



Invasion success and community resistance in single and multiple species invasion models: do the models support the conclusions?

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Abstract

Elton's concept of community-level resistance to invasion has derived significant theoretical support from community assembly models in which species invade (colonize) singly at low densities. Several theoretical models have provided support to this concept and are frequently cited as providing evidence that invasion resistance occurs in nature. The underlying assumptions of these models however, are derived from island or island-like systems in which species invade infrequently at low abundances. We suggest that these island-like models cannot be generalized to systems in which species arrive in greater frequencies and densities. To investigate the effects of altering the basic assumptions of these original models, we utilized assembly algorithms similar to those used in previous studies, but allowed either two species to invade per time step or single species invasions at relatively high inoculation densities. In these models, invasion resistance only occurred when the invasion process was restricted to single species invading at low densities (as in previous models). When two species were allowed to invade per time step, invasion resistant states did not occur in any of 20 simulated communities, even after 10,000 invasion events. Relaxation of the assumption of invasion at low density also resulted in a lack of invasion resistance. These results may explain why the strict concept of complete invasion resistance appears only to operate in island and island-like systems.

Introduction

The introduction of species into new regions is a significant threat to biological diversity (Hatcher et al. 1989; Heywood 1989; Lubchenco et al. 1991; Norse 1993; Suchanek 1994). Yet there is no sound theoretical framework by which to predict which species will invade or which systems are more readily invadable (Williamson 1996; Lonsdale 1999; Mack et al. 2000). Significant attention instead has been focussed on the attributes of invaders that enable successful establishment (e.g., Crawley 1987; Lodge 1993) or alternately, the community or ecosystem attributes of susceptible (i.e., invaded) communities (Elton 1958;

Crawley 1987; Williamson 1996; but see Lonsdale 1999).

One of the primary hypotheses intrinsic to the subdiscipline of invasion ecology is the relationship between diversity and invasibility (e.g., Hengeveld 1986; Lodge 1993; Williamson 1996; Levine and D'Antonio 1999). Elton (1958) proposed a verbal model that communities develop increasing invasion resistance as increasing diversity leads to more tightly connected food webs. This prediction has received significant support from the results of community assembly models (e.g., Post and Pimm 1983; Case 1990, 1991; Drake 1990). Assembly models evaluate the fashion in which ecological communities assemble

through sequential invasions (colonization) and deletions (local extinction) of species mimicking the assembly of real communities (MacArthur and Wilson 1963, 1967; Simberloff and Wilson 1969; Diamond 1975; Dickerson and Robinson 1985). The sequence and timing of species colonization attempts (successful or not) in real communities have been demonstrated to lead either to recurrent turnover in species composition or to invasion resistant states (Robinson and Dickerson 1984, 1987; Hengeveld 1986; Drake 1991).

The results from community assembly models have been held up as the theoretical underpinnings of invasion biology (Hengeveld 1986; Case 1991; Williamson 1996; Levine and D'Antonio 1999). Yet, a number of assumptions are built into the Post and Pimm (1983) and Drake (1990) models: (I) there is a single species source pool that is limited and finite; (II) species attempt to colonise one at a time; (III) colonization density is arbitrarily low relative to Lotka–Volterra equilibrium densities mimicking colonization when rare; and (IV) Lotka–Volterra dynamics and eigenvalue analysis are used to estimate community stability. The first three assumptions do not conform to the invasion biology scenario as empirically observed in several ways: (i) introductions are composed of at least two species pools: the donor pool and recipient pool; (ii) species not only invade singly but also in groups, assemblages or entire communities; and (iii) invasion densities of individual species are often high (e.g., Carlton and Geller 1993). Despite this, these models have been identified as describing biological introductions, and have been extensively cited as supporting the concept of invasion (or biotic) resistance. Our objective was to test whether this latter conclusion is robust, by independently relaxing two of the fundamental assumptions (single colonizers and low density of colonizers) of one of the most cited Lotka–Volterra assembly models (Drake 1990). The extent to which these assumptions modify the development of invasion resistance has not been explored in the literature, yet may have significant consequences to invasion theory.

Methods

The community matrix and Lotka–Volterra equations

The assembly algorithm used in this model incorporates a community matrix focusing on population

growth rates, intra- and interspecific interactions terms, and food web dynamics (Drake 1990). Population growth, intraspecific competition, and interspecific interactions are simulated using a matrix of Lotka–Volterra equations. This leads to the equilibrium density of the i th species given by:

$$\tilde{N}_i = N_i \left(b_i + \sum_{j=1}^n a_{ij} N_j \right), \quad i, j = 1, 2, 3, \dots, n, \quad (1)$$

where N_i is the abundance of i th species, b_i is the per capita rate of increase of the i th species, a_{ij} is the per capita effect of species j on species i , and n , the number of species, which changes during assembly.

Values of b were randomly chosen from a uniform distribution over the intervals $[0 < b_i < 1]$ for producers and $[-1 < b_i < 0]$ for consumers. Values of a_{ij} were chosen from a uniform distribution over the intervals $[0 < a_{ij} < 1]$ for the effect of a prey species on its predator and $[-1 < a_{ij} < 0]$ for the effect of a predator on its prey.

The system dynamics were tracked, as species attempted to colonize or were extirpated, by eigenvalue analysis of local (Lyapunov) stability of the community matrix (Equation (1)). This involved the examination of eigenvalues of the community matrix with elements of $a_{ij} N_j$, where N_j is the equilibrium population density of species j . Linearized differential equations and eigenvalue stability analyses have been criticized in the literature (Case 1991, 1995; Law and Morton 1996), however they have been proven adequate for analyses of systems near equilibrium (see Robinson and Valentine 1979; Post and Pimm 1983) and have been successfully used to demonstrate general patterns in large multi-species systems (Robinson and Valentine 1979; Tregonning and Roberts 1979; Post and Pimm 1983; Yodzis 1989; Drake 1990; Nee 1990). The limitations of these output analyses do not affect the tests of assumptions being made in this paper.

A regional species pool with explicit trophic interactions was constructed consisting of 60 species: 20 primary (1°) producers, 20 primary (1°) consumers, and 20 secondary (2°) consumers. The number of links between trophic levels was set at 180 to give a connectance value of 0.05 (180/60²). This level of connectance creates communities of greater diversity than higher or lower levels of connectance (Huxel and Hewitt, unpublished manuscript). Links between species and the number of links for each species were

randomly assigned. The links were reciprocal, in that, if species i affected species j , species j affected species i .

The assembly algorithm

The assembly model or algorithm used herein (Figure 1) largely follows that of previous studies

(Post and Pimm 1983; Drake 1990) except where explicit tests of two key assumptions were made. The species pool is created with parameter values chosen as described above and two 1° producers are randomly selected to form the base web. As in Drake's study, we allow invasion attempts to be made at each time step with potential colonizers randomly selected

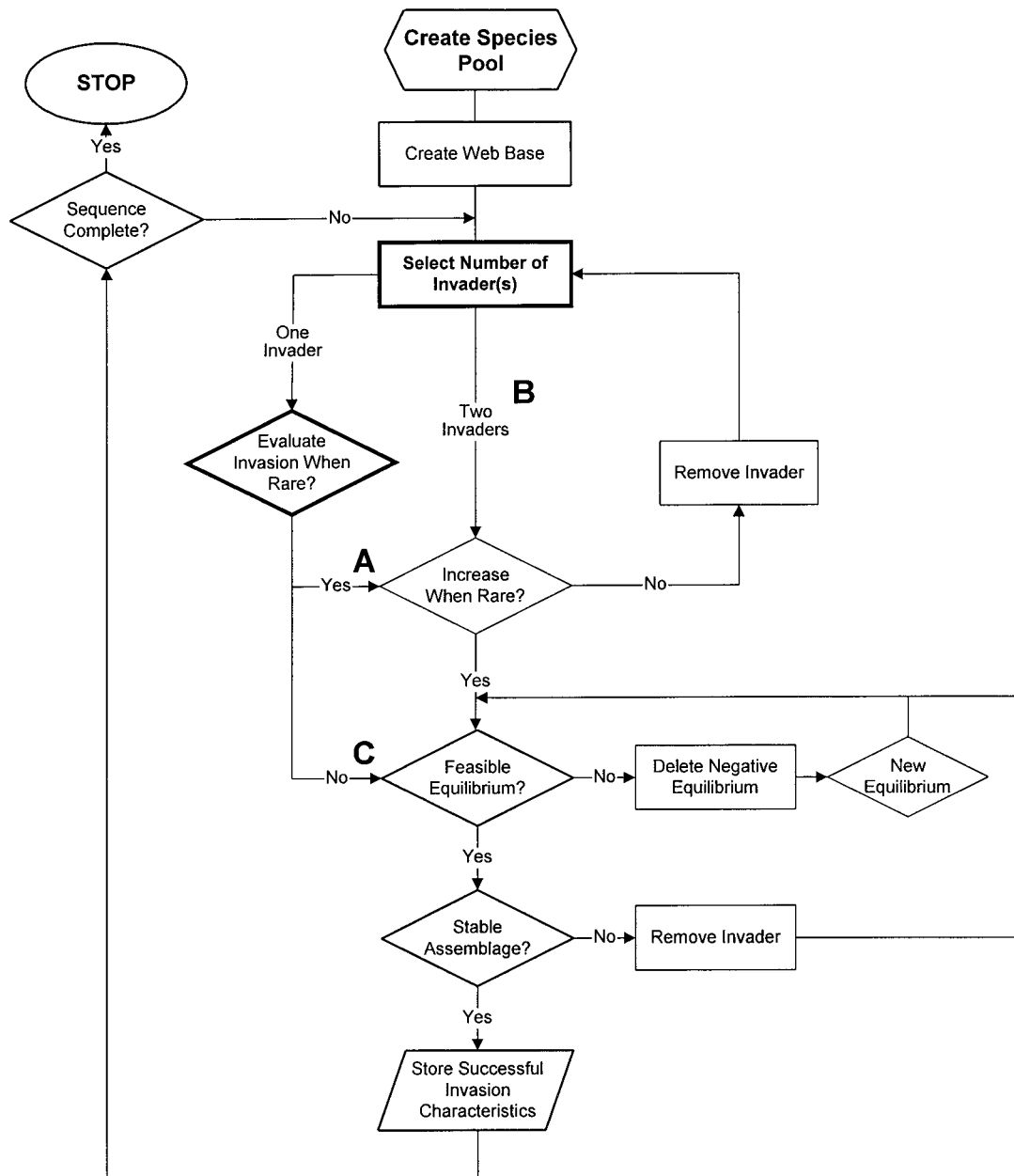


Figure 1. A flow chart of the general assembly model. A denotes the pathway for scenario A where single species invade at low inoculation densities. B denotes scenario B where two species attempt to invade the extant community at low inoculation densities. C denotes scenario C where single species invade near equilibril inoculation densities.

from the available pool that include only those species not already present in the extant community. Species invade at arbitrarily low densities relative to the Lotka–Volterra equilibrium densities. The invading species is added to the community matrix that is then analyzed for stability by performing an eigenvalue test on the augmented system. The eigenvalue analyses give equilibrium densities of all species in the matrix. Species with positive equilibrium densities are maintained in the community. If any of the extant species have negative equilibrium densities, the species with the most negative eigenvalue is deleted from the community (following the methodologies of Tregonning and Roberts 1979 and Drake 1990). The species with the most negative density is assumed to go extinct first. Eigenvalue analyses are then repeated on the remaining community until all remaining species have positive equilibrium densities (Figure 1). Thus, several eigenvalue analyses may be performed during a single invasion step. One of four outcomes may occur following each invasion event: the invasion fails with no change in species composition; the invasion fails, but one or more species is driven extinct; the invasion succeeds and one or more species is driven extinct; or the invasion succeeds augmenting species richness.

Invasion scenarios

We employed three simulation scenarios to test the effect of relaxing two important assumptions of Drake's study (Drake 1990). These assumptions were: (1) only one species invaded per time step; and (2) invasions occurred at low densities. Specifically, the scenarios used in this study were: (A) single invaders at low inoculation densities (this scenario is identical to the previous Drake model); (B) two invaders at low inoculation densities; and (C) single invaders at inoculation densities near equilibrium. For A and C, prior to performing the simulations, matrices were assembled randomly and eigenvalue analyses were used to determine equilibrium densities for all species. Most species densities at equilibrium in these trials were approximately 0.1. Thus, following Drake 1990, species invaded at 0.001 for low inoculation simulations (A), and 0.1 for inoculation densities near equilibrium values for simulations (C). Twenty communities were simulated under each of the three scenarios for 500 time steps. Additionally, two communities were allowed to run for 10,000 time steps for scenarios B and C in order to

ensure that fixation did not occur under these scenarios even over longer time frames.

Results

Assembled communities from the three scenarios

All 20 communities assembled with single species attempting to invade per time step at low densities (scenario A) reached an invasion resistant state (Figure 2). These invasion resistant states represented multiple equilibria, differing in both diversity and species composition. The time to invasion resistance ranged between 16 and 337 time steps ($\bar{x} = 149.8$ and $s.d. = 117.97$). This scenario confirmed that the algorithm is consistent with that of Drake (1990) despite the use of a different species pool with fewer species and trophic levels. In this scenario, colonization success decreased over time as the number of successful colonizations went to zero after reaching an invasion resistant state. The probability of colonization success prior to reaching an invasion resistant state varied greatly, ranging from 4.1% to 50.0% ($\bar{x} = 25.6\%$, $s.d. = 14.9$) with decreasing success as the number of invasion attempts increased prior to reaching an invasion resistant state. However, the overall colonization success rate (over 500 time steps) ranged from 1.6% to 11.8% ($\bar{x} = 2.5\%$, $s.d. = 1.7$).

Communities assembled with two invaders per time step (scenario B) did not lead to a complete invasion resistant state after either 500 (Figure 3) or 10,000 time steps. The per species colonization success did not greatly vary over the first 500 time steps ranging from 19.1% to 30.0% ($\bar{x} = 23.5\%$, $s.d. = 2.3$). Each community assembled under scenario B followed different trajectories of changing species composition due to differences in invasion sequence.

Similarly, the 20 communities assembled where single species invaded at inoculation densities near their equilibrium values (scenario C) did not achieve complete invasion resistance after either 500 (Figure 4) or 10,000 time steps. Colonization success ranged from 43.0% to 59.0% ($\bar{x} = 52.8\%$, $s.d. = 3.6$) and did not exhibit any temporal trend. Again, each community assembled under this scenario followed different trajectories of changing species composition and diversity as a result of random invasion sequences.

Differences between scenarios in colonization success were examined using Student's *t*-test. At low

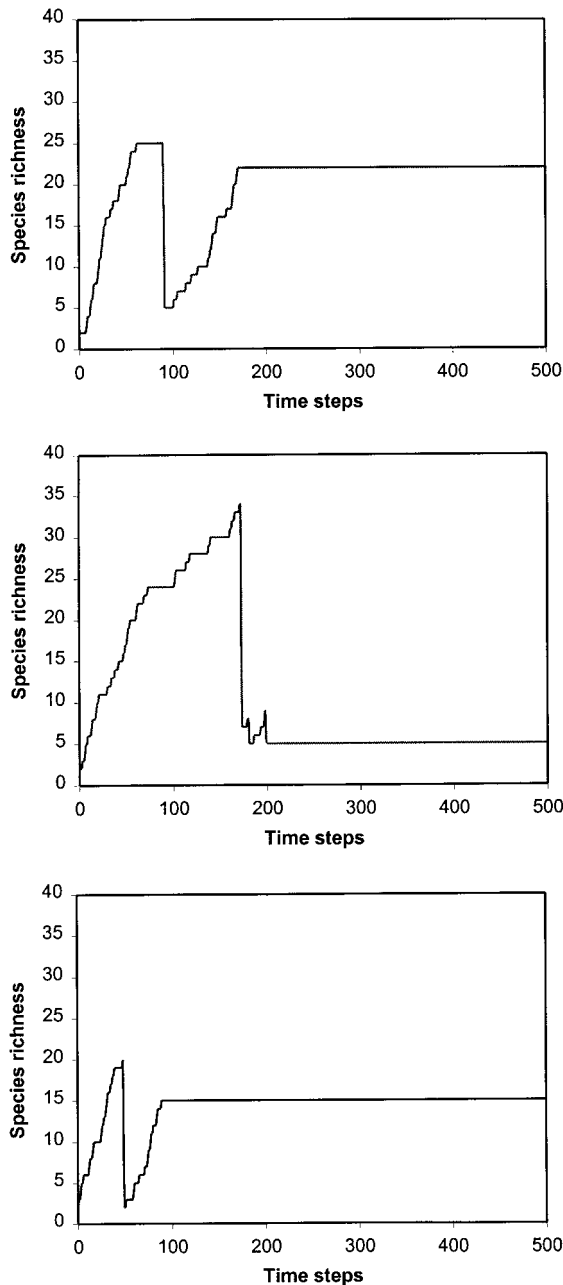


Figure 2. Changes in richness over time during community assembly under scenario A for three simulations. The communities differed in species composition and richness due to differences in invasion history. All communities assembled under the assumptions of single species invading at low densities resulted in complete resistance.

inoculation density (scenarios A *versus* B), invasion success is not significantly different when two species invade rather than one prior to attaining an invasion resistant state in scenario A ($t_{[19]} = 0.62$; $P > 0.05$).

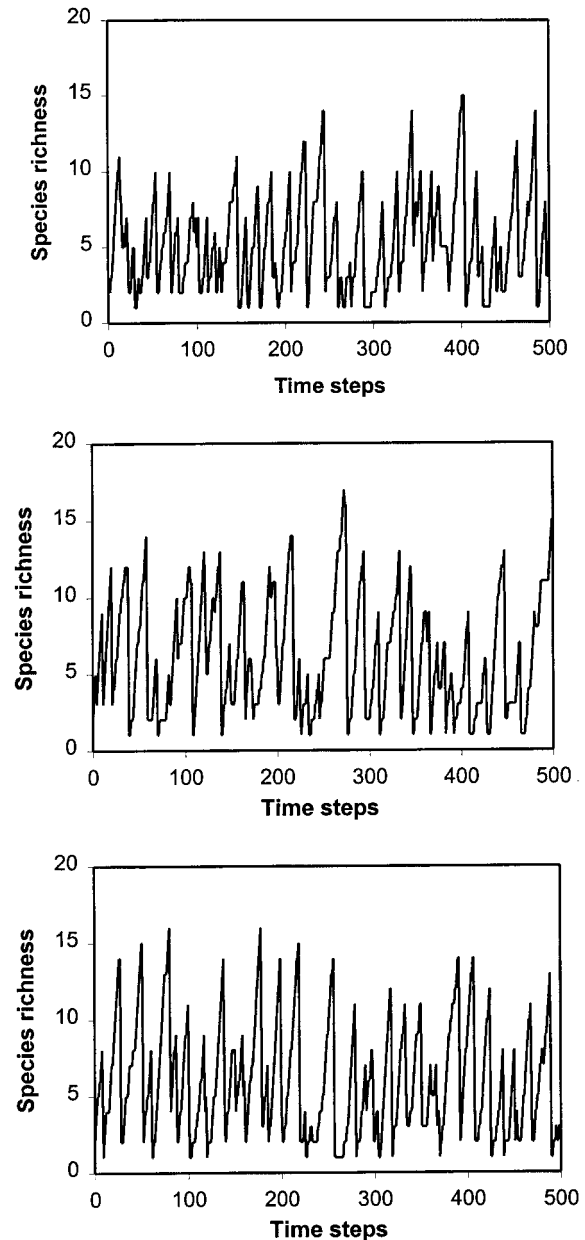


Figure 3. Changes in richness over time during community assembly under scenario B for three simulations. No communities assembled with two species invading per time resulted in complete invasion resistance, but note that there are periods of stasis in each of these simulations.

Overall invasion success however, was significantly different between the two scenarios because of the development of invasion resistance in scenario A ($t_{[19]} = 32.84$; $P < 0.001$). Additionally, colonization success was significantly higher when the assumption

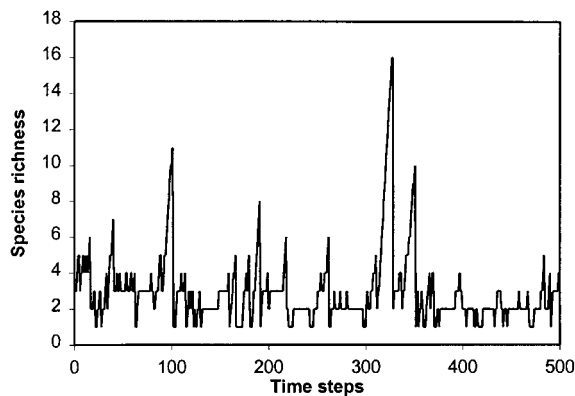


Figure 4. Changes in richness over time during community assembly under scenario C for a typical simulation. No communities assembled with single species invading at high inoculation densities led to complete invasion resistance, but note that there are periods of stasis in each of these simulations.

of invasion at low density was relaxed (scenarios A versus C) both for comparison with the pre-invasion resistant state in scenario A ($t_{19} = 7.94$; $P < 0.001$) and overall success rate ($t_{19} = 56.50$; $P < 0.001$). Per species colonization success is significantly higher in scenario C than in scenario B ($t_{19} = 30.67$; $P < 0.001$). However the total number of successful invasions was not significantly different between the two scenarios.

Discussion

Current theory of biological invasions has evolved from earlier concepts of stability and the 'balance of nature' paradigm (e.g., Hengeveld 1986; Williamson 1996; Levine and D'Antonio 1999). Elton (1958) conceptualized the theory of biological invasions by predicting that the invasibility of communities would decrease as communities became more diverse and formed highly structured food webs. Mathematical community assembly models, such as those by Post and Pimm (1983), Case (1990, 1991), and Drake (1990), are cited as providing fundamental theoretical support to Elton's hypotheses (Groves and Burdon 1986; MacDonald et al. 1986; Mooney and Drake 1986; Joenje et al. 1987; Drake et al. 1989; diCasti et al. 1990; Ruiz et al. 2000). What we are concerned with here is the generality of that support in the light of more realistic assumptions about invasion biology.

To test these assumptions, we utilized a standard Lotka-Volterra assembly model, similar to those used in past studies on biological invasions. These models

have underlying assumptions largely derived from island biogeography theory and specifically drawn from isolated systems (MacArthur and Wilson 1963, 1967). These systems are sufficiently distant from mainland species source pools so that species arrivals are rare (consequently singly) and generally in low numbers. The majority of native systems do not experience the characteristics of isolated islands and while community assembly models have used single species invasions, this assumption appears to have been motivated more by mathematical tractability rather than biological reality. Multiple invaders have been demonstrated to arrive simultaneously and at high densities in a number of native and invaded systems (Simberloff and Wilson 1969; Osman 1978; Carlton 1987, 1989; Carlton and Geller 1993; Hewitt 1993; Robinson et al. 1995; Ruiz et al. 2000).

The implementation of the assembly algorithm under scenario A with identical assumptions as Drake (1990) resulted in all 20 communities attaining invasion resistant states, agreeing with Drake's results and indicating that the model was working accurately. In all scenarios, the communities developed under alternate trajectories based on the random selection of invader. This agrees with the results found in both theoretical (Drake 1990) and empirical (Alford and Wilbur 1985; Barkai and McQuaid 1988; Drake 1991; Drake et al. 1993) studies in which the historical sequence of colonization can have significant effects on community trajectory.

Changing either of the primary assumptions of the Drake (1990) model changes the average invasion success of colonizers and results in a lack of complete invasion resistance in the recipient community, even after 10,000 invasion events (time steps). Relaxing the assumption of a single invading species (scenario B) leads to communities that continue to be susceptible to invasion through time (19–30% of attempts are successful), but are not completely open to all invaders. When the assumption of low invasion densities is relaxed, 50–60% of invasion attempts are successful. These values are similar to the results found in many studies of biological introductions, in which 38–65% of established colonists in the recipient community succeed in establishing 'feral' (self-replacing) populations (Williamson and Brown 1986; Crawley 1987; Weeda 1987).

Previous assembly models have examined the influence of single invaders under different conditions and species pool size. Given a finite species pool,

Drake (1990) demonstrated the development of invasion resistant states and Case (1990, 1991) found that invasion resistance increased with recipient community richness and connectivity. However, when an infinite species pool has been used, the development of invasion resistant states is no longer attained (Post and Pimm 1983; Ginzburg et al. 1988). Instead successful species invasions continue to occur, but the rate of success decreases with increasing community size. While a growing number of field studies have demonstrated partial invasion resistance to specific taxa (Fox 1983; Burns and Sauer 1992; Stachowicz et al. 1999), several others have supported Elton's prediction that some systems will remain 'open' to colonization with frequent extinctions (Paine 1966; Sale 1977, 1978; Paine and Levin 1981; Roughgarden 1989; Lonsdale 1999).

Multiple invaders (at low inoculation densities) or invasion of a single invader at high inoculation densities lead to continuous turnover in species composition similar to long-term successional patterns (Odum 1969; Paine and Levin 1981) and taxon cycling (Wilson 1961) observed in many field systems. Our results suggest that invasion resistance is a matter of degree, varying between complete resistance in insular systems to partial resistance in local communities. Similarly, these findings indicate that inoculation density has a greater influence on invasion success than the number of simultaneous invaders based on the increased rate of invasion success.

Thus as human activities and transport mechanisms continue to reduce the isolation of regional biotas from one another, the numbers of species and inoculation densities of invaders will increase and result in higher susceptibilities to invasion in recipient regions and communities. For example, human-mediated transport and invasion of species in marine communities has generally involved the movement of entire assemblages with oyster culture transfers, wooden ship hull fouling, and ballast water release (Carlton 1985, 1987, 1989, 1992; Carlton and Geller 1993; Hewitt 1993; Hewitt et al. 1999; Ruiz et al. 2000). We suggest that these results call for a re-examination of current invasion theory and the need for more empirical studies of biological invasions.

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