SRP13776

Risk Analysis, Vol. 24, No. 4, 2004

Habitat Destruction, Fragmentation, and Disturbance Promote Invasion by Habitat Generalists in a Multispecies Metapopulation

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Species invasions are extremely common and are vastly outpacing the ability of resource agencies to address each invasion, one species at a time. Management actions that target the whole landscape or ecosystem may provide more cost-effective protection against the establishment of invasive species than a species-by-species approach. To explore what ecosystem-level actions might effectively reduce invasions, we developed a multispecies, multihabitat metapopulation model. We assume that species that successfully establish themselves outside their native range tend to be habitat generalists and that a tradeoff exists between competitive ability and habitat breadth, such that habitat specialists are competitively superior to habitat generalists. In this model, habitat destruction, fragmentation, and short-term disturbances all favor invasion by habitat generalists, despite the inferior competitive abilities of generalist species. Our model results illustrate that providing relatively undisturbed habitat and preventing further habitat degradation and fragmentation can provide a highly cost-effective defense against invasive species.

KEY WORDS: Ecological specialization; invasive species; nonnative species

1. INTRODUCTION

Exotic species will forever be common components of every ecosystem on Earth. This fact argues for a skeptical examination of invasion research, prevention, and control. Given the current extent of the exotic species problem and the fact that resources for the control of nonindigenous species are limited, ecologists can best contribute to management efforts by helping to identify clear priorities about which battles against invasive species we should fight and which we should forfeit. In this article, we first emphasize that a species-by-species approach to the problem of invasive species, although valuable for building up generalities about invasive species, cannot possibly keep pace with the current rate of species introductions. We then use a simple model to develop a hypothesis that links the success of biological invasions to habitat loss, habitat fragmentation, and short-term disturbance. Our model results lead us to suggest that the protection of relatively undisturbed habitats should be an important component of any strategy of defense against invasive species. If general habitat loss and degradation are key contributors to the success of nonindigenous organisms, then cost-benefit considerations argue that fighting invasions is most likely to be successful when the region has not yet suffered too much habitat loss.

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SRP13777

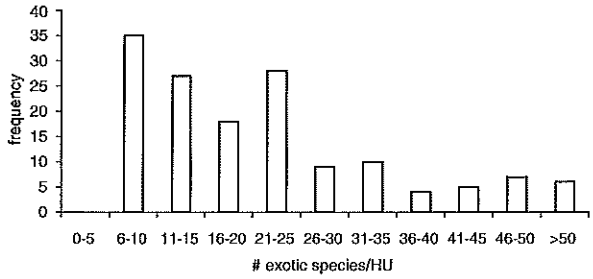

Fig. 1. Total number of exotic species in 149 4th field hydrologic units (HU) of the Columbia River Basin. Animal data are from the CBFWA sub-basin assessments (available at ⟨http: www//cbfwa.org/cfsite/documents.cfm⟩). Plant data are from the Washington Department of Ecology at http://www.ecy.wa.gov/programs/cap/env-info.html.

The introduction of nonnative species has far outpaced the ability of ecologists to study the consequences of each invasion or to develop a management strategy for every exotic species that becomes established. For example, of the 5,862 species in the flora of California, 1,023 (over 17%) are naturalized aliens.[1] At a smaller spatial scale, the Columbia Basin Fish and Wildlife Authority (CBFWA) has assembled data tabulating the exotic species recorded from subbasins within the Columbia Basin (or 4th-field hydrological units, which range in size from 500 to 9,330 km^2). The median number of nonnative species per 4th-field hydrologic unit is 19 species, with over 40 exotic species recorded from many watersheds (Fig. 1). On a larger scale, the numbers of introduced species present in the Unites States, United Kingdom, Australia, South Africa, India, and Brazil range from 2,000 to 50,000 per country and total approximately 480,000 invasions.[2] These statistics demonstrate that there are likely to be numerous exotic species in any particular place, and that it is impractical to expect that detailed risk analyses might be developed for every introduced species in every invaded ecosystem.

The development and parameterization of the detailed models may be important for the management of particularly noxious pests, but given the deluge of exotic species, it would be more efficient to manage habitats and ecosystems to prevent invasions, rather than developing management plans on a species-by-species basis. Thus, the theory we examine is aimed at habitat and ecosystem actions, rather than species-specific strategizing. In our model, we assume that invaders tend to be ecological generalists. Before discussing the details of the model, we first examine the evidence that supports this assumption.

2. WHAT IS THE EVIDENCE THAT INVASIVE SPECIES TEND TO BE HABITAT GENERALISTS?

Because we focus here on a generic habitat-modeling approach rather than a species-specific model, we first consider what might be generic keys to the success of biological invasions. In 1965, Herbert Baker hypothesized that many colonizing or invasive species owed their success to their ability to thrive in a wide variety of habitats or environments.[3,4] Anecdotal tabulations of some of our most notorious animal invaders support this idea. For example, opossums, the Norway rat, and starlings represent vertebrates that have greatly expanded their ranges in North America, due partly to their ability to thrive in a wide variety of habitats. In addition, many studies have attempted to identify the traits of successful invaders, often by comparing the traits of successful invaders to those of noninvasive species.[5,6] Several such studies have found that the degree of habitat generalization is a good indicator of invasion success. For example, the number of "climate types" in which a southern African plant naturally occurs and the geographic extent of the plant's native distribution are good indicators of the plant's weed status within Australia.[7] Goodwin *et al.*[8] similarly point to a species' native geographic range as an important predictor of invasiveness. Although geographic range is not necessarily related to a species' ability to use multiple types of habitats, the two features are often correlated.[9] Comparisons among closely related taxa further support this generalization. For example, among four *Polygonum* species, the most invasive species was the one capable of performing well under the broadest range of environmental conditions.[10] A similar comparison of two cyprinid fish species suggests that the more successful invasion by one of the species is likely due to a higher degree of phenotypic plasticity and the ability to do well under a broader range of conditions.[11] Finally, the invasive *Senecio madagascariensis* (Asteraceae) performs well under a broader range of habitats than its noninvasive congener *S. lautus*.[12]

A related issue pertains to the likelihood of extinction. In particular, if generalists are more successful at establishing, spreading, and attaining high population densities, then, arguably, they should also be less likely to become extinct. Evidence from both fossil and modern species assemblages supports the notion that species with generalized habitat needs are indeed less prone to extinction.[13] For example, among the 197 freshwater fish species historically native to

Virginia, extirpated species tended to be more ecologically specialized.[14]

Although not every invasive species is a habitat generalist, comparisons within taxa indicate that invasive species (and species that are less extinction prone) tend to exhibit habitat preferences that are broad relative to those of closely related noninvasive species. Given this pattern, we turn our attention to the effects of habitat disturbance on the persistence of specialist (and presumably native) species and an invading habitat generalist, coexisting in a patchy habitat.

3. A SIMPLE METAPOPULATION MODEL CONNECTING HABITAT LOSS TO INVASIONS BY GENERALIST SPECIES

Here, we consider a multispecies metapopulation model that tracks the proportion of sites occupied by species that represent different degrees of habitat specialization. Specifically, our model represents an extension of metapopulation analyses aimed at asking how habitat destruction alters competitive coexistence.[15–17] These previous models have typically divided the world into "habitat" versus "nonhabitat," and used the increase of "nonhabitat" to represent habitat destruction. We adopt a similar approach here, but add the complication that there is more than one type of suitable habitat. We consider an environment consisting of an infinite number of sites or patches, of which only a fraction are suitable for occupancy by any species, with some habitable patches being empty at any given time. For simplicity, our model includes two types of usable habitat, types A and B, and three different species. Species a, which occupies the fraction $p_a(t)$ of the entire collection of sites at time t, can occupy only habitats of type A. Species b, which occupies the fraction $p_b(t)$ of all sites, can occupy only habitats of type B. Finally, there is a habitat generalist, species g, which occupies the fraction $p_g(t)$ of both habitat types A and B. The entire landscape is divided into three categories: the fraction of sites that is uninhabitable (denoted as U), the fraction of sites that is habitat A (denoted A), and the fraction of sites that is habitat B (denoted as B), such that $U + A + B = 1$. Under these assumptions, we can track the changing proportions of site occupancy for each of the three species using a system of differential equations that depends on species-specific colonization and extinction rates:

$$\frac{dp_a}{dt} = c_a p_a(A - p_a) - e_a p_a, \tag{1}$$

$$\frac{dp_b}{dt} = c_b p_b(B - p_b) - e_b p_b, \tag{2}$$

$$\frac{dp_g}{dt} = c_g p_g(1 - p_g - p_a - p_b - U) - e_g p_g - c_a p_a p_g\left(\frac{A}{A+B}\right) - c_b p_b p_g\left(\frac{B}{A+B}\right). \tag{3}$$

Here, e_a, e_b, and e_g denote the extinction rate per patch for species a, b, and g, respectively. Similarly, c_a, c_b, and c_g respectively denote the probability of successful colonization per patch for species a, b, and g. We assume that colonists can disperse from any occupied patch to any other suitable patch. In using Equations (1)–(3), we assume that generalists are less-effective competitors when challenged by habitat specialists in the preferred habitat of the specialists. In fact, implicit in the first term of Equation (3) is the assumption that the generalist species is so competitively inferior to specialists that the generalist is unable to invade any site that is already occupied by a specialist. In addition, with the last two terms of Equation (3), we assume that, when a specialist colonizes a site that is occupied by the generalist, the generalist is immediately eliminated. Consider, for example, the last term of Equation (3). With this term we assume that species b can eliminate species g only from habitat of type B. Because generalists have no preference for either habitat type, we assume that, of the habitat occupied by generalists, the fraction $B/(A+B)$ is of type B.

The notion that a "jack of all trades is the master of none" has enjoyed a rich history in the ecological literature.[18,19] Table I provides a summary of several studies that document a tradeoff between competitive ability and ecological breadth. If we were to reverse the assumed competitive hierarchy and make the generalist species the competitive superior, the generalist species would always exclude the specialists—a result that is clearly unrealistic given the existence of specialist species in nature.

There is a unique positive (i.e., nonzero) equilibrium state of Equations (1)–(3):

$$\hat{p}_a = A - \frac{e_a}{c_a}, \tag{4}$$

$$\hat{p}_b = B - \frac{e_b}{c_b}, \tag{5}$$

$$\hat{p}_g = 1 - U - \hat{p}_a - \hat{p}_b - \frac{e_g}{c_g} - \frac{Ac_a\hat{p}_a + Bc_b\hat{p}_b}{(A+B)c_g}. \tag{6}$$

Table I. A Sample of Studies that Tested Whether a Tradeoff Exists Between Resource Breadth and Competitive Ability

Comparison	Finding
Foraging efficiency of a specialist pollinator species versus that of four generalist pollinator species[29]	Specialist was the most efficient forager.
Habitat selectivity and competitive ability of three small mammal species[30]	The habitat generalist was the weakest competitor, the habitat specialist was the strongest competitor, and the third species was intermediate in both respects.
Specialist (lac−, mal+) versus generalist (lac+, mal+) *E. coli*[31]	The specialist was more efficient at using maltose and outcompeted the generalist in a laczose-free environment.
Habitat selectivity and competitive ability of four small mammal species[32]	The three specialist species were competitively superior to the one generalist species.
Jackdaws forced to be either specialist or generalist feeders[33]	In most instances, generalists were less efficient feeders than specialists for each of the three different feeding modes.
Two species of copepod that parasitize flatfish[34]	The generalist copepod was more sensitive to competition than the specialist.
Two spiny mice, a microhabitat specialist and a microhabitat generalist[35]	The specialist appeared to be a more efficient forager than the generalist.
Specialist versus generalist nematodes parasitizing *Drosophila*[36]	Specialist was more efficient at infecting hosts and reproducing. Specialist outcompeted generalist in mixed infections.
Performance of specialist and generalist herbivores[37]	Review of bioassay studies found that specialist herbivores have higher survival and growth rate than generalists on diet of leaf discs containing phytochemicals from the specialist's host plants.

The equilibrium corresponds to a situation in which the fraction of sites occupied by species a, b, and g are unchanging. This equilibrium is positive if $A > (e_a/c_a)$, $B > (e_b/c_b)$, and

$$\frac{e_a}{c_a} + \frac{e_b}{c_b} > \frac{A(Ac_a - e_a) + B(Bc_b - e_b)}{(A+B)c_g} + \frac{e_g}{c_g}. \quad (7)$$

The equilibrium is stable whenever it is positive; that is, a sufficiently small perturbation of the equilibrium will eventually vanish (although the deviation may initially grow before shrinking).[20] Numerical simulations suggest that, if Equation (7) is satisfied, any initial condition with all three species present yields a solution that converges to this equilibrium.

To simplify the model further, we assume that extinction rates are identical across the three species ($e = e_a = e_b = e_g$), as are the colonization rates ($c = c_a = c_b = c_g$). Although other combinations of extinction and colonization are possible and even plausible (e.g., generalists might have higher colonization rates than specialists), we sought to examine how disturbance affects the balance among species that differ only in ecological breadth and competitive abilities, with all else being equal. We also assume that habitable patches are equally divided among types A and B and that the effects of habitat loss are symmetric, meaning that as U increases, habitat is lost equally from the two habitat types (i.e., $A = B$). These symmetry assumptions reduce the distinction among species to only two features: the degree of habitat specialization and the absolute competitive superiority of habitat specialists over habitat generalists. The assumptions also imply that species a and b are completely interchangeable; we therefore show results for one of these specialist species in the figures presented below.

Given these assumptions, the equilibrium state of Equations (4)–(6) simplifies to:

$$\hat{p}_a = \hat{p}_b = \frac{1-U}{2} - \frac{e}{c}, \quad (8)$$

$$\hat{p}_g = \frac{2e}{c} - \frac{1-U}{2}. \quad (9)$$

This equilibrium is positive if

$$1 - \frac{4e}{c} < U < 1 - \frac{2e}{c}. \quad (10)$$

We use our model to examine how habitat loss, habitat fragmentation, and disturbance affect the persistence of generalist and specialist species because these three factors represent major forms of generic human-induced stress in ecosystems.[21] First, we divide the two-dimensional parameter space defined by colonization rates (c) and extinction rates (e) into four different qualitative outcomes: the two specialists persist but not the generalist ($p_a > 0$, $p_b > 0$, $p_g = 0$), both the specialists and the generalist species persist ($p_a > 0$, $p_b > 0$, $p_g > 0$), only the generalist persists ($p_a = p_b = 0$, $p_g > 0$), or no species persists ($p_a = p_b = p_g = 0$). Dividing parameter space according

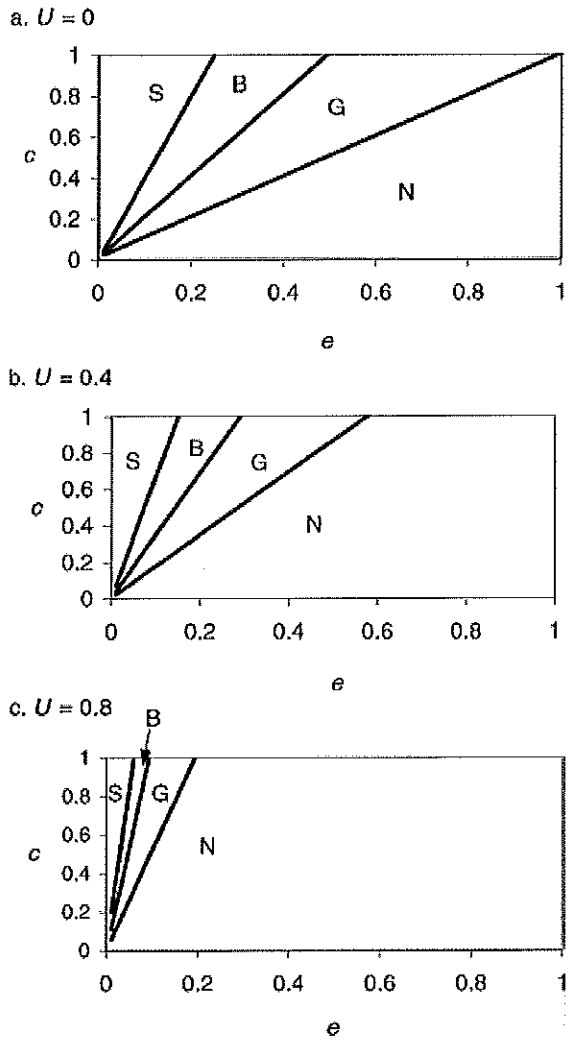

Fig. 2. Combinations of values for colonization (c) and extinction (e) in which particular sets of species persist. S: only specialist species persist; B: both specialists and generalists persist; G: only generalist species persists; and N: no species persist.

to these outcomes, we can examine different degrees of habitat loss (i.e., different values for U) and ask how increasing U alters the opportunities for species coexistence (Fig. 2). As expected, any increase in U reduces the amount of parameter space in which any species can persist. More interesting is the fact that increasing U tends to convert conditions (particular combinations of c and e) under which only specialists can persist to conditions in which the generalist can invade. Similarly, any increase in U tends to convert conditions that can support all three species (the two specialists and the generalist) to a situation in which only the generalist can persist. Of course, continued habitat destruction would ultimately lead to the elimination of all three species, even before all of the suitable habitat has been destroyed.[15] What is interesting is that at levels of habitat destruction short of those needed to cause the extinction of all species, habitat loss tends to convert communities filled with habitat specialists to communities that include or are primarily composed of generalists.

One way to visualize the shift in community composition (shown in Fig. 2) is to select a particular combination of c and e and then examine how the equilibrium fractions of sites occupied by specialists versus the generalist change as U is gradually increased (Fig. 3). When all patches are habitable ($U = 0$ and $A = B = 0.5$), species with specialized habitat preferences tend to be present and often persist on more patches than the generalist species. As the proportion of habitat that is unsuitable for any of the species increases, the equilibrium fraction of patches occupied by the specialist species declines and persistence of the generalist becomes increasingly likely. At intermediate amounts of habitat destruction, all three species may coexist, but the specialists are eventually lost from the metapopulation as habitat destruction continues. Occupancy by the generalist species peaks at the level of habitat destruction that eliminates the specialist, but beyond that degree of habitat loss all further habitat destruction reduces occupancy by the generalist. Eventually, so much of the habitat is destroyed that none of the species can persist.

Second, habitat destruction typically occurs in patterns that result in habitat fragmentation,[22] and fragmentation frequently reduces the likelihood of successful colonization, either by hindering movement of individuals among habitat patches or by increasing mortality during interpatch movement.[23] Such an effect can be visualized by plotting the changing equilibrium fractions of patch occupancy versus the colonization rate (increasing fragmentation results in lower values of c) for any given extinction rate and degree of habitat loss (U). When all three species have high colonization rates, specialist species are strongly favored. But as colonization rates decline, the habitat generalist becomes increasingly favored (Fig. 4). At some point, however, colonization rates become so low that no species can persist.

Finally, we used the model to consider the transient dynamics of specialist versus generalist species following a short-term disturbance (Fig. 5). As a first approach, we simulated a disturbance as a reduction in patch occupancy, affecting all three species simultaneously. To examine the short-term dynamics of the

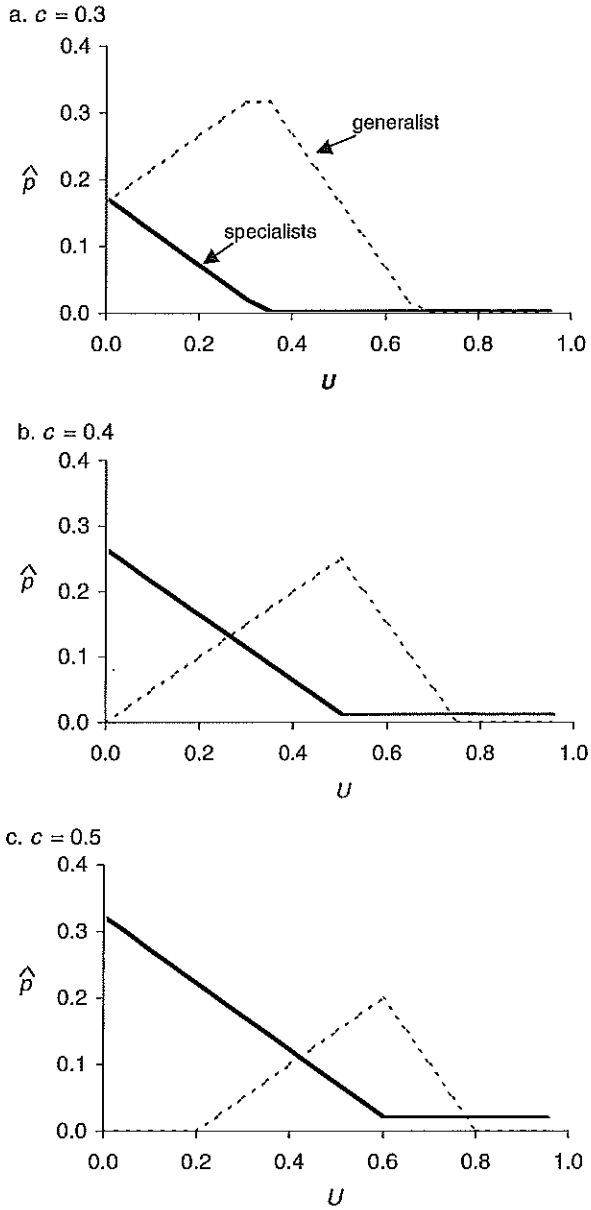

Fig. 3. Effect of habitat destruction on the equilibrium proportion of habitat occupied by specialist and generalist species ($e = 0.1$). The solid line represents either species a or species b because they exhibit identical dynamics.

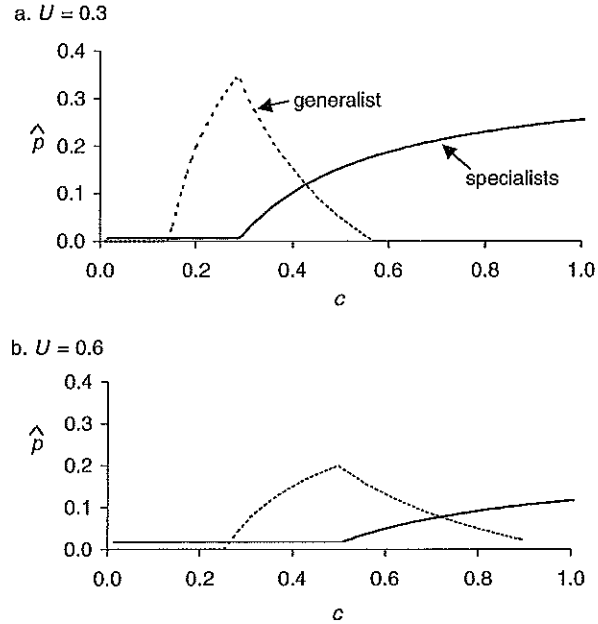

Fig. 4. Effect of habitat fragmentation on the equilibrium proportion of habitat occupied by specialist and generalist species. Because habitat fragmentation would likely reduce colonization rates (see text for rationale), an increase in habitat fragmentation can be thought of as a shift to the left along the x-axis. Results are shown for $e = 0.1$ and for two levels of habitat destruction. The solid line represents either species a or species b because they exhibit identical dynamics.

model following a perturbation, we subtracted 0.01 from the equilibrium proportion of patches occupied by each of the three species. Immediately following this disturbance, all three species begin to recover, but the generalist enjoys a temporary advantage (Fig. 5). This temporary advantage exists because the disturbance removes specialists from sites, thereby reducing the inhibiting effect of specialists on generalist occupancy. The interesting point is that the transient benefits to generalists vary with different degrees of habitat loss (or U). When habitat loss is negligible, disturbance causes only minor temporary increases in the generalist species. In contrast, as habitat loss is increased (U gets larger), the transient increase in generalists is relatively larger (Fig. 5).

To examine the transient dynamics of this model more thoroughly, we used a suite of analytical metrics developed by Neubert and Caswell.[20] The first measure of transient dynamics is *resilience*, which can be defined as the asymptotic rate of decay of a small perturbation to a stable equilibrium point. *Reactivity*, is the maximum instantaneous growth rate of a small perturbation. Finally, the *amplification envelope* gives the maximum possible amplification of a small perturbation and is characterized by a maximum ($\rho_{\max}$), and the time at which the maximum occurs ($t_{\max}$). Collectively, these metrics describe what happens immediately following a perturbation, such as a flood, fire, or other nonselective disturbance. They provide

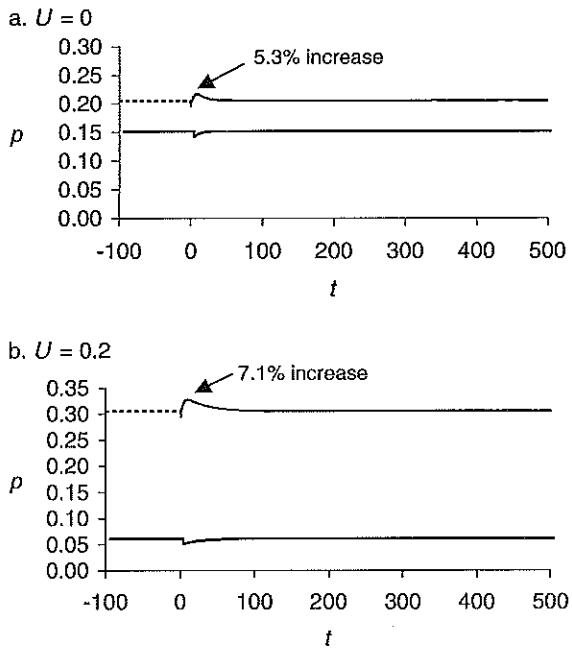

Fig. 5. Effect of short-term disturbance on the fraction of habitat occupied by specialist and generalist species. At time 0, a disturbance event reduces the fraction occupied by each species by a constant amount (0.01), where $e = 0.3$ and $c = 0.85$. Solid and dashed lines represent the proportion of patches occupied by the specialist and generalist species, respectively. The solid line represents either species a or species b because they exhibit identical dynamics.

analytical measures of how much and how rapidly the pattern of habitat occupancy can change following a disturbance, and how quickly the pattern can return to the previous equilibrium. We calculated these indices for the linearization of our model in the neighborhood of the coexistence equilibrium (Equations (4)–(6)) over a range of colonization rates and degrees of habitat loss (Fig. 6). Several of these indexes indicate that a decrease in habitable area leads to the possibility of more violent transient behavior. In particular, as U increases, the potential for the species to exhibit transient growth increases (i.e., reactivity and ρ_{max} both increase), and the duration of that transient growth is longer (i.e., t_{max} increases). Resilience also changes as habitat gets destroyed, however, resilience can initially increase with the modest levels of habitat destruction, but later consistently decreases as habitat destruction continues. Overall, our results suggest that the habitat loss is likely to exaggerate the response of species to short-term disturbances. Not only does habitat loss directly favor generalist invaders, but perturbations can also result in large, albeit temporary, increases in occupancy by the generalist.

The idea that disturbance favors competitively inferior species dates back to the earliest discussions of fugitive species and life history theory.[24] However, most discussions of life history theory examine a coordinated suite of traits that include competitive prowess, intrinsic rates of population growth, and dispersal,[25,26] whereas our specialists/generalist metapopulation model includes no differences in dispersal rates or population growth rates among the three species. Moreover, the nonlinear interaction between disturbance and habitat loss with regard to favoring generalist invaders has not previously been emphasized.

In summary, our simple three species metapopulation model suggests that habitat loss, habitat fragmentation, and temporary disturbances all conspire to favor generalists, relative to specialists. In any real landscape affected by the habitat destruction, all three factors are likely to be acting simultaneously. Because the model assumes absolute (and instantaneous) competitive superiority on the part of habitat specialists, its results underestimate the benefits accrued by the habitat generalists due to these three forms of environmental degradation. For example, if sites occupied by the generalists were not instantly usurped by a colonizing specialist species, then generalists would enjoy much greater success upon habitat loss than is shown in Fig. 3.

Those involved in on-the-ground management of exotic species may wonder if our model could be parameterized and used to estimate amounts of habitat destruction that would facilitate the invasion of particular species. We doubt that such quantitative predictions would be useful. In a spatially explicit version of an earlier multispecies metapopulation model, predictions regarding the order of extinction were qualitatively robust, but quantitative predictions depended sensitively on details such as the precise pattern of habitat destruction and the nature of the species' dispersal behavior.[27] Although our model is a "strategic model" in the sense that it cannot predict any particular invasion scenario, the very fact that it is such a simple model, with a minimal distinction between generalists and specialists, means that its broad conclusions are likely robust. Indeed, our model results concur with field observations, which document that habitats characterized by a high degree of anthropogenic or natural disturbance tend to include a higher proportion of nonnative species.[28] We conclude that extensive environmental degradation or frequent habitat

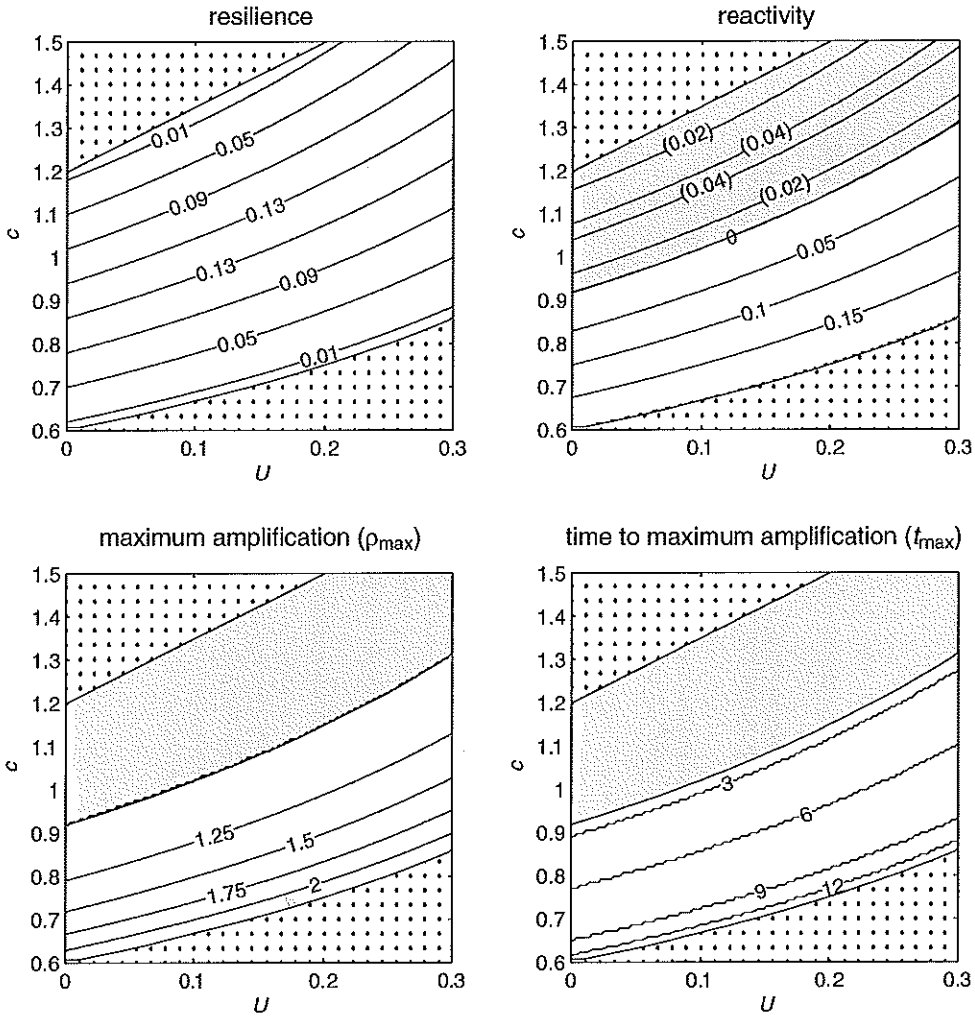

Fig. 6. Indices of responses to perturbation (as described in the text) for the coexistence equilibrium (Equations (4)–(6)) of model (Equations (1)–(3)). For this set of graphs, $e = 0.3$, and negative numbers appear in parentheses. In the stippled areas, the equilibrium is not positive. In the gray areas, the reactivity is negative, and hence $\rho_{max} = 1$ and $t_{max} = 0$.

disturbance will almost inevitably favor the invasion of communities by generalist species.

4. AN ECOSYSTEM MANAGEMENT PERSPECTIVE ON BIOLOGICAL INVASIONS

One way theoretical ecologists can contribute to the control of invasive species is by modeling the spatial spread of particular invaders, with detailed demographic and life history simulations in real landscapes. These modeling exercises can be useful for building generalizations regarding the life history traits of invasive species, but it is impractical to expect management for each invasion on a species-by-species basis. Thus, it may be more fruitful to lump exotic species in a common pool and think of them as a form of biological pollution, the impact and influx of which should be minimized at an ecosystem level.

Our model highlights that invasive species are a major concern because they are often a symptom of additional conservation problems, such as habitat destruction, disturbance, and fragmentation. In addition, invasive species are likely to change the composition of ecological communities, shifting communities toward higher frequencies of generalist species and relatively fewer specialists. Based on our findings,

we suggest that management may well attain its broadest success by simply aiming to identify and protect large intact expanses of minimally disturbed and relatively unfragmented habitats. A management strategy aimed at maintaining large stands of intact habitat is likely to help deter a wide variety of exotic species, whereas species-by-species analyses cannot possibly keep pace with the fast-rising tide of exotic species.

ACKNOWLEDGMENTS

We thank Mark Anderson for organizing a stimulating workshop on risk assessment applied to introduced species and for critical feedback and suggestions that greatly improved an earlier version of this manuscript. We are also grateful to Will Satterthwaite for helpful feedback. MGN acknowledges the National Science Foundation (DEB-99073518, DMS-9973212, OCE-0083976) and the Environmental Protection Agency (R-82908901-0) for their support.

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