibility relationship. The probability of invaders colonizing an area was inversely related to the density of natives, creating a negative nativeexotic correlation when invaders first arrived. Over time, native and exotic populations were both shaped by the same post-introduction processes (disturbance, dispersal, and recolonization), shifting their correlation to positive. The rate of temporal change in the diversityinvasibility relationship was mainly dependent upon the fecundity of invaders. Greater fecundity meant that invaders spread through the landscape faster and were subject to postintroduction processes sooner. We propose a unified conceptual model where the diversityinvasiblity relationship is a function of both spatial and temporal scales.

Key words: biotic resistance; dispersal; disturbance; invasion paradox; resource availability; temporal scale.

# INTRODUCTION

The "invasion paradox" refers to opposing trends in experimental and observational studies of the diversityinvasibility relationship, and has been a topical conundrum in community ecology over the past two decades (Levine and D'Antonio 1999, Fridley et al. 2007). Experiments have usually involved adding seeds of invaders to plot-sized plant communities, and generally find a negative relationship between species richness and invasibility (Naeem et al. 2000, Kennedy et al. 2002). Surveys typically observe the number of native and exotic species occurring in a given area of natural landscape, and generally find a positive relationship (Lonsdale 1999, Stohlgren et al. 1999). Understanding the mechanisms behind this apparent conflict is a major step toward developing general theories of community invasibility and the functional role of species diversity.

Currently, the most popular explanation for the paradox is that it is driven by differences in spatial scale (Fridley et al. 2007). Most suggest that diversity increases invasion resistance at small scales to produce a negative diversity–invasibility relationship, but at larger scales, other factors that promote diversity (e.g., propagule supply and disturbance) are positively correlated with

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invasion to produce a positive relationship (Levine 2000, Shea and Chesson 2002). Field studies have tested this theory by measuring native and exotic species richness at a range of spatial scales. Some support the theory of spatial scale dependence (Brown and Peet 2003, Davies et al. 2005, Knight and Reich 2005), but others report a mostly positive relationship at all spatial scales (Sax 2002, Keeley et al. 2003, Gilbert and Lechowicz 2005). Patterns within spatial scales also vary with habitat type: At the 1-m<sup>2</sup> scale, Stohlgren et al. (1999) found a negative relationship in the Central Grasslands (USA) but a positive relationship in the Colorado Rockies. These results suggest that spatial scale is not the only factor contributing to the invasion paradox, and that other mechanisms might also be important.

As well as differing in spatial scale, experiments and surveys measure invasion at different temporal scales. Experiments essentially measure the initial stages of invasion over an ecologically brief period (usually 1–4 years), whereas field surveys measure a history of invasion over an unknown period, perhaps decades or centuries. These methodologies may therefore be measuring different invasion processes: Experiments mostly measure invader colonization, while surveys predominantly measure invader persistence. If the mechanisms that govern each stage of invasion differ, then the diversity–invasibility relationship might be expected to change through time. A recent experiment showed that when a disturbance regime is present, the direction of the

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diversity-invasibility relationship can change from negative to positive though time (Clark and Johnston 2011). This was demonstrated across a fixed gradient of disturbance conditions in a marine system, but what remains unclear is the role of temporal scales in other systems.

Simulation models are a powerful tool for uncovering the underlying mechanisms that drive emergent patterns (Peck 2004). They can reduce complex systems to a few key variables, and allow us to determine the range of scenarios in which certain patterns should occur. In this study we used simulation models to explore the generality of temporal change in the diversity-invasibility relationship. We built a cellular automata model that incorporated community dynamics, dispersal, and disturbance, and observed invasion patterns through time. We parameterized the model in three ways to represent neutral theory, and with empirical estimates from terrestrial and marine systems. In all scenarios the simulations showed temporal change in the diversityinvasibility relationship, and clearly illustrate the disturbance-based mechanism of this change.

# MATERIALS AND METHODS

We began with the simplest cellular automata model that contained the relevant characteristics. We used a dynamic stochastic competitive Lotka-Volterra metacommunity model, incorporating a negative-exponential dispersal kernel and propagule pressure. We used Latin hypercube sampling for sensitivity analysis (McKay et al. 1979). We assumed a homogeneous landscape over an  $M \times M$  matrix, where disturbance occurred at a rate (Q) randomly across the landscape. When disturbance occurred, all individuals within the local cell were eliminated, but could recolonize via dispersal.

To model community dynamics we used a Lotka-Volterra competition model:

$$\frac{ds_i}{dt} = r_i s_i \left( 1 - \frac{\sum_{j=1}^{S} \alpha_{ij} s_j}{K_i} \right) \tag{1}$$

where  $s_i$  is the local population size of species i, r is the intrinsic rate of population growth,  $K_i$  is the local carrying capacity for species i, and  $\alpha_{ij}$  is the competitive effect of species j on species i. We modeled the relationship stochastically, converting it to expected numbers of births  $(b_i)$  and deaths  $(m_i)$  (i.e., the birth and death rate multiplied by the population size) as follows:

$$b_i = r_i s_i \tag{2}$$

$$m_i = r_i s_i \frac{\sum_{j=1}^{S} \alpha_{ij} s_j}{K_i}$$
(3)

such that the point estimate expectation of population

growth followed the Lotka-Volterra model (Eq. 1). We modeled the dynamics stochastically using Poisson distributions to model the expected number of births and deaths within a given time interval. For computational purposes, we discretized the relation for each time interval within each local cell. Overall, for each species i in location x, y, we have

$$s_{i,x,y,t+1} = s_{i,x,y,t} + b_{i,x,y,t} - m_{i,x,y,t} + \sum_{x'=1}^{M} \sum_{y'=1}^{M} D_{i,x',y',x,y,t} \quad (4)$$

where population size at each time (t + 1) is determined by previous population size (s), births (b), deaths (m), and the number of surviving immigrants from all other cells (D).

The number of immigrants (*D*) to a given cell implicitly incorporated the number dispersing, the probability of reaching a cell, the probability of propagule survival. The probability of reaching a cell and the probability of survival were modeled simultaneously using a dispersal submodel, again using a Poisson model to stochastically generate values of dispersal. Fecundity was the rate at which each individual produced dispersing propagules. The probability of survival was incorporated as a reduction in this rate, so both could be described by a single parameter ( $\delta$ ) to simplify the model. Thus, from a given cell (*x*, *y*), the total expected number of dispersers was  $\delta s_{i,x,y,t}$ . We used a negative exponential dispersal kernel to determine the distance moved by each propagule:

$$pdf = \beta_i e^{-\beta_i d} \tag{5}$$

where pdf is the probability density function,  $\beta$  is a scalar, and *d* is the distance dispersed [i.e.,  $d = \sqrt{(x'-x)^2 + (y'-y)^2}$ ]. Direction was determined randomly.

For each simulation, we allowed 30 native species to equilibrate for 100 time steps before introducing 30 exotic species (one per cell). We simulated an additional 100 time steps to allow the general dynamical properties of the invasion to play out (see Plate 1). For all simulations we used a  $10 \times 10$  matrix of cells as our meta-population. We modeled homogeneous individuals and environmental conditions, to remove the potential for spatial heterogeneity to influence patterns (Davies et al. 2005) and focus on the temporal dynamics of invasions.

We parameterized the model with three sets of values: (1) according to neutral theory, and with values derived from published studies from (2) terrestrial grasslands and (3) marine sessile invertebrates. Grassland and sessile marine invertebrate systems were chosen for their prevalence in the invasion paradox. Methods to obtain parameters and parameter ranges are reported in the Appendix. Simulations were run 1000 times per set of parameters, and results are averages across repeat simulations. For each simulation, parameter sets were chosen using Latin hypercube sampling, to allow sensitivity analysis (see Appendix for parameter ranges used).

We performed sensitivity analysis (backward stepwise selection) on neutral model simulations to determine which parameters were correlated with the rate of temporal change in the diversity-invasibility relationship. This was defined as the time at which the relationship first switched from negative to positive in each simulation. Simulations models were programmed in C++, and source code is included in the Supplement. Statistical analyses and plotting were conducted in R version 2.15.0 (R Development Core Team 2012) using base packages and 'ggplot2' (Wickham 2009).

## RESULTS

Temporal change in the diversity-invasibility relationship occurred similarly with all three sets of parameters (Fig. 1). The correlation between native and exotic diversity (r) was negative (approximately r = -0.5) when exotics were first introduced and became positive after several time steps. By 40 time intervals it had stabilized at approximately r = 0.4 for neutral and marine simulations, and r = 0.3 for terrestrial stimulations.

Fig. 2 shows the disturbance-based mechanism of temporal change. Native diversity was lower in cells that were recently disturbed, and increased towards maximum diversity (30 spp.) in cells that had not been disturbed for some time. This pattern was stable through time. In contrast, when exotics were first introduced they were most diverse in recently disturbed cells where there was less competition with natives. This created a negative correlation between native and exotic diversity within the first few time steps. Over time, new disturbances inflicted mortality to both natives and exotics, and the diversity of exotics across all cells was reduced by competition with natives. The cohort of exotics that initially invaded disturbed cells comprised a diminishing proportion of total exotics, and the relationship between exotic diversity and disturbance progressively changed to resemble that between native diversity and disturbance. At 10 time steps, the correlation between native and exotic diversity was neutral, and by 20 time steps a significant positive correlation had emerged. The positive correlation strengthened over time, as more of the exotics that initially invaded disturbed cells were removed.

Sensitivity analysis revealed that the rate of temporal change mainly depended on the fecundity of invaders ( $\delta$ ), with higher fecundity resulting in faster temporal change (Fig. 3). To a lesser extent the timing of change was also related to (in decreasing order of importance) the carrying capacity (K) of each cell in the landscape, the intrinsic rate of population growth (r), and distance dispersed (d).

### DISCUSSION

Temporal change in the diversity-invasibility relationship was common in model simulations, regardless



FIG. 1. Temporal change in the correlation between native and exotic diversity (r) in model simulations. The model was parameterized to represent neutral theory, and with data from published studies in terrestrial and marine systems. Open circles are average r at each time step, and solid lines are loess smoothers. "Time since introduction" represents time steps in the model.

of the parameters used. The only requirement for temporal change was heterogeneous disturbance within a landscape, and there were no constraints on the spatial distribution of disturbance (i.e., disturbance was randomized). A previous study experimentally demonstrated similar temporal change across a fixed gradient of disturbance within a marine system (Clark and Johnston 2011). Here we demonstrate that temporal change may occur more generally in any spatially structured system where species compete for simple resources (e.g., plants, marine algae and invertebrates, bacteria) and are subject to disturbance. It may therefore explain some of the contrasting diversity–invasibility patterns in the invasion paradox, where studies have measured different stages of invasion.

The mechanism of temporal change was contrasting effects of disturbance on the initial vs. later stages of invasion. When invaders first enter a landscape they are advantaged by recent disturbance due to high resource availability (Davis et al. 2000) and less competition with natives (Hobbs and Huenneke 1992). Native diversity is Reports



FIG. 2. Relationships between disturbance history, native diversity, and exotic diversity at multiple times since introduction. Points are averages of cells with a given "time since disturbance" across all neutral model simulations. Temporal change in the native–exotic correlation is driven by disturbance, which facilitates invader entry before causing invader mortality. "Time since introduction" represents time steps in the model, and species richness shows the actual number of species.

reduced by disturbance in these same areas, creating a negative diversity-invasibility relationship. Subsequent disturbances then reduce both exotic and native diversity together, until both bear similar relationships to disturbance history and are positively correlated with one another. In essence, incoming propagules exploit unused resources more efficiently than residents, but local processes of disturbance and recolonization eventually overcome effects of the initial pulse of introduction. As long as there is heterogeneity in disturbance within the sampling area, there are no spatial constraints on this mechanism. The timing of temporal change was dependent on the fecundity of invaders, since this determines the rate at which invaders disseminate through the landscape (Seabloom et al. 2003) and are exposed to the same population-shaping pressures as natives.

Shea and Chesson (2002) used patch dynamics to explain the role of spatial scale in the invasion paradox. They suggested that diversity inhibits invasion within patches through local mechanisms such as the sampling effect (Huston 1997) and species complementarity





FIG. 3. Timing of change in the direction of the native– exotic correlation (from negative to positive) relative to the fecundity of invaders. Data are from neutral model simulations where all individuals in a given simulation had the same fecundity. Axes use  $\log_{10}$  scales, points are jittered to reduce over-plotting, and the line is a loess smoother.

(Kennedy et al. 2002), but a positive diversity–invasibility relationship emerges between patches due to differences in habitat quality. Some patches have greater carrying capacity than others, so support more native and exotic species than less habitable patches. In comparison, the temporal mechanism here operates exclusively between patches, where patches are represented by cells in the landscape, and habitat quality is represented by disturbance. Both negative and positive diversity–invasibility relationships are possible between patches, depending on the time since introduction.

Effects of spatial and temporal scales on the diversity– invasibility relationship can be combined in a unified conceptual model. We propose that the diversity– invasibility relationship is a composite function of spatial and temporal scales, increasing positively with both (Fig. 4). Only temporal scale was examined in our simulations, but for illustrative purposes we assume that effects of both spatial and temporal scale are logarithmic in shape and are additive. The small spatial and temporal scales of experiments would sample the region close to the origin of the x- and y-axes in Fig. 4, where the correlation between native and exotic diversity is lower. Surveys typically sample at large spatial scales, longer after introduction, where the correlation is higher.

Our model mimics experimental studies by introducing invaders simultaneously into a native community, and describes patterns generated by those invaders. In nature it is common for exotics to be gradually introduced into areas where invaders already exist, and past invaders in these areas may already be redistributed from high- to low-disturbance patches. In these cases, the initial negative relationship generated by new invaders may be overwhelmed by a positive relationship from past invaders. The community-wide native-exotic correlation, therefore, depends on the proportion of new vs. old invaders, and could be continually positive if the rate of introduction is low. This further explains the ubiquitous positive relationships in natural systems and represents another point of difference between the processes measured in field surveys and experiments. Temporal change would still be detectable for new invaders assessed against the pool of natives and past invaders, but the distinction between new and old invaders is important in observing temporal dynamics.

Empirical evidence of temporal change in the diversity-invasibility relationship in terrestrial systems is scarce due to the logistic difficulties of long-term experiments, but several studies have detected or commented upon multistage invasion dynamics. In a five-year experiment of grassland invasion, Thompson et al. (2001) found that the variables predicting invasion changed over the course of the study, and identified two distinct stages that they termed "colonization" and "consolidation." Resource availability was of central importance throughout the experiment, but the importance of different combinations of resources changed through time. A 40-year study of plant succession in an abandoned field also found temporal change in the strength and slope of correlation between native to



FIG. 4. Conceptual model of the effects of spatial and temporal scales on the diversity–invasibility relationship. The native–exotic correlation increases independently with space and time, which together determine the direction and strength of correlation.



PLATE 1. Example of the disturbance mosaic model landscape shortly (1 time step) and some time (100 time steps) after invasion. When first introduced, exotics invade with the most frequency in recently disturbed cells, but native and exotic distributions converge over time. Points represent the presence of a species in a given cell.

exotic richness (Meiners et al. 2002). Patterns showed some irregularity with history of use, but generally become increasingly positive through time.

Others have recognized that the processes important to invasion change during the invasion processes (Dietz and Edwards 2006, Theoharides and Dukes 2007). Theoharides and Dukes (2007) provide a detailed review of factors affecting four stages of invasion: transport, colonization, establishment, and landscape spread. Dietz and Edwards (2006) refer to a primary and secondary phase, where invasion is facilitated by disturbance in the primary phase, but in the secondary-phase invader spread is related to genetic adaptation. Rigorous tests of effects of temporal scale would require experiments over extended periods, but logistical constraints are clearly prohibitive. Alternatively, distance from source could be used as a proxy for "time since introduction" in cases where an invasion is expanding as a front. We would then predict surveys to show negative correlations between diversity and invasion near the invasion front, but positive correlations in areas invaded some time ago.

Patterns of invasion are likely to be shaped by multiple factors that vary with spatial and temporal scales and heterogeneity (Stachowicz et al. 1999, Davies et al. 2005). The relative importance of spatial and temporal processes will depend on properties of the study system and component species, together with traits of potential invaders. The model here provides clarity in a mechanism driving temporal change in diversity–invasibility relationships, and a context with which to better incorporate temporal dynamics into invasion theory.

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#### SUPPLEMENTAL MATERIAL

## Appendix

Parameter values used in simulation models and methods for their derivation (Ecological Archives E094-004-A1).

#### Supplement

C++ source code containing the algorithms described in this paper and a short description of the program and its options (*Ecological Archives* E094-004-S1).