

# Modeling the Risks of Nonindigenous Species Introductions Using a Patch-Dynamics Approach Incorporating Contaminant Effects as a Disturbance

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The establishment and spread of invasive or nonindigenous species has caused concern from stakeholders in affected areas, and has prompted many field and modeling studies. We used stochastic two species, circular three patch dynamic models to investigate the patterns of invasion and impacts upon the affected species. Both persistent and degradable toxicants were incorporated as parts of the model system to act as disturbance regimens. There is a clear series of patterns that result from these simulations. Competition increases population variability, but decreases the number of distinct outcomes possible from the same initial conditions. Isolation of the patch of the introduction was the main determinant of successful establishment through a process we call the beachhead effect. Coexistence of species was often possible in local patches, contrary to the analytical solutions of Lotka-Volterra equations and numerous modeling studies. Contaminants and their resultant disturbances are important as contributors to the stochastic nature of models. The stochasticity leads to a variety of outcomes from some sets of initial conditions. Different outcomes have different probabilities of occurrence and are dependent upon the specific initial conditions of the simulation. A clear pattern that is apparent is the "beachhead effect," where the invasive establishes a population within a relatively remote patch before migrating to the remainder of the landscape. We make predictions and provide specific research hypotheses as to the causes and effects of invasive species establishment, spread, and impacts.

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**KEY WORDS:** Contaminants; nonindigenous species; patch dynamics; risk assessment

## 1. INTRODUCTION

The risks of invasive or nonindigenous species to marine, freshwater, and terrestrial environments are one of the dominant issues in environmental management. Estimates of nonindigenous species for the

United States range as high as 50,000 species, with estimated costs to the economy as high as \$120 billion per year (Pimentel *et al.*, 2005). Global transportation of materials and goods, disturbance of native habitat, and the widespread purposeful introduction of nonindigenous species have increased the rates of invasion events in North America over the last 200 years (Ruiz *et al.*, 2000).

It is clear that there is a growing interest in developing tools for assessing the risks due to nonindigenous or invasive species. The recently published series of articles in *Risk Analysis* demonstrates this interest (Anderson *et al.*, 2004a, 2004b). The articles have covered a variety of topics. Landscape

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factors that promoted the establishment of invasive species were investigated by Marvier *et al.* (2004), Neubert and Parker (2004), and With (2004). In risk assessment terminology these would correspond to the exposure and persistence of the stressors section of the analysis. Landis (2004) presented a generalized conceptual model for the risk assessment of invasive species that included landscape structure and other stressors as confounding elements. Bartell and Nair (2004) presented the most complete risk analysis with most of the major components present. Maguire (2004) provided an example of decision making for the control of invasive species by using Hawaiian feral pigs as a case study. The bioeconomics of controlling invasive species with barrier zones was discussed by Sharov (2004). These diverse articles demonstrate that the risk assessment of invasive species is a developing area in risk assessment with implications for ecological systems, human health, and in the arena of intentional introductions to produce economic, health, and ecological impacts.

*Invasive Species:* The goal of this article is to further the development of this subdiscipline by examining both the spread and resultant impacts of invasive species in a patchy landscape. We present a simple stochastic two species three patch dynamic model derived from Wu *et al.* (1993) and Spromberg *et al.* (1998) to explore patterns in the establishment of invasive species and impacts upon a local population. We find that competition increases population variability, but decreases the number of distinct outcomes possible from the same initial conditions. The main determinant of successful establishment is isolation of the patch of the introduction through a process we call the beachhead effect. Coexistence of species was often possible in local patches, contrary to analytical solutions of Lotka-Volterra equations and numerous modeling studies. Toxic contaminants were important as contributors to the stochastic nature of models, leading to a variety of outcomes from some sets of initial conditions.

The next sections review previous studies of invasive species, outline the specific characteristics that are unique to modeling nonindigenous species, present our modeling approach, summarize our simulation outcomes, and compare our results to other modeling and empirical studies. The last section will present the implications of these studies for future risk assessments of invasive species and list the research needs.

### **1.1. Studies of the Establishment and Effects of Nonindigenous Species**

The study of invasive species has been approached largely on a case-by-case basis and field studies often have been too idiosyncratic to be used to derive general hypothesis of invasive species establishment (Vermeij, 1996). Laboratory and garden studies are hampered by problems of scale, replication, and control (Doak *et al.*, 1998; Wardle, 2001). Hypothesized mechanisms for invasive species establishment and spread abound and most may be separated into two general categories: (1) attributes of the nonindigenous species and (2) attributes of the community into which the invasive species has arrived. Studies considering the former are typically searches for lists of common traits among the various species of invasive species, and exceptions to these lists are common (Mack *et al.*, 2000).

First, one of the strongest predictors of plant introductions is if the species has established in another location (Kolar & Lodge, 2001). In fish invasions of the Great Lakes, factors like relative slower growth rate, tolerance of a wide temperature range, and poor survival at higher temperatures were associated with the rapid spread (Kolar & Lodge, 2002). Examining the past patterns of invasion or home range characteristics can also prove predictive for a variety of species (Kolar, 2004). The second category of hypotheses includes vacant niche, enemy escape, disturbance, and species richness or diversity (Mack *et al.*, 2000; Shea & Chesson, 2002). However, we may not yet know enough about ecosystem functioning to relate these types of observations to the larger questions of prediction, policy, and management (National Science and Technology Council Committee on the Environment and Natural Resources, 1999).

### **1.2. The Characteristics of Invasive Species Critical for Ecological Risk Assessment**

There are four features of invasive species ecological risk assessment that are in contrast to risk assessment for chemicals and other abiotic stressors (Landis, 2004).

First, the exposure to the stressor becomes the probability of a biological invasion event even if a permanent introduction throughout the landscape does not occur. The success of an introduction over a specified timeframe is clearly tied to migration rates, the habitat specificity, suitability of the new

environment, the isolation of the receiving habitat, the size of the receiving environment, the frequency of disturbance within the landscape, and historical events that may preclude or enhance invasion.

Second, the population size of the invasive species can increase, fluctuate, or even become extinct. Crowding effects, competition from native species, and variation in migration pathways can change rates of migration within and between habitat patches. Risk assessment for invasive species requires understanding of the life history, population dynamics, and ecology of the introduced species.

Third, there is a broad range of mechanisms by which invasive species can directly and indirectly impact the valued characteristics of the receiving environment. For example, direct and indirect competition, physical habitat alteration, and changes in prey-predator interactions are typically named. Landscape-level impacts may also occur by a change in the ecological matrix through which migration occurs, altering the spatial relationships of important habitat patches.

Fourth, the processes that govern impacts are fundamentally ecological and evolutionary. These processes are therefore contingent, probabilistic, and dynamic. The dynamics of both the invasive species and the affected population are critical factors in estimating the risk, especially if the ecological services being delivered to the stakeholders are based upon the taking of resources such as a fishery, silviculture, or subsistence harvesting. Because of the stochastic nature of ecological systems there may be several outcomes possible from the exact same initial conditions and the risk assessment should account for this possibility.

Each of these four factors also takes place within an ecological landscape with a variety of patches containing species with populations of varying characteristics. Migration between habitat patches may be an important factor; therefore, the characteristics of the environment in these migration corridors need to be incorporated.

### 1.3. Model Background

There are two common formulations of metapopulation models used to describe species interactions. The first, patch occupancy models, are the oldest, simplest (McLaughlin & Landis, 2000), and most common. In its simplest form, patch occupancy determines the fraction of occupied patches based on the rates of colonization and extinction of species in patches.

However, patch occupancy excludes the possibility of local coexistence (Amarasekare & Nisbet, 2001). Bengtsson (1991) used patch occupancy to determine that interspecific competition of *Daphnia* species is important for their distributional dynamics and coexistence in rockpools around Sweden and the Baltic Sea.

A patch occupancy model that examines disturbance, habitat fragmentation, and habitat loss on the risk due to invasives has been created by Marvier *et al.* (2004). In this model framework, disturbance was a reduction in the amount of habitat occupied by either a specialist or generalist species. The output suggested that the higher the degree of disturbance within a system, the greater the likelihood of invasion. The species that will be favored will also be generalists rather than specialists.

The second type of model is based upon the work of Wu *et al.* (1993) that simulates the dynamic of a population within a patch and the movement of organisms between patches. Modification of this approach by Spromberg *et al.* (1998) and McLaughlin and Landis (2000) was used to investigate the importance of environmental contaminants in spatially structured population. These studies demonstrated that toxicants may have dramatic impacts on neighbor populations through action at a distance (Spromberg *et al.*, 1998). The type of model developed here is a derivation of these models with competition added between two species.

Application of the classic Lotka-Volterra (LV) formulation for competing species can be applied to the patch dynamics simulations. Spatial LV metapopulation models observe how space influences the coexistence of competing species when nonspatial formulations of the LV model predict otherwise (Bolker *et al.*, 2003). Spatial variants of LV relax or remove the assumption in patch occupancy models of a homogenous environment and LV allows local (patch) population dynamics to influence the dynamics of the metapopulation.

Amarasekare and Nisbet (2001) review empirical evidence demonstrating the local coexistence of superior and inferior competitors. Using a two patch Lotka-Volterra competition model they demonstrate a source-sink system is better able to describe the dynamics of asymmetrically competing species coexistence than a colonization extinction approach. Buttel *et al.* (2002) have drawn a similar conclusion using a spatially explicit patch model.

Our goal is to examine the invasion and impacts of an invasive species in a relatively simple patch model

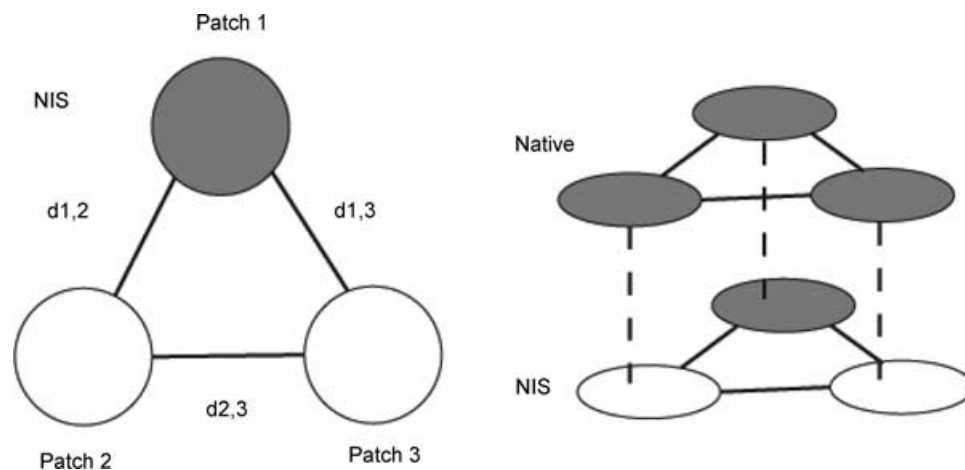
that incorporates competition, a toxicant, and flexibility in the shape of the landscape. The application of a toxicant in these models occurs only within a portion of a habitable patch. Depending upon the concentration, toxicity, and persistence of the toxicant, the population may persist within the patch. The persistence of the population within a patch during disturbance allows a different type of population dynamic to be investigated compared to a patch occupancy model as in Marvier *et al.* (2004). The next section describes our model development and the conditions under which the simulations were performed.

## 2. METHODS

The patch dynamic models were developed in this study to simulate the spread and trends of invasive species establishment with toxicant exposure and effects. Both models were derivatives of the circular three patch dynamic model of Spromberg *et al.* (1998) with either persistent or nonpersistent toxicants in the system. The diagram of the model and the Stella code can be obtained by contacting Wayne Landis at landis@cc.wvu.edu.

### 2.1. Patch Arrangements

Three patches were connected in a circular form (Fig. 1). The distance between the neighboring patches was 1. The distance between the neighboring



**Fig. 1.** Basic layout of the patch dynamic model. The basic form is the three patch circular model as found in Spromberg *et al.* (1998). Essentially, each layer represents the dynamics of either the native or nonindigenous species and each layer is connected to calculate the interactions between each species. Three patches are arranged in a circular fashion to represent the three patches in the landscape. The distances between the patches can vary and relate to the relative rate of migration of the organisms between patches. The introduced species typically starts in Patch 1 and the native can be found in every patch (shaded areas). The relative competitive ability of each species, the amount of toxicant, and the initial population size can be set for each patch.

patches with the patch of introduction varied from 1 to 100. A distance of 10 indicates that 10 times less migration occurs when compared to a distance of 1.

### 2.2. Competition and Crowding-Based Growth Rates

The growth rate of a single species in the previous models was based on the crowding of the single species in the local patch based on a growth curve. The growth curve defines both the assumptions of minimum viable population (MVP) and carrying capacity (CC) of a patch. For a two species one resource system, there is a CC for both species where the sum of both species cannot persist above. Using a single growth curve for both species by calculating combined growth meets the assumption of carrying capacity but does not meet the assumption of MVP because the individuals would persist in a patch as long as the sum of the two populations is larger than either of their MVPs. If separate growth curves are used to meet the assumption of MVP, then the assumption CC is not met, but rather the model simulates the presence of two equally abundant resources. In order to meet both the assumptions of MVP and CC, the growth rate of a species near its MVP is dependent only on its own density and the growth rate of a population that exists near the carrying capacity depends on the total crowding in the patch. This approach is similar to an Allee effect at low densities where the growth rate of a

**Table I.** Scenarios for Simulation. Each Set of Scenarios was Run with Persistent and Nonpersistent Toxicants for a Set of Eight Different Types of Combinations

Scenarios	Variables				
	Initial Number of Native Species	Dose Application	Toxicant Dose	Distances	Competition
1	200% MVP	All patches	LD0 – LD100	1–100	0.1 – 100
2	200% MVP	Patch of introduction	LD0 – LD100	1–100	0.1 – 100
3	CC	All patches	LD0 – LD100	1–100	0.1 – 100
4	CC	Patch of introduction	LD0 – LD100	1–100	0.1 – 100

population decreases (Ferdy & Molofsky, 2002). Both species have identical growth curves at low crowding, but “share” a growth curve at high crowding.

Competition was modeled by ranking the two species present on a ratio scale, dividing each ranking by their sum, and forming relative rankings. Competition was made relevant at the local scale by multiplying the relative competitive ability by the local crowding of a species. The resulting competitive terms determined the fitness of the species and in turn determined the growth of the species.

**2.3. Migration**

The competition terms for both species were added to create a total competition factor for each patch. Total competition was used to determine migration between patches conceptually as a flow down a competition gradient. The total competition function allows migration to be dependent on both intra- and interspecific competition.

**2.4. Scenarios**

The scenarios for both the persistent and nonpersistent toxicant models were the same, with minor deviations (Table I). Each model consisted of four different scenarios with varying competition, toxicant dose, distance between patch of introduction to neighboring patches, and initial native population.

**2.5. Simulation Conditions**

Each initial condition in the four scenarios was run from 10 to over 100 times in order to obtain a representative proportion of results. Baseline simulations for the persistent toxicant model were conducted in the absence of a second species and produced results comparable to Spromberg *et al.* (1998) for both species. Baseline simulations for the nonpersistent toxicant model were conducted with a dose of LD0

and gave comparable results to the persistent toxicant model.

**2.6. Initial Number of Organisms**

The introduced species was initiated in the patch of introduction at 110% of the MVP and the native species was initiated at either 200% of the MVP or at CC.

**2.7. Toxicant Characteristics**

One set of simulations had a persistent exposure function and the other had a nonpersistent exposure function. The nonpersistent toxicant degraded at a constant rate over time during the simulation. The toxicant dose was based on a standard dose-response curve. At LD100, the toxicant dose degraded to 0 before the 60th iteration. In all scenarios, only the native species was dosed. The toxicant dose for all scenarios was varied at LD0, LD25, LD50, and LD100. The toxicant was applied to all patches or the patch of introduction only. Modifications were made to the previous models to estimate the crowding-based growth rates, competition, and migration.

**2.8. Competition**

In all scenarios, the competition of the invasive species was initiated at 10 times less competitive, equal competitive, and 2, 10, 50, and 100 times more competitive. A competition of 1 indicates that both species are equally competitive and a competition of 10 indicates that the invasive species is 10 times more competitive than the native species.

**2.9. Running the Models**

The model was constructed and run using the program STELLA (v.7.0.3 and v. 8.1 HPS Inc., www.hps-inc.com). The model was run for 300 time iterations in

each simulation, with 0.25 step intervals with Euler's Method.

### 3. RESULTS

The outcomes of the simulations with the persistent and then the nonpersistent or degradative toxicant are presented below. Table II presents the types of outcomes for both kinds of toxicants listing each type according to the results in each patch. Table III presents a detailed accounting for the results of the persistent toxicant simulations, with the type of outcome and the percentage occurrence.

#### 3.1. Persistent Toxicant Simulations

Population variability was a result of stochastic toxicant exposure, and the amount of variability increased with increasing dose. Larger variation was evident in all doses, though only in the dose of LD100 was the variation large enough for multiple outcomes to occur. Increasing the competitive ability of the introduced species while maintaining a constant dose increased variability in runs that included toxicant exposure (Fig. 2). As can be seen within scenarios in Table II, increased population variability due to competition decreased the number of distinct outcomes, causing an overall decrease in the number of distinct runs. In these instances, the increased variation in a population due to competition acted to increase the probability that the population will be driven below the MVP. As more patches experienced increased variability, the possible outcomes quickly converged on a few simple monospecific source-sink dynamics or extinction, rather than on multiple source-sink dynamics involving regional and local coexistence. The increase in variability in native populations remained, even after the extinction of introduced species.

#### 3.2. Distinct Outcomes

There were a total of 16 distinct outcomes represented in the persistent model (Table II), though no set of initial conditions for a simulation displayed more than seven outcomes. Only simulations with LD100 in at least one patch showed more than one outcome for a set of initial conditions. The outcomes were ranked based on decreasing native species population and patch structure and increasing introduced species population and patch structure, i.e., a rank of 1 indicates that the native species reached carrying

**Table II.** Summary of the Types of Outcomes for All Simulations. For the Invasive Species, Only the Results of the Patch 1 for the Invasive Species are Shown, when Established in Patch 1 the Invasive Species Would Move into the Other Patches of the Landscape

Persistent Toxicant				
Native Species		Invasive Species		
P1	P3	P3	P1	
<b>Persistent Toxicant Outcomes</b>				
1	Persist <sup>3</sup>	Persist	Persist	Extinct
2	Persist	Persist	Persist	Establish <sup>4</sup>
3	Persist	Persist	Persist	Est. Mid <sup>5</sup>
4	MVP <sup>6</sup>	Persist	Persist	MVP
5	Est. Mid	Persist	Persist	Est. High <sup>7</sup>
6	Sink	Persist	Persist	Extinct
7	Sink	Persist	Persist	Establish
8	Extinct	Persist	Persist	Est. Mid.
9	Extinct	Persist	Persist	Dominant <sup>8</sup>
10	Sink	Sink	Persist	Extinct
11	Sink	Sink	Persist	Establish
12	Extinct	Sink	Persist	Dominant
13	Extinct	Extinct	Extinct	Extinct
14	Extinct	Extinct	Extinct	Establish
15	Extinct	Extinct	Extinct	Dominant
16	Extinct	Extinct	Extinct	Dominant-3 <sup>9</sup>
<b>Nonpersistent Toxicant Outcomes</b>				
1	Persist	Persist	Persist	Extinct
2	Persist	Persist	Persist	Establish
3	Est. high	Persist	Persist	Establish
4	Est. mid	Persist	Persist	Establish
5	Est. mid	Est. mid	Est. mid	Est. mid
6	MVP	Persist	Persist	MVP
7	Sink	Persist	Persist	Establish

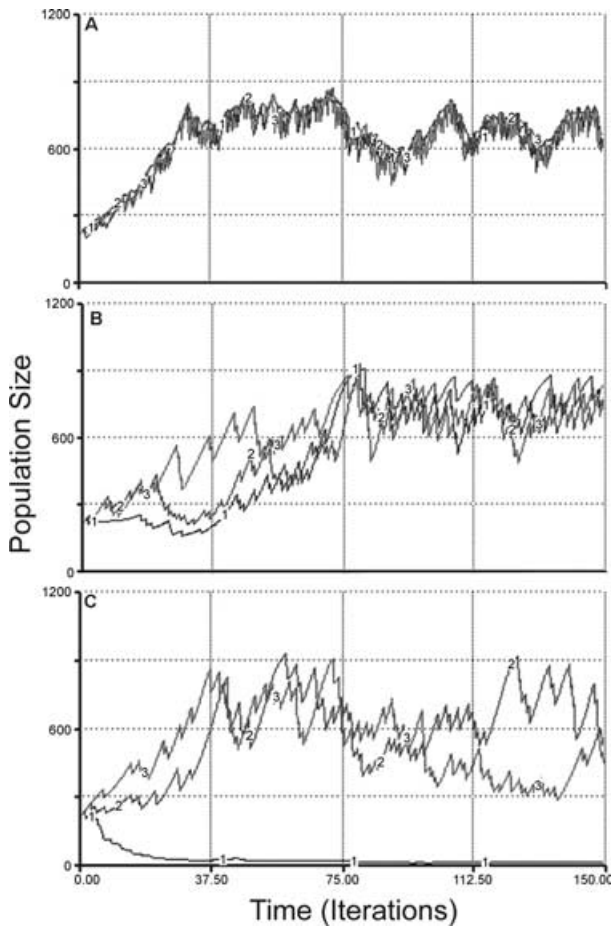
<sup>1</sup>Patch of the introduction.  
<sup>2</sup>Patches 2 and 3 are interchangeable in terms of dynamic shown.  
<sup>3</sup>Population persists at or near the CC.  
<sup>4</sup>Persistence at the population of introduction.  
<sup>5</sup>Population persists between the MVP and CC indefinitely.  
<sup>6</sup>Persistence at the MVP.  
<sup>7</sup>Persistence indefinitely nearer to the CC than MVP.  
<sup>8</sup>Invasive species established and then excluded the native species.  
<sup>9</sup>The invasive species reached carrying capacity in all three patches.

capacity in every patch and the introduced species did not establish. A rank of 16 indicates that the introduced species established, spread, and dominated every patch while the native species went extinct. Rankings did not indicate the frequency a particular outcome occurred. Table II describes the outcome types and Table III presents their probabilities of occurrence at LD100. Outcomes 7, 8, 9, 11, and 12 demonstrated regional coexistence where both species never occupied the same patch by the end of the simulation. Outcomes 2, 3, 4, and 5 showed local

**Table III.** Distribution of Outcomes at a Dose of LD100 for the Persistent Toxicant Simulations; the Numbers Refer to the Type of Outcome Listed in Table II under the Persistent Toxicant Simulation Heading, for Instance, under Scenario 1, Distance 1 and Competitive Ability 1 (see outlined cell), Outcome Type 1 Occurred in 46% of the Simulations and Outcome Type 13 Occurred in 54% of the Simulations

		Competitive Ability						
Distance		1	2	10	25	50	75	100
Scenario 1 <sup>1</sup>	0.1	<b>1(70)<sup>5</sup>, 13(30)</b>	<b>1(51), 6(47), 14(2)</b>	<b>1(65), 3(1), 9(1), 10(2), 13(2), 14(3), 15(27)</b>	<b>2(67), 9(1), 11(4), 14(3), 15(25)</b>	<b>2(26), 7(22), 9(10), 11(13), 14(1), 15(28)</b>	<b>2(30), 7(15), 9(14), 11(10), 14(1), 15(33)</b>	<b>2(25), 7(14), 9(21), 11(11), 15(29)</b>
	1	<b>1(46), 13(54)</b>	<b>1(48), 13(38), 14(14)</b>	<b>1(12), 2(27), 7(5), 9(1), 10(1), 14(1), 16(54)</b>	<b>7(24), 16(76)</b>	<b>2(1), 9(55), 15(38), 16(6)</b>	<b>2(1), 9(61), 14(1), 15(37)</b>	<b>9(56), 15(44)</b>
	2	<b>1(33), 13(67)</b>	<b>1(50), 7(1), 13(29), 14(20)</b>	<b>7(11), 9(1), 16(89)</b>	16	<b>9(6), 15(48), 16(46)</b>	<b>9(50), 15(49), 16(1)</b>	<b>8(64), 15(36)</b>
	10	<b>1(28), 10(26), 13(46)</b>	<b>7(46), 11(33), 14(31)</b>	16	16	<b>15(86), 16(14)</b>	16	<b>9(12), 15(88)</b>
	50	<b>6(13), 10(40), 13(47)</b>	<b>7(30), 11(49), 14(21), 7(24), 11(46), 14(30)</b>	16	16	15	15	15
	100	<b>6(9), 10(27), 13(64)</b>	<b>7(24), 11(46), 14(30)</b>	<b>9(1), 16(99)</b>	16	15	15	15
	Scenario 2 <sup>2</sup>	0.1	1 <sup>6</sup>	1	2	2	2	<b>2(71), 7(29)</b>
1		1	<b>1(55), 2(45)</b>	2	2	<b>2(14), 7(86)</b>	<b>2(10), 7(90)</b>	11
2		1	<b>1(55), 7(45)</b>	2	11	8	8	8
10		1	7	8	8	8	8	8
50		6	7	8	8	8	8	8
100		6	7	8	8	8	8	8
Scenario 3 <sup>3</sup>		0.1	1	1	1	4	4	4
	1	1	1	<b>1(80), 2(20)</b>	<b>2(42), 7(52), 9(4), 16(2)</b>	<b>2(13), 7(28), 9(58), 16(1)</b>	<b>2(10), 7(10), 9(80)</b>	<b>2(1), 7(7), 9(91)</b>
	2	1	1	<b>2(6), 7(69), 16(25)</b>	<b>7(5), 16(95), 9(2)</b>	<b>7(49), 9(1), 16(50)</b>	<b>9(93), 15(7)</b>	<b>9(97), 15(3)</b>
	10	1	<b>6(4), 5(79), 11(2), 14(1), 16(9)</b>	16	16	<b>15(70), 16(30)</b>	<b>9(2), 15(98)</b>	<b>9(55), 15(45)</b>
	50	<b>6(85), 10(12), 13(3)</b>	<b>7(9), 16(91)</b>	16	16	15	15	<b>16(90), 12(10)</b>
	100	<b>6(64), 10(18), 13(5), 16(8)</b>	<b>16(98), 14(1), 11(1)</b>	16	16	15	15	15
	Scenario 4 <sup>4</sup>	0.1	<b>1(38), 2(62)</b>	2	2	2	2	2
1		<b>1(5), 2(95)</b>	2	2	2	<b>2(79), 7(21)</b>	<b>2(37), 7(63)</b>	<b>3(21), 2(80)</b>
2		2	2	2	<b>2(3), 7(95), 9(2)</b>	<b>7(3), 9(97)</b>	9	9
10		2	<b>7(10), 9(90)</b>	9	9	9	9	9
50		9	9	9	9	9	9	9
100		9	9	9	9	9	9	9

<sup>1</sup>Scenario 1: Native population initiated at 200% MVP, toxicant in all patches.  
<sup>2</sup>Scenario 2: Native population initiated at 200% MVP, toxicant in patch of the introduction only.  
<sup>3</sup>Scenario 3: Native population initiated at CC, toxicant in all patches.  
<sup>4</sup>Scenario 4: Native population initiated at CC, toxicant in patch of the introduction only.  
<sup>5</sup>Numbers in parenthesis indicate percents of outcomes of given type.  
<sup>6</sup>Rankings represent 100% of the runs for the simulation, unless otherwise noted.



**Fig. 2.** Competition increases the variability in population dynamics of the native species. (A) No competition; (B) invasive species is five times more competitive; (C) invasive species 100 times more competitive and note extinction in Patch 1. The introduced invasive went extinct in each of the simulations shown. Other parameters were: toxicant LD100 in all patches, distance between patches of 1, and native species initiated at 200% of the minimum viable population size.

coexistence of competing species, where species occupied the same patch indefinitely.

### 3.3. Percent Establishment

Establishment was defined as persistence of the introduced species until the end of the run at any population above the MVP. At LD0, LD25, and LD50, when the native species was initiated at 200% of the carrying capacity, establishment occurred at all distances greater than 1 and at all competitive abilities except when the introduced species was less competitive. In the less competitive case, establishment occurred in all runs where distance was greater than 2.

Toxicant placement did not change the probability of establishment in these runs. Establishment occurred in all runs when the native species was initiated at carrying capacity and LD0, 25, or 50 in all patches.

At LD100 establishment was slightly more likely when the native species was initiated at 200% of the MVP than if initiated at carrying capacity (Fig. 3). When the native was initiated at carry capacity, toxicant decreased the potential for establishment when compared to the lower dosed runs at carrying capacity. When the native species was initiated at carrying capacity and experienced high toxicity, it was less likely that the introduced species would establish than when the native species was not experiencing toxicity.

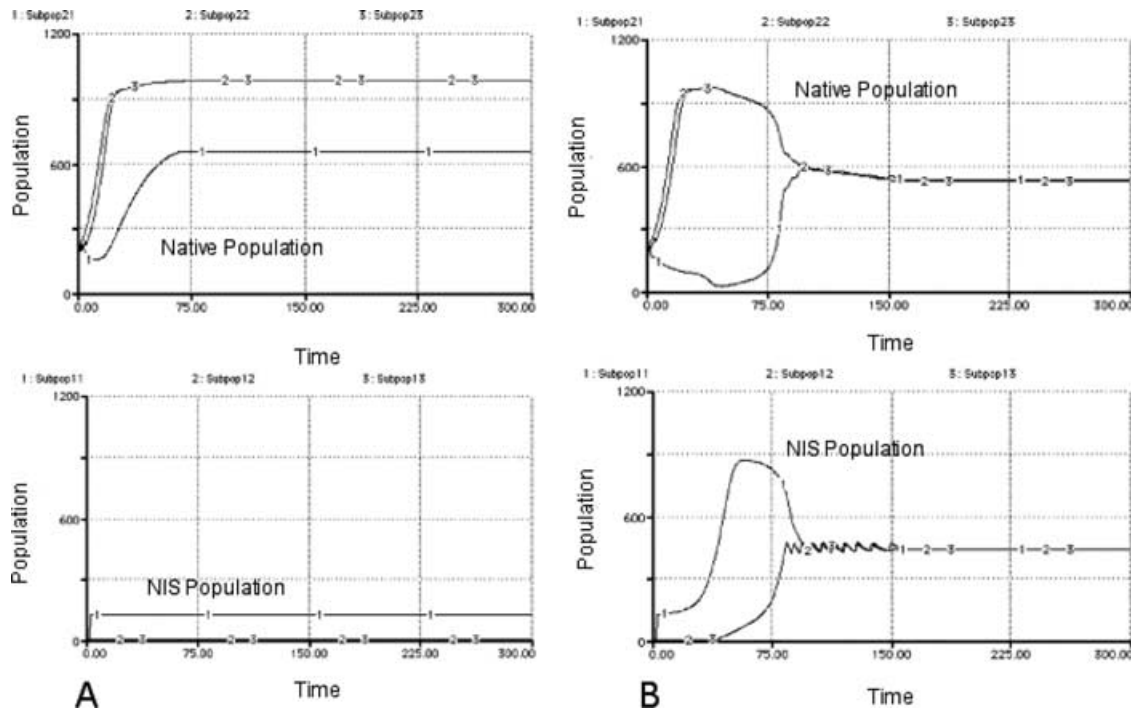
### 3.4. Percent Spread

The introduced species only spread from the patch of the introduction when toxicant dose was LD100 and present in all patches. Spread only occurred after initial establishment and domination of the invasive species in the patch of the introduction. Spread was observed both when the native species was initiated at 200% of the MVP and at carrying capacity. The latter increased the range of distances the introduced species was able to spread, but to do so the introduced species needed to be at least twice as competitive as the native species. As distance, and to a lesser degree, competitive ability increased, percent spread increased rapidly to 100% of the runs. When the simulation starts at carrying capacity, spread occurred in 9% of the runs at a distance of 1 when the competitive ability of the introduced species is 100 times that of the native species. The 200% MVP scenario showed spread at a distance of 25 while at carrying capacity (6b) the probability of a spread outcome was greater at the same distance. It would appear that the system that lacked available resources prompted spread when compared to the 200% MVP situation where resources were initially abundant as “low-hanging fruit.”

### 3.5. Nonpersistent Toxicant Simulations

#### 3.5.1. Scenario 1

All seven of the outcomes found in the nonpersistent toxicant results appeared in this scenario. The invasive species did not establish in any of the runs where the distance was 1. There was only one outcome for all initial conditions where the toxicant dose was LD0, LD25, and LD50. No initial condition had



**Fig. 3.** Two possible outcomes of simulation of the nonpersistent model initiated at a distance of 50, competition of 10, and LD100. The graphs of (A) and (B) are individual outcomes that appeared with the same initial conditions. The top section of each graph represents the population of the native species and the bottom graphs represent the population of the invasive species.

more than two outcomes. There were multiple outcomes when the initial condition had toxicant dose of LD100, competition of 10, and when the distance was 2, 10, 25, 50, 75, or 100 (see Fig. 3 for an example). There was a correlation between distances and competition with invasive species establishment. The invasive species establishment increased slightly with increasing distance when considering all initial competition conditions. For example, at LD0, the invasive species did not establish in any of the runs with a distance 1 but established in all of the runs with a distance of 100. The invasive species establishment increased with increasing competition when the distance was larger than 1. With increasing distances, there was a slight increase in variability and the number of outcomes. At LD0, LD25, and LD50, invasive species spread occurred when the competition was 50 and 100 with a distance of 10, 25, 50, 75, and 100. At LD100, invasive species spread occurred when the competition was 10, 50, and 100 with a distance of 10, 25, 50, 75, and 100.

### 3.5.2. Scenario 2

The result was very similar to Scenario 1. Like Scenario 1, all seven outcomes appeared. Invasive

species establishment only occurred when the distance was more than one run. Most runs had single outcomes except for runs where the model was initiated at LD100, a distance of 10, 50, or 100, and competition was 10. The correlation between distances and competition with invasive species establishment was similar to that of Scenario 1. The proportions of outcomes when there were multiple outcomes were slightly different than that of Scenario 1. At LD0, LD25, and LD50, invasive species spread occurred when the competition was 50 and 100 with a distance of 10, 25, 50, 75, and 100. There was little spread when initiated at LD100, competition of 10, and a distance of 10 and larger. At LD100, competition of 50 and 100, and a distance of 10 and larger, there was 100% spread in all runs.

### 3.5.3. Scenario 3

The outcomes 1, 2, 3, 4, 5, and 7 appeared. The invasive species did not establish in any of the runs with a distance of 1 but did establish in some or all of the runs with distances of 2, 10, 50, and 100. All but one run had single outcomes. The one run with multiple outcomes occurred when the model was initiated at LD100, a distance of 2, and a competition

of 50. There was a correlation between distances and competition with invasive species establishment. The invasive species establishment increased slightly with increasing distance when considering all initial competition conditions. At all toxicant doses, the invasive species spread when the competition was 50 and higher and the distance was 50 and higher.

#### 3.5.4. Scenario 4

Outcomes 1, 2, 3, 4, 5, and 7 appeared in this scenario. Single outcomes appeared in all runs except for one set of conditions where the model was initiated at LD 100, distance of 2, and competition of 50. There was no invasive species establishment at a distance of 1 and the establishment increased with increasing distances and competition. The proportion of outcome 1 decreased with increasing distances when considering all competition. The invasive species spread in the same initial competition and distance as Scenario 3.

### 3.6. Summary of Simulation Results

The models with different toxicant functions had different number of outcomes. Each outcome of the two models was assigned a number in order to record and analyze data (Table II). The outcome where the native species persists in all patches and the invasive species becomes extinct was assigned 1. As the population of native species decreased and the population of invasive species that establish increased the outcomes were assigned a larger number. The persistent toxicant model had a total of 16 outcomes and no simulation had more than seven outcomes. The nonpersistent toxicant model had a total of seven outcomes. Outcome 16 in the persistent toxicant model is when the invasive species established, spread, and dominated every patch while the native species went extinct. Outcome 7 in the nonpersistent toxicant model is when two native patches persist, one native patch becomes a sink, and the invasive species establishes and spreads. In both models, multiple outcomes only occurred when the models were initiated at LD100.

### 3.7. Population Variability

The trends in variability were similar for both the toxicant models. For all of the simulations, there was an increase in population variability with increasing competition across the same toxicant dose. The variability in some cases was very small and did not change the outcome. The initial variability was large

in other cases and caused different outcomes to occur. An increase in toxicant dose increases the population variability to a lesser degree. The increase in variability due to an increase in toxicant dose does not have as large an effect on the outcomes as competition. As more patches experienced increased variability, the possible outcomes quickly converged on monospecific-source sink dynamics or extinction, rather than on multiple-source sink dynamics involving regional and local coexistence. The increase in variability in native populations remained, even after the extinction of introduced species.

Even though those trends are similar, the effect of the increase in variability was different. In the persistent toxicant model, an increase in competition did not decrease the number of distinct outcomes, and might have slightly increased the number of outcomes. In the nonpersistent toxicant model, the variability increase due to competition caused a decrease in the number of distinct outcomes.

### 3.8. Establishment of Invasive Species

Establishment was defined as persistence of the introduced species until the end of the run at any population above the MVP. Establishment trends for both toxicant models were similar. With the persistent toxicant model, at LD0, LD25, and LD50 and when the native species was initiated at 200 of the MVP, establishment occurred at all distances greater than 1 and at all competitive abilities except when the introduced species was less competitive. In the less competitive case, establishment occurred in all runs where distance was greater than 2. Establishment occurred in all runs when the native species was initiated at carrying capacity and LD0, 25, or 50 in all patches. At LD100 establishment was slightly more likely when the native species was initiated at 200% of the MVP, than if initiated at carrying capacity. When the native species was initiated at carrying capacity, toxicant decreased the potential for establishment when compared to the lower dosed runs at carrying capacity. For the nonpersistent toxicant model, the invasive species established when the distance was greater than 1 in some or all of the simulations in all scenarios. Establishment increased with increasing distance and competition.

### 3.9. Spread of Invasive Species

In the persistent toxicant model, the introduced species only spread from the patch of the introduction

when toxicant dose was LD100 and present in all patches. When the native species was initiated at CC, the range of distances the introduced species was able to spread increased, but to do so the introduced species needed to be at least twice as competitive as the native species. As distance, and to a lesser degree, competitive ability increased, percent spread increased rapidly to 100% of the runs.

With the nonpersistent toxicant model, spread of the invasive species mostly occurred only when it was much more competitive than the native species and at a larger distance. Whether the toxicant was added to the patch of introduction only or to all of the patches had little effect on the invasive species spread. When spread occurred at a competitive level, it usually occurred at increasing distances. From the various trends in the simulations, there was usually establishment with no spread followed by establishments with spread.

In both toxicant models, spread only occurred after initial establishment and domination of the invasive species in the patch of the introduction. Spread of the invasive species was observed both when the native species was initiated at 200% of the MVP and at carrying capacity.

#### 4. DISCUSSION

The models are clearly idealized representations of a simple three patch, patchy population without age structure and no delays between exposure to the toxicant (disturbance) and death. The competition between the species native to the patch and the invasive is also a simple Lotka-Volterra model with no mechanism specified and parameters such as competition coefficient and carrying capacity incorporated. In these models there is an assumption of a MVP, so there is not a scenario where the introduction by one parthenogenic organism can lead to its establishment in the landscape. The models used a toxicant with a typical concentration response as the disturbance, but other kinds of disturbances with their specific exposure response could easily be incorporated. However, even with these limitations the simulations present interesting patterns that could be important in understanding the risks due to invasive species.

##### 4.1. The Beachhead Effect and Competition

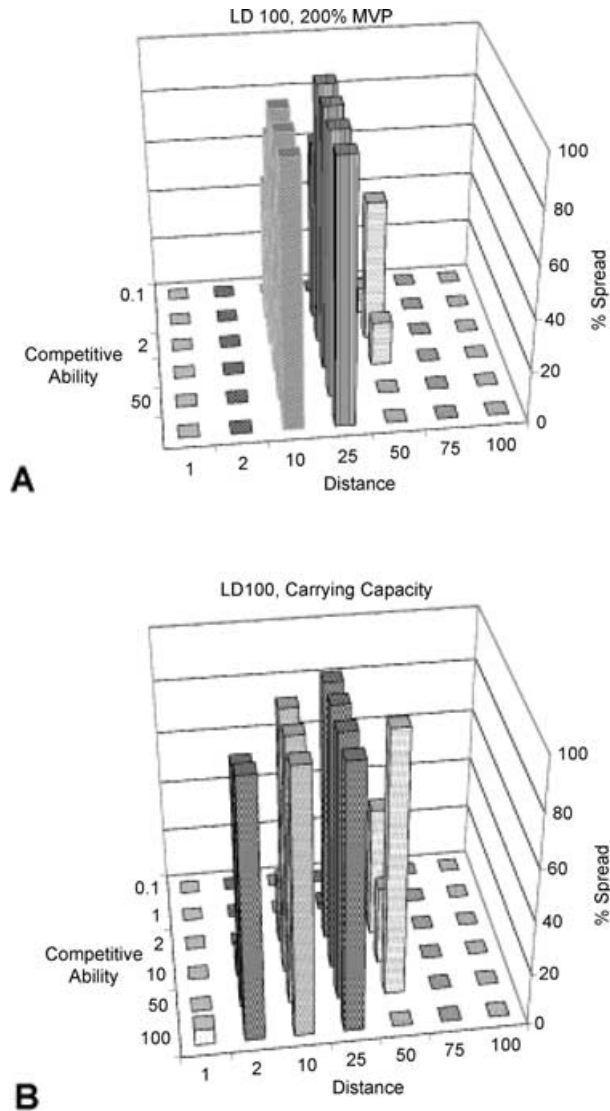
The dynamics of the introduced species in this model may be described as the establishment of a beachhead population in the patch of the introduc-

tion. The beachhead effect describes initial isolation leading to establishment, coexistence, and possible spread of an introduced species. Habitat availability alters dispersal rates in the cases discussed above of (1) higher native toxicity decreasing the chance of establishment, and (2) increasing chance of spread when the native species is at carrying capacity. In the former, dispersal is increased and establishment occurs less often. In the latter, dispersal is decreased and establishment is possible. Increasing the isolation of the patch of the introduction also decreases initial dispersal but increases the probability of establishment in a patch and spread throughout the model landscape (Fig. 4).

These counterintuitive results are the result of the invasive species population being introduced very near the MVP, a likely situation for a successful introduction. After the introduction event, if dispersal is low due to lack of habitat in neighbor patches or large distances between patches, the population grows above the MVP and persists. The presence of toxicant and competitive abilities has little influence on this initial establishment. If dispersal between patches is high due to ample resource availability or near neighbors, then the introduced population may migrate out of the patch of the introduction causing a decline in the population in that patch to below the MVP.

Solving for the equilibriums of a two patch system, Amarasekare and Nisbet (2001) also found a threshold effect where dispersal above a certain level was disadvantageous in the same way as the observed beachhead effect discussed above. As in Spromberg *et al.* (1998) and Wu *et al.* (1993), the spatial arrangement of patches contributes greatly to the extinction or persistence of species. Here, we show that the local coexistence of two species is also heavily dependent on the spatial component of patches.

Analytical solutions of Lotka-Volterra equations often cited in introductory ecology courses predict species coexistence in a homogenous environment under most situations is not possible. Recent studies have continued to find in even more elaborate models that regional coexistence requires spatial or temporal separation of competing species (Doncaster *et al.*, 2003; Ferdy & Molofsky, 2002; Higgins & Cain, 2002; Levin, 1974), particularly via habitat heterogeneity (Wang *et al.*, 2002). Alternatively to these findings, the number of coexisting species cannot be greater than the number of types of local resources, or for coexistence to occur there must be at least one area in the region where each species exists with higher productivity than the other in that region (Iwasa &



**Fig. 4.** Beachhead effect-persistent toxicant. Panel A represents the percent spread at LD 100 and native species initiated at 200% minimal viable population. Panel B presents the percent spread at LD 100 and native species initiated at the carrying capacity. Note that with the native species at carrying capacity, the invasive species could be successful under a wider range of initial conditions.

Roughgarden, 1986), i.e., in a source-sink fashion. Most models, until now, have robustly predicted that at the local, or within-patch scale, coexistence is not possible (Doncaster *et al.*, 2003; Hassell *et al.*, 1994), or possible only when recolonization events from outside the system occur (Taneyhill, 2000).

The exception to the above is the spatial LV model by Amarasekara and Nisbet (2001), who found analytically that local coexistence may be possible under

the condition of spatial heterogeneity of competitive ability. In our model such heterogeneity is not an explicit parameter of the model, but may have resulted from the dependence of competitive ability on crowding. The iterative, instead of analytical, approach we used to simulate introduction and competition means that the competitive abilities of a population are often very different by the end of simulation than at the beginning.

Local species segregation is not necessary for coexistence in our model. In the persistent toxicant model outcomes, numbers 2, 3, 4, and 5 show coexistence of both species in the patch of the introduction above their MVP, indicating that neither species required immigrants to maintain that population. Outcome 3 only occurred once during all simulations, other outcomes occurred 41%, 19%, and 5% of all runs, respectively. Together, outcomes showing local coexistence make up the majority (65%) of the runs. The patch of the introduction is occupied indefinitely by both species at a variety of initial conditions, with isolation of the patch and dispersal of the invasive species the primary determinates of establishment. However, neither regional nor local coexistence is observed if the introduced species spreads from the patch of the introduction, as the invasive species always dominates the system after spread.

Spread is only observed when toxicant dose and competitive ability of the invasive species are very high, causing large variability in the dynamics of the population. The dynamics in the patch of the introduction may be different from establishment in subsequent patches because the former is driven by a single introduction event, rather than multiple events. Once established, spread would be in the form of multiple introductions with the neighbors receiving new individuals during each time step, rapidly raising the new colony above the MVP. Subsequent domination of neighbor patches is achieved through a combination both of competitive ability and stochastic toxicant death of the native species. The former is demonstrated by increasing spread with increasing competitive ability in Fig. 4. The latter is evidenced by the fact that spread only occurs at the highest levels of variability.

Bengtsson (1989) found that interspecific competition in *Daphnia* species in rockpools increased the rates of local extinction. Our analysis provides a mechanism. Extinction of *Daphnia* in these rockpools may be a result that interspecific competition increases variability and outcomes converge on extinction of one species. Unfortunately, the reported

coefficients of variation for population density in this article are not adequate to test this hypothesis.

Goldwasser *et al.* (1994) modeled the effect of variability on invasion dynamics for plants and reported that a few highly dispersive individuals could increase the rate of spread of species. Durrett and Levins (1998) also predict that the ability to disperse at longer distances can allow a weaker competitor to overcome a stronger competitor. We show that for the case of a population being near the MVP, a few fast dispersers could drive an introduced species to extinction by decreasing the initial population below the MVP. Outcomes also demonstrate there is not a required tradeoff between competitive and dispersal ability for coexistence to occur regionally as the models by Durrett and Levins (1998) and Hassell *et al.* (1994) predict. The current model is in agreement with Higgins and Cain (2002), Doncaster *et al.* (2003), and Gourbiere and Gourbiere (2002) concerning the competition dispersal trade-off.

Some of the general predictions are in agreement with a few previous studies. Vermeij (1996) postulates that the characteristics that make for a good disperser may differ from those that make a species good at establishing a beachhead. We provide a reasonable mechanism for this observation.

#### 4.2. Disturbance

Disturbance as portrayed in this model had different properties compared to the patch occupancy model of Marvier *et al.* (2004). In these models the organisms interact with the toxicant on a stochastic basis and since migration from other patches can rescue the population, extinction within a patch is not the only outcome. In our model the toxicant alters the dynamics of the population growth and of the migration between patches.

The outputs and conclusions of Marvier *et al.* (2004) do have some common features with the results of our models. An increase in disturbance and habitat fragmentation does increase the likelihood of an invasive species becoming established. In our models this corresponds to the distances between patches. In arrangements when the patches are closer, migration can save patches under invasion and prevent establishment of the invasive species. At longer distances between patches the establishment of the invasive is more likely. The increase in patch distance corresponds to the fragmentation as set in a patch occupancy model. At very long patch distances the

habitat is so fragmented that invasion is unlikely because of the low probability of immigration.

The toxicant disturbance did increase the variation in the dynamics and because a stochastic function described the interaction, multiple outcomes were possible from some sets of initial conditions. Other kinds of stressors may also disturb patches in similar ways. Heterogeneity within a patch due to erosion, fire, flood, or sedimentation may have effects similar to that of a toxicant.

#### 5. CONCLUSION

So as a summary, what properties of a species would enhance its ability to invade a new landscape? Our results suggest that a species that is very competitive, resistant to contaminants, and one that can delay its dispersal until it has established a “beachhead” in the landscape. The beachhead patch ensures that there is a source for further migration into the landscape. Even with these characteristics the invasive does not often persist in the landscape under the conditions of the simulation. Note that even in situations where the invasive is much more competitive, invasion is not a common outcome per infection. However, even low probability events can occur if the number of occurrences is high.

The implication is that a fragmented or patchy environment will be more likely to contain an invasive because of the increasing number of areas that can be colonized and used as beachheads for further colonization. If the invasive can remain cryptic so that eradication efforts are limited until established in several refugia patches, the probability of a successful invasion should increase.

The models confirm work by many other researchers (see Anderson *et al.*, 2004a, 2004b; Marvier *et al.*, 2004) that there is a clear interaction between the landscape, competing species, and the invasive species. Spatial structure must be incorporated if an understanding of the possible outcomes is to be factored into the risk analysis. The interaction between the toxic contaminant and the native species demonstrated that only in high doses did the contaminant influence the outcome of the invasion. Nonetheless, the stochastic nature of the exposure to the contaminant allowed multiple outcomes to result from the same initial conditions. Stressors other than contaminants may also interact with the competing species in a stochastic manner. In order to reduce uncertainty in the risk estimate the interactions of the stressors

with the invasive species and the assessment species should be understood and computed.

The process of invasive species risk assessment and the findings of this study also have applications in at least two other areas. The first is the risk assessment of genetically modified organisms and the associated genetic elements. The second is in the arena of intentionally introduced organisms, whether for agriculture, aquaculture, or for malicious intent.

The dynamics of these models also have applicability to the estimate of risks due to novel introduced elements in genetically modified organisms. Watrud *et al.* (2004) has demonstrated that landscape-level gene flow does occur in bentgrass using a glyphosate herbicide resistance marker. Introgression into native plants was detected 14 km from the source and at 21 km in sentinel plants. Glyphosate resistance was transferred to seed sets of plants within the landscape to an area of approximately 310 km<sup>2</sup>. Landis *et al.* (2000) have modeled the patch dynamics of genetic elements moving between bacterial hosts and the concomitant alterations in the dynamics of the host populations. A variety of dynamics resulted, depending upon the selective advantage and the rate of transmission of the genetic element. It is possible to model movable genetic elements or the gametes from genetically modified organisms as replicating units in an invasive species framework. It is time to combine field studies and the modeling of the patch dynamics to generate likely hypothesis and to generate risk assessment tools for genetically modified organisms.

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