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Authors
Drury, Kevin L. S.
Rothlisberger, John D.

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Offense and Defense in Landscape-level Invasion Control

Kevin L. S. Drury[†]
and

John D. Rothlisberger

Department of Biological Sciences,
The University of Notre Dame,
Notre Dame, IN 46556

Abstract

Biological invasions are multi-stage processes comprising chance demographic events, species interactions, and dispersal. Despite this complexity, simple models can increase understanding of the invasion process. We model the spread of aquatic invasive species through a network of lakes to evaluate the effectiveness of two intervention strategies. The first, which we call offense, contains the invader at sources; the second, which we call defense, protects uninvaded destinations. Deterministic models reveal the effects of these intervention strategies on spread rates. Practical applications involve finite collections of uninvaded lakes, however, and we therefore also present a stochastic model to describe how these strategies affect expected times to important invasion milestones. When the goal is to reduce overall spread rates, both approaches agree that offense is better early in invasions, but that defense is better after 1/2 the lakes are invaded. When the goal is to protect areas of high conservation value, however, defensive site protection provides lower per site introduction rates. Although we focus on lakes,

our results are quite general, and could be applied to any discrete habitat patches including, for example, fragmented terrestrial habitats.

Introduction

Translocation of people and products introduces a wide variety of organisms to novel habitats at rates, and over distances, independent of inherent dispersal ability (Mack et al. 2000). These human-mediated dispersals are likely to be especially important in discontinuous habitats, such as freshwater lakes (Puth and Post 2005). The spread of invasive species to such habitat patches is conceptually similar to both the colonization of islands, and the transmission of pathogens from infected to susceptible individuals. We therefore frame our analysis in terms of the theory of island biogeography (MacArthur and Wilson 1967) and use simple models of epidemics to explore the landscape-level consequences of facilitated dispersals, and strategies for impeding them.

Experience shows that intervening early in the invasion process by, for example, removing organisms from transportation pathways, is more effective than post-establishment eradication (Lodge et al. 2006) and indeed, is economically optimal (Leung et al. 2002). Because resources

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[†]Corresponding author:
current address: drury@nceas.ucsb.edu
National Center for Ecological Analysis and Synthesis
University of California, Santa Barbara

for the management of invasive species are limited, however, decisions about when, where and how to prevent introductions remain necessary. We therefore consider the relative effectiveness of two intervention strategies: (1) preventing spread *from* invaded source patches and (2) blocking spread *to* uninvaded destination patches. We refer to the former as offense and the latter as defense and show that a threshold exists for switching between them. As a concrete example, we focus on inadvertent, between–lake spread of aquatic invasive species by transient recreational boaters (Johnson et al. 2001).

Because aquatic organisms spread among unconnected lakes via occasional discrete jumps from invaded to uninvaded sites, colonizations form "disjunct foci" (Moody and Mack 1988), which expand locally via diffusive spread (Shigesada and Kawasaki 1997, chap. 5). This pattern stands in contrast to the continuously radiating wavefront associated with some range expansions (e.g., Skellam 1951). Furthermore, in the case of inter-lake spread, random arrivals of individuals are offset by elevated mortality rates caused by emersion and transit stress. This demographic stochasticity, accompanied by local extinctions (see, e.g., Mack et al. 2000), may explain some slow initial range expansions (Shigesada and Kawasaki 1997, chap. 2) because many sites with invasive species may initially be population sinks that contribute little, if at all, to regional spread. Under continued immigration, however, these may eventually achieve positive population growth and convert to source populations.

We therefore assume that invaders arrive at random times, in small random quantities, and with high post–introduction mortality rates. Given these assumptions, the colonization–extinction equilibrium concept from island biogeography (MacArthur and Wilson 1967) immediately leads to the general hypothesis that interactions among introduction rates, mortality rates (Ricciardi et al. 1995, Facon et al. 2004) and regional geography (Facon and David 2006) influence colonization success. Neverthe-

less, without models, it is not obvious how these processes interact with offensive and defensive intervention strategies to determine the rate at which an invading species spreads through a collection of lakes.

We begin with simple, deterministic SEIR epidemic models (S$\rightarrow$ susceptible, E$\rightarrow$ exposed, I$\rightarrow$ infected, R$\rightarrow$ recovered) to describe transmission of invaders among lakes. This approach reveals differences in introduction rates, according to intervention strategy, but because it approximates the number of invaded lakes as a continuous variable, it is not well–suited for exploring the effect of strategy on elapsed time until full invasion of a finite collection of lakes. We therefore also use a stochastic *SI* epidemic model to evaluate offense and defense with respect to expected time to the half–invaded and fully invaded states. Note that these approaches rely on the assumption of equally likely contacts among lakes, an assumption that we relax in forthcoming work. Finally, we show how to evaluate trade-offs between the number of protected lakes, the duration of protection, and the effectiveness of intervention.

Lessons from Biogeography and Epidemiology

There are clear parallels between isolated lakes and the islands of island biogeography; in both cases, suitable habitats are embedded in a background matrix of unsuitable habitat. Indeed, the equilibrium between immigration and mortality in a lake can be understood using the graphical approach of island biogeography (Fig. 1a). Immigration rates (horizontal lines) are constant because arrival events are independent of previous arrivals, but differ depending on distance from sources. In contrast, population-level mortality rates are proportional to the per capita death rate μ and generate the linearly increasing dashed mortality line. When the equilibrium is large enough to sustain positive local population growth, lakes convert from exposed to invaded and become sources for further spread.
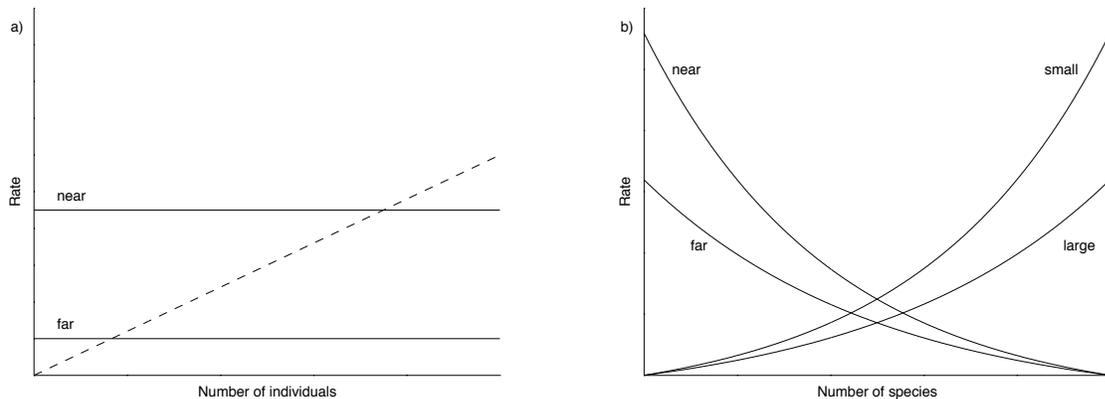
Fig. 1.— a) MacArthur and Wilson equilibrium number of species for large and small islands that are either near or far from a mainland species pool. b) equilibrium number of live individuals of an invading aquatic species carried across land by boaters from a source lake that is either near or far away. c) As in b except that Allee dynamics suggest that for equal introduction sizes, density is lower in large lakes so that mortality rates as described by the Nagumo equation are higher.

Offensive containment is conceptually similar to increasing distance between islands and the mainland (Fig. 1b), because intervention at sources decreases the per lake probability of introduction for all destinations. An example of this type of intervention is removal of organisms from boats leaving lakes. In constrast, the defensive strategy is more analogous to decreasing the size of particular islands because smaller lakes are less attractive to boaters (Reed-Andersen et al. 2000). Thus, destination intervention decreases the probability of introduction for particular protected lakes. The conceptual framework of island biogeography therefore provides a useful metaphor, which we use to interpret our simple models and provide a useful link between epidemiological and ecological approaches for understanding how intervention slows the spread of invasions.

We first develop a simple deterministic model based on global movement behavior of individuals between identical lakes so that neither distance between lakes nor lake size matter. Although these assumptions are unrealistic for many networks (see, e.g., Barabasi and Albert 1999), they can nevertheless provide useful descriptions of epidemics (Keeling 2005). Indeed,

because lake-to-lake transmission of invasive species is conceptually so similar to the spread of disease via contacts between infectious and susceptible individuals, we restrict our attention to the so-called "well-mixed" case here, and explore the consequences of variability in these network features in forthcoming work.

For small collections of lakes, it is feasible to enumerate all possible contacts between invaded and uninvaded lakes, under all possible intervention configurations. For example, Fig. 2a shows the number of contacts when the invader is contained at zero, one, and all invaded sources. Figure 2b shows the possible contacts when destinations are instead protected. The number of connections is directly proportional to the number of actual introductions.

These diagrams illustrate that intervening at sources or destinations generates identical results when occurring at either all lakes, or none of the lakes. When the numbers in each class vary, however, protecting identical numbers of lakes can lead to different numbers of contacts. Thus, identifying the most effective intervention strategy requires knowing how the number of potential contacts depends on the numbers of lakes in each class. We therefore de-

3

rive formulæ for these contacts under each intervention strategy, assuming that all are equally likely. For example, when intervention occurs at source lakes, the relationship illustrated in Fig. 2a leads to the generalization,

$$E_{\mho} = (I - P_{\mho})S, \tag{1}$$

where $E_{\mho}$ is the total number of potential new exposures, $P_{\mho} \in (0, I)$ is the number of sources contained, and I and S are invaded sources and unexposed destinations respectively. When destinations are protected, the relationship illustrated in Fig. 2b leads to the generalization,

$$E_{\mathcal{D}} = I(S - P_{\mathcal{D}}), \tag{2}$$

where $E_{\mathcal{D}}$ is the total number of possible new exposures, and $P_{\mathcal{D}} \in (0, S)$ is the number of protected destinations. Our question is therefore, for what values of I, S, and P are these two expressions for exposures equal, and for which values is one greater than the other?

$$(I - P)S \overset{?}{>} I(S - P) \tag{3}$$

Inequality (3) is true when more than half the total number of lakes are invaded, which can be seen by replacing S with $(N - I)$, where $N = S + I$ is total lake number, and solving for I. Figure 3a shows this relationship for a population of 50 lakes with varying numbers of initially invaded sources and protected lakes. Positive regions of the surface indicate that $E_{\mathcal{D}} > E_{\mho}$, which means that intervention should focus on containing sources, the offensive strategy. Negative regions of the surface indicate the opposite so that protecting destinations results in fewer new exposures. Note that the switchpoint between positive and negative, and hence between offensive containment and defensive protection, occurs at precisely $\frac{n}{2}$. Flat regions of the surface represent nonsensical parameter pairs, such as containment in more invaded sources than exist.

Invasion Rates

The combinatorial nature of potential introductions for fixed I and S depicted in Fig. 2 is suggestive of mass-action, an assumption of the SEIR model of disease transmission (pg. 611, Murray 2002). Mass-action means that some fraction α of all possible new introductions occurs in each time interval. This fraction can express the rate of change in susceptible lakes with either

$$\frac{dS_{\mho}}{dt} = -\alpha(I - \rho P_{\mho})S, \tag{4}$$

or

$$\frac{dS_{\mathcal{D}}}{dt} = -\alpha(S - \rho P_{\mathcal{D}})I, \tag{5}$$

depending whether sources are contained or destinations are protected, with effectiveness ρ, respectively. Here we hold I constant and model the rate of change in exposures $(S \rightarrow E)$, which is distinct from transitions from uninvaded to invaded $(S \rightarrow I)$. The rate described by Eqs. (4)–(5) is therefore proportional to, but less than, the number of sites that are ultimately invaded $(E \rightarrow I)$, because many exposures ultimately revert to susceptible $(E \rightarrow S)$. The constant of proportionality obviously depends on the population biology of the invading species, whereas the introduction (i.e., exposure) process we model here does not.

Note that Eq. (4) is similar to a metapopulation model with no extinction (Hanski 1999). Metapopulation models have equilibrium patch occupancy frequencies, however, while the equilibria of Eq. (4) occur only when there is no containment at invaded source lakes $(P_{\mho} = I)$ or the system is fully invaded $(S = 0)$. Thus, as is often observed empirically, Eq. (4) suggests that invasions proceed to habitat saturation.

With perfect intervention effectiveness $(\rho = 1)$ in Equations (4)-(5), there are no accidental transmissions from contained source lakes or to protected destination lakes. In practice, this is not likely to be the case. Considering efficacy $\rho < 1$ therefore allows us to explore the effects
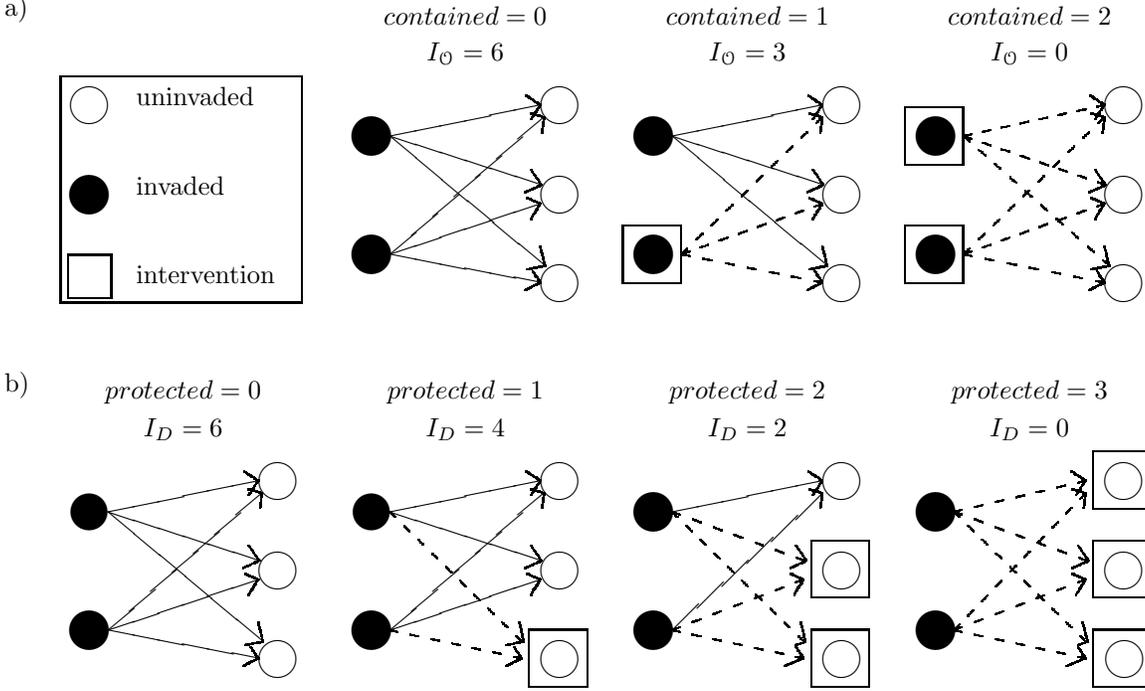
Fig. 2.— a) Schematic diagram representing the effects of intervention that prevents invaders from leaving sources on pathways of spread to uninvaded sites. I_S is the number of possible introductions when intervention prevents invaders from leaving source lakes. b) As in a) except that intervention occurs at destinations and prevents entry into univaded lakes. I_D is the number of possible introductions when intervention prevents invaders from enteriering uninvaded destination lakes.

of imperfect intervention on exposure rate. Solving Equations (4)–(5) yields, respectively,

$$S_{\mho}(t) = S_0 e^{-\alpha t(I - \rho P_{\mho})} \qquad (6)$$

and

$$S_{\mathcal{D}}(t) = \rho P_D + (S_0 - \rho P_D) e^{-\alpha I t}. \qquad (7)$$

Equation (6) reveals that the number of uninfected destinations decays exponentially with time when sources are contained, if $I > \rho P_{\mho}$. In contrast, when destinations are protected, the number of uninfected destinations decays exponentially to the constant,

$$S_{\mathcal{D}}^*(\infty) = \rho P_{\mathcal{D}}. \qquad (8)$$

Thus, under the offensive strategy, the number of unexposed lakes will decrease to 0, at a rate proportional to the difference, $I - \rho P_{\mho}$, the introduction rate α, and time t. In contrast, Eq. (8) formalizes the common-sense notion that blocking introductions to $P_{\mathcal{D}}$ protected lakes will result in $P_{\mathcal{D}}$ unexposed lakes in the long run. With imperfect intervention, however, the quantity $\rho P_{\mathcal{D}}$ indicates that on average, we expect only the success rate fraction ρ of the $P_{\mathcal{D}}$ lakes to remain unexposed. When no lakes are protected, $P = 0$ and solutions (6)–(7) are identical.

Manipulation of these equations yields quantitative predictions about how system-wide invasion outcomes will vary according to introduction rate, intervention strategy, efficacy, and number of sites. For example, rearranging Eq. (6) yields

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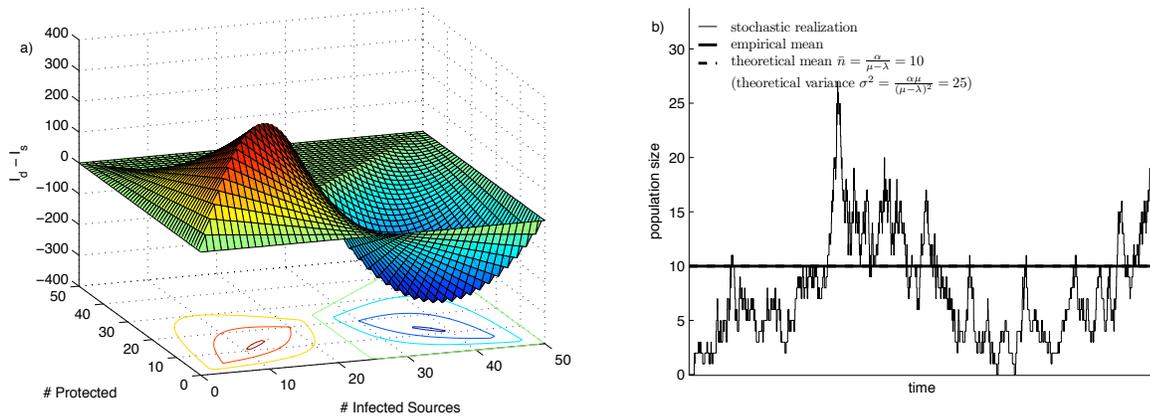
Fig. 3.— The potential contact surface showing relationship between # of infected sources, the number of sources or destinations protected, and the difference between the number of possible ways for an infection to occur in each strategy $E_{\mathcal{D}} - E_{\mathcal{O}}$, represented by surface height on the z-axis. The positive portion of the surface loosely means that infections are more likely when protection is concentrated at destinations *vs.* sources, while the negative surface indicates the opposite. Note that the deterministic switching point is at exactly $\frac{1}{2}$ total lake number.

$$-ln\left[\frac{S_{\mathcal{O}}(t)}{S_0}\right] = \alpha t(I - \rho P_{\mathcal{O}}), \qquad S_0 > 0, \quad (9)$$

revealing a linear relationship among the introduction rate α, time t, and the difference $I - \rho P_{\mathcal{O}}$. This relationship provides a useful model for comparison with empirical data (see, e.g., Dwyer et al. 1997), because for given t and number of infected sources I, it provides an obvious means of estimating introduction rate α. The analogous transformation of Eq. (7),

$$-ln\left[\frac{S_{\mathcal{D}}(t)}{S_0}\right] = -ln\left[e^{-\alpha It} + \rho \tilde{P}_{\mathcal{D}}(1 - e^{-\alpha It})\right], \quad (10)$$

$$\text{where, } \tilde{P}_{\mathcal{D}} = \frac{P_{\mathcal{D}}}{S_0}, \text{ and, } S_0 > 0.$$

describes the effects of introduction rate α and time t on the development of an invasion when destinations are protected. Comparing the predictions of the two intervention strategies is now a simple matter of specifying model parameters, solving equations (9)-(10), and plotting the results (Fig. 4).

When source lakes are contained, the rate of new introductions is affected sim-

ilarly by changing the number of intervention lakes or the introduction rate from infected sources to susceptible destinations (Fig. 4a). In contrast, changing the number of protected destinations has no effect on the rate of introduction (dot-dashed line), but does affect the asymptotic number of uninfected destinations $S_{\mathcal{D}}(\infty)$ (Fig. 4b). Changing the introduction rate does not affect this asymptote, but changes the rate at which it is approached (dotted line).

This deterministic approach thus reveals important qualitative and quantitative differences in the dynamics resulting from containment versus protection. Nevertheless, it does not allow calculation of the expected time to invasion milestones, such as the half–invaded or fully–invaded states, another meaningful way to compare offense to defense.

Full Invasion Times

Calculating the expected time until all lakes become invaded requires a stochastic model (Nasell 1999). Using a simple stochastic epidemic model (see, e.g., Ross 1996, pg. 238) and again assuming that

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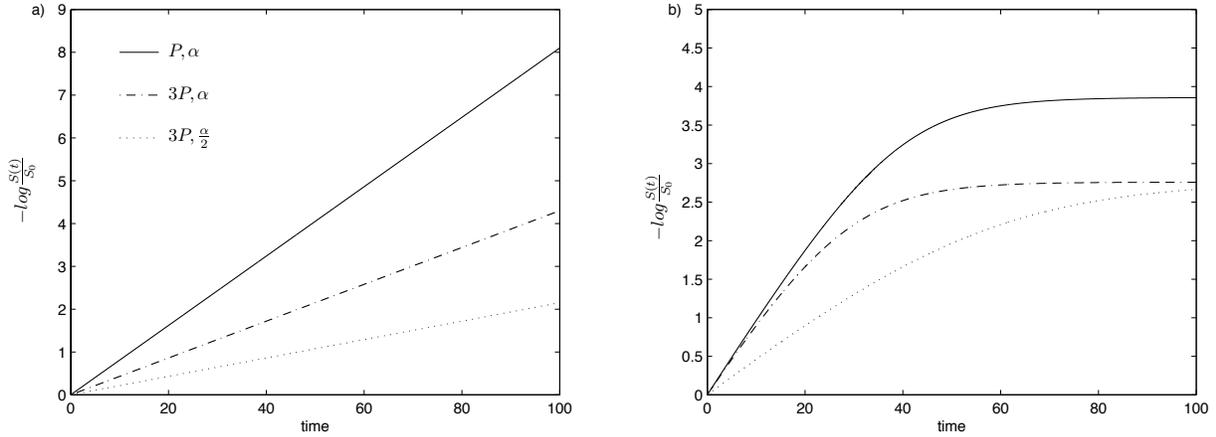
Fig. 4.— a) Offense: Solutions to equation (9) for a system of $n = 100$ lakes with initial susceptible destinations $S_0 = 90$, protection effectiveness $\rho = 0.99$, infected sources $I = 10$ and P and α varied as indicated in the figure legend. Note that increasing the number of protected infected sources P has a similar effect on overall infection rates as decreasing contacts α between infected and susceptible lakes. b) Defense: The analogous solutions to equation (10), using the same values as in a), except that here it is susceptible destination lakes that are protected. Note the asymptotic behavior as rate of new infections declines and total infections approach $S_D^*(\infty)$ of equation (8). Introduction rate α affects the rate at which the asymptote is approached, but not the ultimate value, while changing the number of protected susceptible destinations P_D does affect the asymptote.

spread is equally likely from all invaded source lakes to all uninvaded destination lakes, the probability of the nth infection when invaders are contained at source lakes can be expressed as

$$\lambda_{n,\mathcal{O}} = \begin{cases} (m-n)(n-p_s)\alpha + (m-n)p_s\alpha_{\mathcal{O}}, \\ \qquad \text{for, } n = 1, \ldots, m-1, \\ 0, \qquad \text{otherwise,} \end{cases} \tag{11}$$

where m is the total number of lakes, n is the number of invaded sources and p_s is the number of contained sources. The unprotected and protected rates of introduction to the $(m-n)$ uninvaded destinations are therefore expressed as $(n-p_s)\alpha$ and $p_s\alpha_{\mathcal{O}}$, respectively. Thus, in this section we consider transitions directly from $S \to I$ with no intermediate exposed state E.

With the length of time that the system remains at n invaded lakes being independent of the amount of time spent at $n-1$ invaded lakes, the process is, by definition, Markovian. The inter-event times are

therefore exponentially distributed with rate λ_n. Using the approximating integrals and definitions for the constants C and $\tilde{\alpha}$ in Appendix A, the expected time to full invasion starting from n_0 initially invaded lakes is,

$$E[T_{Offense}] \approx \tag{12}$$
$$C\log\left[\frac{(m-n_0)\left[m-1-p(1-\tilde{\alpha})\right]}{\left[n_0-p(1-\tilde{\alpha})\right]}\right].$$

Equation (12) is an explicit formula for the expected time until all lakes are invaded, given intervention at p sources, in terms of the protected and unprotected conversion rates. Following a similar approach for the defensive strategy yields,

$$E[T_{Defense}] \approx \tag{13}$$
$$C\log\left[\frac{(m-p-1)(m-n_0-p(1-\tilde{\alpha}))}{n_0(1+p\tilde{\alpha})}\right]$$
$$+ \frac{1}{m\alpha_D}\log\left[\frac{p(m-1)}{(m-p)}\right].$$

7

Equations (12) and (13) provide another straightforward tool for comparing containment to defensive protection. For example, the expected time to full invasion from n_0 intially invaded lakes, under each strategy, with p intervention lakes and relative effectiveness of protection $\tilde{\alpha}$ can be represented by level curves of $E[T]$ (Fig. 5a and b). Furthermore, Eqs. (12) and (13) facilitate decision-making even within a particular intervention strategy. For example, $E[T]$ can be calculated for a variety of combinations of p and $\tilde{\alpha}$ allowing selection of a strategy based on these practical considerations. Note that $\tilde{\alpha} \approx 1$ indicates that intervention provides little protection, while values close to 0 indicate effective protection at the p lakes (see Appendix A.1).

Comparison of Figs. 5a and b reveals that time until full invasion is greatly extended by defensively protecting destinations. As can be seen in Eqs. (12), expected time to full invasion when containing invaded lakes depends on a single system-wide decrease in introduction probabilities. In contrast, Eq. (13) contains two terms, the first corresponding to the relatively rapid invasion of all unprotected destinations (but also allowing for invasion of protected destinations at rate $\tilde{\alpha}$), and the second corresponding to the subsequent, and relatively slower, invasion of the protected destinations (Figs. 5c and d). Thus, at the regional scale, the advantage of offense is realized early in the invasion process (Fig. 6a), while the benefits of defense accrue late in the process. The dominating effects of defense late in the process do not justify wholesale endorsement of defensive intervention, however, because the collection of lakes remains below the half–invasion threshold much longer with source containment (Figs. 6a and b). Nevertheless, over the entire invasion epoch

$$E[T_O] \ll E[T_D]. \tag{14}$$

These results agree with the qualitative predictions from Eqs. (9)–(10) and Figs. 4a and b. Furthermore, carrying out the necessary algebra and solving an inequality involving the rate of decrease of uninvaded lakes under each strategy,

$$\lambda_{n,S} \overset{?}{>} \lambda_{n,D}, \tag{15}$$

$$(m-n)\left[(n-p_S)\alpha_0 + p_s\alpha_S\right] \overset{?}{>}$$
$$(m-n-p_D)n\alpha_0 + p_D n\alpha_D, \tag{16}$$

reassuringly demonstrates the existence of the switchpoint, $n > \frac{m}{2}$, in this model as well.

Figure 5d illustrates the relationship between protection effectiveness $\tilde{\alpha}$, the number of protected lakes p, and mean first passage time to full invasion $E[T]$, using the switching point at $n/2$. These passage times are, respectively, approximately 294% and 6% longer than source or destination protection alone, showing that employing knowledge of the switching point in developing intervention strategies can substantially prolong time to full invasion.

Discussion

Resources for slowing the spread of invasive species are finite, making intervention strategy an important consideration in managing invasions. Nevertheless, without a model, the magnitudes of differences among competing strategies are not obvious. Our simple models address the question of whether containing invasive species at invaded sources slows spread more than preventing entry to uninvaded destinations. The results indicate that the answer depends on how many lakes are already invaded. The best strategy for maximally prolonging the expected time to full invasion contains sources until the number of invaded lakes $n = \frac{m}{2}$ and protects destinations thereafter. Thus, counterintuitively, early in an invasion, when slowing spread through the collection of lakes is the priority, the best way to protect uninvaded areas is to allocate resources to containing invaded areas. The switch–point then suggests that as an invasion progresses, this species–specific containment at sources should give way to protection of uninvaded sites.
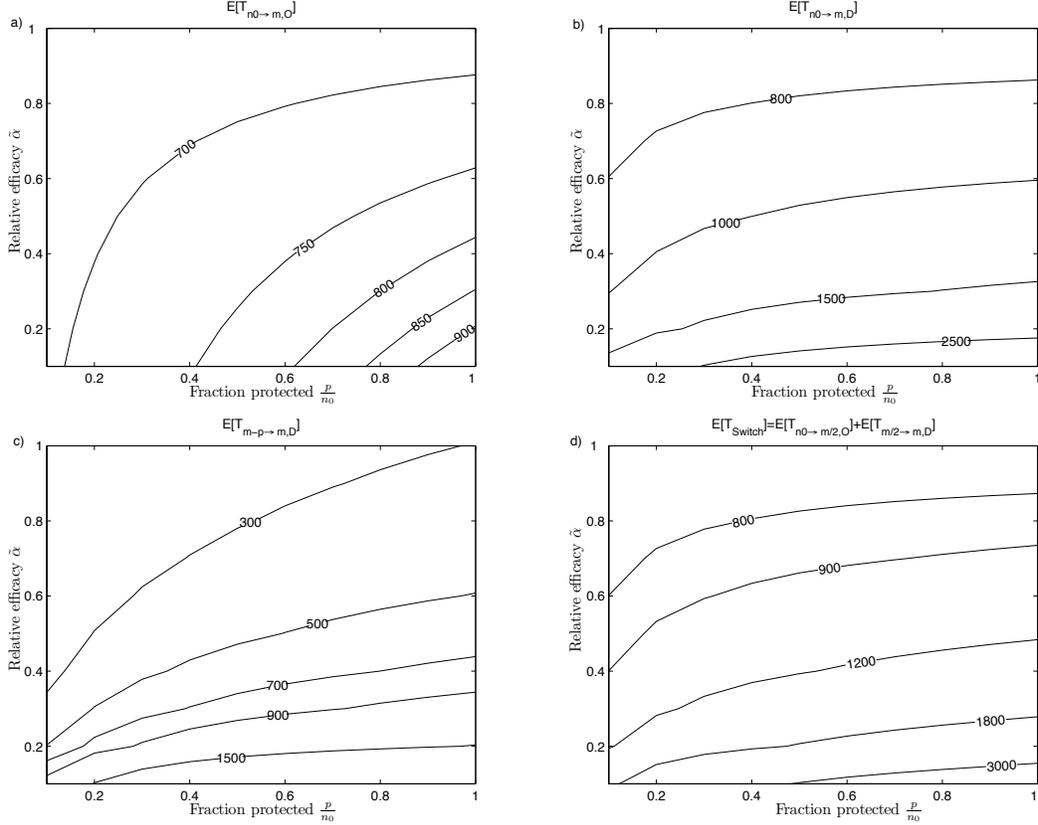
Fig. 5.— Expected time to invasion for the stochastic epidemic model (**??**). a) time to full invasion when sources are protected, b) time until all unprotected destinations are invaded when destinations are protected, c) time for invasion through protected destinations, d) time until full invasion when sources are protected until $m/2$ lakes are invaded, then intervention is switched to the same number of destinations.

Our analyses provide tools for understanding intuitively how this switchpoint arises. Specifically, protecting isolated destinations early in the invasion process allows organisms to spread from sources at the unprotected rate to many unprotected destinations, which then become sources and contribute to the system-wide spread rate. The ever-increasing number of sources eventually overwhelms protection measures at remaining destinations. Protecting destinations is nevertheless the best strategy late in the process because it yields lower per destination introduction rates at protected sites than containment at the same number of sources. Note that when the goal is to prevent introductions at areas with high conservation value, for example, this lower per–site introduction rate suggests that destination protection always provides the best strategy. Thus, the best intervention strategy depends on the scale of management goals. Specifically, at the landscape–level, source containment and the switchpoint are optimal, while at the local site–scale, destination protection is optimal.

The approximating integrals allow direct calculation of the expected time to reach the switching point at $m/2$ invaded lakes $E[T_{m/2}]$, given numbers of invaded sites, intervention sites, and intervention efficacy. These calculations can thus quantify expected differences between strategies in terms of average time to reaching some invasion milestone. For example, using the half-invaded milestone at $m/2$, and somewhat arbitrary choices of parameters for

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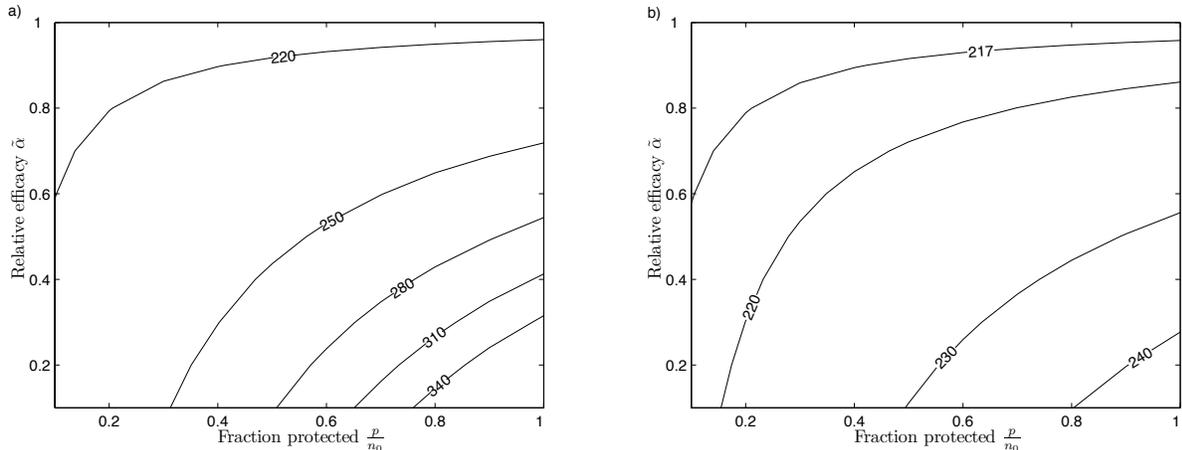
Fig. 6.— a) Level curves of mean first passage time to the 1/2–invaded state given a) offensive intervention at invaded p/n_0 sources that prevents spread at efficacy $\tilde{\alpha}$, and b) defensive intervtion for the same. p/n_0 is the fraction of initially invaded lakes that become intervention sites and $\tilde{alpha}$ is the ratio of intevention effectiveness to unmanipulated transmission.

illustration purposes, source containment yields $E[T_{m/2}]$ of approximately 340 time units, while site protection yields 240. If we imagine these time units to be weeks, and boating seasons of 16 weeks duration, this yields approximately 21 years for offense, compared to 15 years for defense.

Analysis of the error introduced by approximating $E[T]$ with integrals (Appendix A.1) reveals that the approximation is more accurate when more lakes are protected, which also leads to the longest expected times to full invasion. This analysis also reveals that as lake number increases, for a fixed number of contained sources, the expected time to full invasion decreases (Fig. 7). This counter–intuitive result suggests that for a given number of initially invaded and protected lakes, regions with more lakes reach full invasion more rapidly than regions with fewer lakes. This arises because the larger number of unprotected lakes convert to sources and contribute to spread. Thus, the fraction of initially invaded lakes contained early in the invasion is a crucial parameter, because unprotected destination lakes quickly become uncontained sources.

Given finite resources, another practical issue is whether to use highly effective methods at a few lakes, or less effective methods at many lakes. This trade–off too can be analysed with the level curves of expected time to full invasion. Indeed, this approach complements previous results, which showed that causing the extinction of nascent foci dramatically reduces invasion spread rates (Moody and Mack 1988). Because eradication of aquatic invaders is so rare (but see Mack et al. 2000, for some exceptions), we have not modeled extinctions. Thus, in our formulation of the problem, intervention that affects nascent foci is captured by increasing the effectiveness of intervention at either sources or destinations, because both effectively reduce new colonization success. Our results contribute to this understanding by demonstrating the conditions under which each strategy is most effective. Moody and Mack conclude that most efforts address the most conspicuous invasions, when in fact they should focus on exterminating nascent foci. Our results suggest that when post-establishment eradication is unlikely, the most effective way to inhibit new foci is to reduce spread from established colonies to uninvaded habitat patches.

Conceptual similarities between the theory of island biogeography and invasion of
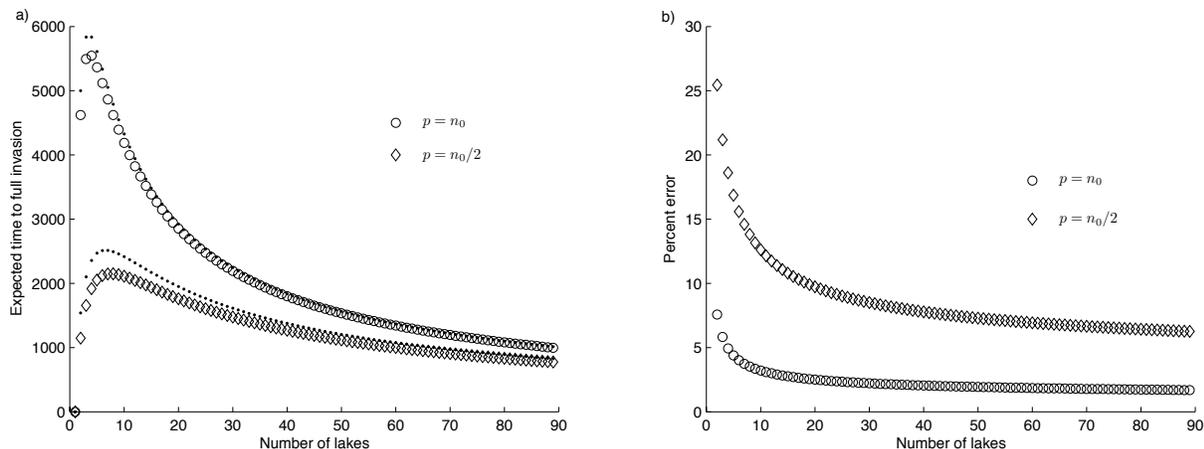
Fig. 7.— a) Level curves of mean first passage time to the 1/2–invaded state given a) offensive intervention at invaded p/n_0 sources that prevents spread at efficacy $\tilde{\alpha}$, and b) defensive intervtion for the same. p/n_0 is the fraction of initially invaded lakes that become intervention sites and $a\tilde{l}pha$ is the ratio of intevention effectiveness to unmanipulated transmission.

a network suggest that the elegant graphical model typifying the former can usefully synthesize our results. For example, in the language of island biogeography, source intervention metaphorically moves the "mainland" (i.e., contained invaded lakes) further away from the "islands" (i.e., uninvaded lakes), whereas destination intervention makes the "islands" smaller (i.e., protected destinations become less likely to receive invaders). In the present context, the equilibria between colonization and extinction represent within–lake population sizes, which are related to probabilities of transitions between uninvaded, exposed, and invaded lakes. Thus, the introduction–extinction equilibrium concept provides an intuitive connection between within–lake population dynamics and between–lake spread. Our approach adds to this understanding by quantifying the switchpoint, and showing how to balance intervention effectiveness with intervention site number.

Acknowledgments

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11

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Appendix A. Time to Full Invasion

Appendix A.1. Offense: Source Containment

When interactions among all invaded and uninvaded lakes are equally likely, and sources are contained (i.e., offense 0), the "birth rate" of new invasions is

$$\lambda_{n,\mathcal{O}} = (m-n)(n-p)\alpha_0 \quad \text{(A-1)}$$
$$+(m-n)p\alpha_p,$$
$$= (m-n)[(n-p)\alpha_0 + p\alpha_p] \text{(A-2)}$$

where m is the total number of lakes, of which n are invaded, and p are protected. The rates of invasion for unprotected and protected lakes are α_0 abd α_p respectively. When the time between the $(n-1)^{th}$ and n^{th} invasion is independent of the time between the nth and $(n+1)^{th}$, the process is Markovian and the expected time between invasions is exponentially distributed at rate $\lambda_{n,\mathcal{O}}$ (Ross 1996). Thus, the expected time between the nth and $(n+1)^{th}$ invasion is

$$E[T_n] = \frac{1}{\lambda_{n,\mathcal{O}}},$$
$$= \frac{1}{(m-n)[(n-p)\alpha_0 + p\alpha_p]}, \text{(A-3)}$$

and the expected time until all m lakes become invaded, starting with n_0 initially invaded lakes is

$$E[T_{n_0 \to m,\mathcal{O}}] =$$
$$\sum_{i=n_0}^{m-1} \frac{1}{(m-i)[(i-p)\alpha_0 + p\alpha_p]}. \quad \text{(A-4)}$$

When m is large (see Fig. 7), Eq. (A-4) can be approximated by the integral,

$$E[T_{n_0 \to m,\mathcal{O}}] \approx$$
$$\int_{n_0}^{m-1} \frac{1}{(m-t)[(t-p)\alpha_0 + p\alpha_p]} dt, \text{(A-5)}$$
$$\approx C \int_{n_0}^{m-1} \left[\frac{1}{(m-t)} + \frac{1}{(t-p(1-\tilde{\alpha}))} \right] dt, \quad \text{(A-6)}$$

$$\text{where,} \quad C = \frac{1}{\alpha_0[m - p(1-\tilde{\alpha})]}, \quad \text{(A-7)}$$

$$\text{and,} \quad \tilde{\alpha} = \frac{\alpha_p}{\alpha_0}. \quad \text{(A-8)}$$

Thus, $\tilde{\alpha}$ is the relative effectiveness of intervention, compared with unmanipulated introduction rates. Solving Eq. (A-6) yields,

$$E[T_{n_0 \to m,O}] \approx$$
$$C\, ln \left[\frac{(m-n_0)(m-1-p(1-\tilde{\alpha}))}{(n_0 - p(1-\tilde{\alpha}))} \right], \quad \text{(A-9)}$$

which makes it clear that full invasion time increases with total lake number m, decreases as the number initially invaded n_0 increases, increases with the number protected p, and increases with relative intervention effectiveness $\tilde{\alpha}$.

Figure 7a shows that the approximate solution behaves qualitatively like the exact summation, while Fig. 7b quantifies the error, when all invaded lakes are intervention sites ($e < 5\%$), and when only half are intervention sites ($e < 10\%$), for numbers of lakes $n > \approx 20$.

Appendix A.2. Defense: Site Protection

Following a similar strategy for defense yields the invasion rate equation,

$$\lambda_{n,\mathcal{D}} = (m-n-p)n\alpha_0 + pn\alpha_p, \quad \text{(A-10)}$$
$$= n[(m-n-p)\alpha_0 + p\alpha_p], \quad \text{(A-11)}$$

with expected inter-event time,

$$E[T_{n \to n+1}] = \frac{1}{\lambda_{n,\mathcal{D}}}$$
$$= \frac{1}{n[(m-n-p)\alpha_0 + p\alpha_p]}. \text{(A-12)}$$

Summing Eq. (A-12) over all inter-event times only provides an approximation, because although protected lakes p can be invaded and thus contribute to n, the sum does not account for this. Nevertheless, Eq. (A-12) is exact at $\tilde{\alpha} = 0$ and $\tilde{\alpha} = 1$, the y–axis bounds in Figs. 6a–d. Thus, at these bounds, the summation is exact, while for intermediate values of $\tilde{\alpha}$, $E[T]$ is slightly over-estimated.

The calculation for defense also differs because the approximating integral,

$$E[T_{n_0 \to m-p-1, \mathcal{D}}] \approx$$
$$C \int_{n_0}^{m-p-1} \left[\frac{1}{t} + \frac{1}{(m-t-p(1-\tilde{\alpha}))} \right] dt, \text{(A-13)}$$

13

is only valid up to $m - p$ lakes. Thus, the invasion of the remaining p lakes requires a separate calculation, and because we do not assume that p is large enough to approximate the sum with an integral ($p \approx 10$), in practice we directly calculated the sum,

$$E[T_{m-p \to m, \mathcal{D}}] = \frac{1}{\alpha_p} \sum_{i=m-p}^{m-1} \frac{1}{i(m-i)}. \quad \text{(A-14)}$$

Time to full invasion under defense is therefore,

$$E[T_{n_0 \to m-1, \mathcal{D}}] \approx$$
$$C \ln \left[\frac{(m-p-1)(m-n_0 - p(1-\tilde{\alpha}))}{n_0(1+p\tilde{\alpha})} \right]$$
$$+ \frac{1}{\alpha_p} \sum_{i=m-p}^{m-1} \frac{1}{i(m-i)}, \quad \text{(A-15)}$$

where the first term is the solution to Eq. (A-13), and C and $\tilde{\alpha}$ are given by Eqs. (A-7) and (A-8) respectively.

Appendix A.3. Strategy Switch

The expected time to full invasion, given a strategy switch from offense to defense when the number of invaded lakes is $m/2$ has 3 components. First, we calculate the expected time until $m/2$ lakes are invaded, given source intervention with

$$E[T_{n_0 \to n/2-1, \mathcal{O}}] \approx$$
$$C \int_n^{m/2} \left[\frac{1}{(m-t)} + \frac{1}{t - p(1-\tilde{\alpha})} \right) \right] dt, \quad \text{(A-16)}$$

which has solution,

$$E[T_{n_0 \to n/2-1, \mathcal{O}}] \approx$$
$$C \log \left[\frac{(m-n_0)\left[m/2 - 1 - p(1-\tilde{\alpha}) \right]}{(m/2+1)(n_0 - p(1-\tilde{\alpha}))} \right]. \quad \text{(A-17)}$$

We then approximate the expected time to invasion of the $(m-p)-(m/2+1)$ unprotected destination lakes with

$$E[T_{n/2 \to m-p-1, \mathcal{D}}] \approx$$
$$C \int_{m/2}^{m-p-1} \left[\frac{1}{(t)} + \frac{1}{m - t - p(1-\tilde{\alpha})} \right) \right] dt, \quad \text{(A-18)}$$

with solution,

$$E[T_{n/2 \to m-p-1, \mathcal{D}}] \approx$$
$$C \ln \left[\frac{(m-p-1)(m/2 - p(1-\tilde{\alpha}))}{m/2(1+p\tilde{\alpha})} \right]. \quad \text{(A-19)}$$

The third time component of the invasion process is given by Eq. (A-14). Thus, incorporating the strategy switch at $m/2$, the time to full invasion shown in Fig. 5d is the sum,

$$E[T_{switch}] =$$
$$E[T_{n_0 \to n/2-1, \mathcal{O}}] + E[T_{n/2 \to m-p-1, \mathcal{D}}]$$
$$+ E[T_{m-p \to m, \mathcal{D}}]. \quad \text{(A-20)}$$