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Spatially Explicit Models for the Population Dynamics of a Species Colonizing an Island

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ABSTRACT

We construct reaction-diffusion models for the population dynamics of a species colonizing an island from a source population on a continent. We view the source population as inducing a density or flux of immigrants onto the island and interpret colonization as succeeding if the population on the island is predicted to persist even when immigration from the continent is stopped. To capture the observation that a sufficiently large population or density must be attained for colonization to succeed, we assume Allee (i.e., bistable) dynamics rather than logistic dynamics for the colonizing population. We consider the cases of colonization in both the absence and presence of a competitor. We use reaction-diffusion theory, especially comparison methods and sub- and supersolutions, to determine how parameters such as the distance from the continent to the island and the dispersal, birth and mortality rates, carrying capacity, and minimum viable population density of the colonizing species affect the outcome of the attempted colonization. In the case of colonization in the presence of a competitor we consider a number of scenarios involving different types and strengths of competition. Our analysis permits us to draw conclusions about the characteristics of a species that make it a good colonizer.

1. INTRODUCTION

The study of island populations has been an important and sometimes influential part of ecological and evolutionary theory ever since Darwin's celebrated visit to the Galapagos. The island biogeography theory of MacArthur and Wilson [1] has stimulated much research and some controversy over the last quarter of a century (see [2,3] for discussion and references) and has been applied to issues of conserva-

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tion and refuge design, with the application sometimes engendering further controversy (see [2,4]). The MacArthur–Wilson theory is based on the idea that the species composing an island community are determined by stochastic events of colonization and extinction, with the total number of species remaining roughly constant at a dynamic equilibrium induced by a balance between colonizations and extinctions. A limitation of the MacArthur–Wilson theory is that the underlying models are not spatially explicit and use population dynamics only indirectly to determine the influence of birth and death rates and carrying capacities on the probability of colonization or extinction. Furthermore, there are some difficulties in defining successful colonization; see [1, p. 64; 3, p. 86]. Both theoretical and empirical considerations suggest that the size of an island and its distance from a source of colonists should affect the number and nature of species inhabiting it [1,3]. Area effects were derived by Preston [5] by assuming the total population of all species on an island to be proportional to the area of the island and the relative abundances of species to be given by a lognormal distribution. In [2] two of the co-authors derived species area curves from spatially explicit population dynamical models based on reaction-diffusion equations. In that work only extinctions were considered as a structuring factor. In the present work we construct spatially explicit models for island colonization, again based on reaction-diffusion equations, use them to give a precise definition of successful colonization, and study them to see how the distance of the island from a source of colonists interacts with the population dynamical and dispersal characteristics of those colonists to affect the prediction of success or failure of colonization. We perform qualitative and quantitative analyses for the case of a single colonizing species and a qualitative analysis for the case of colonization in the presence of a competitor. In both situations we obtain criteria for successful colonizing; the difference is that for a single species we also examine the parameter dependence of the criteria in some detail. The parameters include dispersal rates, population growth or mortality rates, carrying capacity, minimum viable population density, island size, and the distance of the island from the source population.

Our models are based on considerations somewhat similar to those used to study spatial effects in the population dynamics of the spruce budworm in [7] and in a more general context in [6] and use methods of analysis developed in those works. However, since we are modeling a different phenomenon our models differ considerably in detail from those of [6,7]. We envision colonization as a two-step process: First, we think of emigration from a continent inducing a density or flux of potential colonists via diffusive random dispersal with mortality; then we use that induced density or flux as an initial condition for population dynamics with dispersal on the island. We define the colonization to be successful if the colonizing species would be predicted to persist on the island in the absence of further immigration or emigration. For this formulation to yield meaningful results we must assume some sort of Allee effect for the population dynamics on the island, at least in the case of a single species. By an Allee effect we mean that the population will decrease at low densities, increase at moderate densities, and decrease again at high densities (see [8–10]). Roughly, the presence of the Allee effect requires that the colonizing species attain a density above some threshold over a region of sufficient size if colonization is to succeed. This is plausible from a biological viewpoint [1, Chap. 4; 3, p. 86]. The threshold can be interpreted as a minimum viable population density of the sort discussed in [11]. Without an Allee effect the models would always predict successful colonization in the single-species case. For the case of two competitors, it turns out that if there are no Allee effects and there is a globally stable coexistence equilibrium then colonization always succeeds, but if the states with only one species present are locally stable or if there are Allee effects then history and geography determine the success or failure of colonization.

The article is structured as follows: The models are formulated in Section 2; the simplest version of the single species model is analyzed in Section 3; a more sophisticated single-species model is analyzed in Section 4; and models for colonization in the presence of competition are discussed in Section 5. Conclusions and comparisons with related work are drawn in Section 6. The most sophisticated mathematical analysis is in Sections 4 and 5; the conclusions of Section 6 are mostly stated in nonmathematical terms.

2. DISCUSSION OF MODELING

We envision a source population on a continent producing via dispersal a population on an island at some distance from the continent. We assume the dispersal takes place along a somewhat inhospitable transit corridor, which typically we would view as a body of water or a region of unsuitable habitat. We interpret colonization as successful if the population on the island persists when immigration from the continent ceases. We employ two different regimes for determining a population density profile on the island to be considered as the initial profile at the cessation of immigration. The first and simplest is to take the distribution that would be expected over the transit corridor under the assumption of immigration over a prolonged period of time and use it directly. A second approach is to view immigration as inducing a flux of individuals into the island, which then interact with the island environment to produce a density profile. The first approach is perhaps a more accurate description for airborne immigrants, such as birds or flying insects, since they might fly over the island in the same way as over the transit corridor. The second approach might be a more accurate description for terrestrial animals swimming to an island and then interacting with its boundary. In either regime we then use the initial profile as the starting point for a population model on the island that assumes no further immigration occurs. We base our analysis on diffusion models. Since we wish to study situations in which some threshold level of immigration is needed for colonization to succeed, we assume an Allee effect in the population dynamics on the island. We treat two scenarios, the first in which the immigrant species is considered without specific reference to any other species and the second in which the immigrant species competes with a species that is already established on the island.

Let us now describe the modeling process in more detail, treating first the scenario in which we consider only a single species. We then discuss the case in which the immigrant species competes with an established species. We begin by idealizing to a single space dimension. We assume that the island to be colonized is of length l and that the distance from the continent to the near edge of the island is L. We assume that the species emigrates from the continent at its carrying capacity (K_c) for the continent. The species does not reproduce in transit from the continent to the island. Consequently, there will be a net reduction in the density of the species as it moves toward the island, due to factors such as physical inability to survive the trip and predators along the transit corridor. We assume this reduction is proportional to the population density. Consequently, if we locate the continent, island, and transit corridor along the x-axis with the edge of the continent nearest the island at 0, the population density obeys the linear population law

$$u_t = \mu_0 u_{xx} - r_0 u \tag{2.1}$$

in the transit corridor, where $\mu_0 > 0$ is the rate of diffusion of the species through the transit corridor medium and $r_0 > 0$ is the constant of proportionality for the decay of the species in the transit corridor. If this population law (2.1) is subject to the constraints

$$u(0,t) = K_c, \qquad u(\infty,t) = 0,$$

it has stable equilibrium

$$u(x) = K_c e^{-\sqrt{(r_0/\mu_0)}x}, \qquad x > 0. \tag{2.2}$$

(This form of expected density is also used in [3; p. 68] and [7].)

We use the equilibrium (2.2) to determine the population density profile of the immigrant species at the time immigration ceases in our first regime and also the influx of the immigrant species to the island in our second. In the first regime, we simply take $K_c e^{-\sqrt{(r_0/\mu_0)}x}, x \in [L, L+l]$ as the population density profile of the immigrant species at the cessation of immigration. If we now translate the x-axis so that the edge of the island nearest the continent corresponds to the origin, we have

$$u(x) = K_c e^{-\sqrt{(r_0/\mu_0)}(x+L)}, \tag{2.3}$$

$x \in [0, l]$, as population density profile at the cessation of immigration in the first regime. For the second regime, we have from (2.3) that the influx into the island $\mu_0 u_x(0)$ is given by

$$\mu_0 u_x(0) = -K_c\sqrt{r_0\mu_0}\, e^{-\sqrt{(r_0/\mu_0)}L}. \tag{2.4}$$

We use (2.4) in deriving the population density profile of the immigrant species at the cessation of immigration in our second regime. However, this derivation also employs in an essential way the population law that the immigrant species obeys on the island. As a consequence, we discuss next the population dynamics of the immigrant species on the island. We follow this discussion with the derivation of the population density profile of the immigrant species at the cessation of immigration for the second regime. Once we have derived the initial population density profile in this case, we describe in more detail what is meant by successful colonization.

As previously indicated, we suppose the dynamics on the island to be of the Allee type. By the Allee type, we mean that the local population law follows a pattern of decline for small populations or population densities, growth for some intermediate range of populations or population densities (i.e., up to a carrying capacity), and decline for populations or population densities above this range. In [10], Lewis and Kareiva mention a number of reasons why such an effect could occur, among them less efficient feeding at low densities, reduced effectiveness of vigilance and antipredator defences, and inbreeding depression.

Perhaps the simplest mathematical model reflecting the Allee effect is given by the initial value problem

$$\begin{aligned} \frac{du}{dt} &= u(u-a)(K-u) \\ u(0) &= u_0 \end{aligned} \tag{2.5}$$

with $0 < a < K$. In (2.5), u represents the population of a species in a uniform environment, K the carrying capacity of the population, and a/K the "fraction of carrying capacity below which the ill-effects of a low density produce negative population growth" [10, p. 143]. See also the discussions in [8,9]. It is easy to calculate that (2.5) has as its general solution

$$\frac{|u-a|^K}{|u|^{K-a}|K-u|^a} = C_0 e^{aK(K-a)t},$$

where $C_0 = |u_0 - a|^K / (|u_0|^{K-a}|K - u_0|^a)$, provided $u_0 > 0$ and $u_0 \neq a$ or K. (Note that $0, a$, and K are equilibria for (2.5).) If $u_0 < a$, then $u \to 0$ as $t \to \infty$, while if $u_0 > a$, $u \to K$ as $t \to \infty$. Hence, in this model, any population of initial size less than a is doomed to extinction, so that a is referred to as the *minimal viable population.* In corresponding reaction-diffusion models (i.e., having reaction term of the form $ru(u-a)(K-u)$, u no longer represents a population but rather a population density. In such models, a now represents the minimum *uniform* population density, in the sense that any initial population density below a throughout the island leads to extinction, while any population with initial population density above a throughout the island persists. In our analysis we examine nonuniform initial population densities with the density above a on portions of the island and below a on other portions of the island. As we shall see, a significant aspect of our analysis lies in determining the asymptotic behavior of certain such initial population density profiles. We assume therefore that the imigrating species is subject on the island to the population law

$$u_t = \mu u_{xx} + f(u), \qquad (x,t) \in (0,l) \times (0,\infty), \tag{2.6}$$

where

$$f(u) = ru(u-a)(K-u), \qquad u \in [0,K]. \tag{2.7}$$

Once immigration ceases, we assume in addition that

$$u_x(0,t) = 0 = u_x(l,t), \qquad t \in (0,\infty). \tag{2.8}$$

With (2.8), we are making the simplifying assumption that once members of the species reach the island they remain there, so that we augment the population law (2.6) with a reflecting (i.e., Neumann) boundary condition. (It would also be reasonable to impose a mixed or Robin-type boundary condition, given that the surrounding medium corresponds in part to the transit corridor and should not be viewed as utterly inhospitable to the species.) In (2.7), $K = K_i$, the carrying capacity for the species on the island. We do not assume that $K_i = K_c$. The reason is that the island is some distance from the continent, and hence the topography, vegetation, and freshwater supply may be substantially different on the island. $K_i > K_c$ would reflect better living conditions for the immigrant species on the island than on the continent and $K_i < K_c$ just the reverse. Also in (2.7), r is a parameter reflecting the growth rate of the species. In [10], Lewis and Kareiva note that if $K = K_i = 1$ and if $f(u)$ is to have maximum value 1,

$$r = 27/\left(2\left[\left((1+a)^2 - 9a/2\right)(1+a) + \left((1+a)^2 - 3a\right)^{3/2}\right]\right),$$

where as if $f(u)/u$ is to have maximum value 1, $r = 4/(1-a)^2$. Further, we note that $f(u)$ in (2.7) is defined only for $u \in [0,K]$. In our analysis, we sometimes need to consider $u < 0$ or $u > K$. It does not materially affect the model whether we assume f is the cubic given in (2.7) for all real values of u or we assume that $y = f(u)$ extends linearly in a smooth way from $(0,0)$ and $(K,0)$. However the second assumption is frequently an aid in the mathematical analysis, and for this reason, we make that assumption when needed.

We now turn our attention back to the derivation of the population density profile of the immigrant species at the cessation of immigration in our second regime. Recall that in this case we think of immigration inducing a flux of individuals into the island, which then interact with the island environment to produce the desired density. It is evident that (2.6) is the population law we must use in this situation. Since we assume the immigrant species remains on the island once it arrives, it is reasonable to take $(\partial u/\partial n)(l,t) = u_x(l,t) = 0$ as the augmenting boundary condition to (2.6) at the far end of the island. What remains to determine is $(\partial u/\partial n)(0,t) = -u_x(0,t)$. Recall that the influx from the continent is given by (2.4). From (2.6), the flux from the island at the edge nearest the continent is $\mu u_x(0)$. Following Ludwig et al. [7] we match $\mu_0 u_x(0)$ and $\mu u_x(0)$ to obtain

$$-u_x(0) = K_c \frac{\sqrt{r_0 \mu_0}}{\mu} e^{-\sqrt{(r_0/\mu_0)}L}. \tag{2.9}$$

Consequently, the population density profile of the immigrant species at the cessation of immigration in the second regime is determined by the boundary value problem

$$u_t = \mu u_{xx} + f(u) \qquad \text{in } (0,l)\times(0,\infty) \tag{2.10}$$

$$u_x(0,t) = -\gamma \qquad \text{on } (0,\infty) \tag{2.11}$$

$$u_x(l,t) = 0 \qquad \text{on } (0,\infty), \tag{2.12}$$

where $f(u)$ is as in (2.7) and $\gamma = K_c(\sqrt{r_0 \mu_0}/\mu)e^{-\sqrt{(r_0/\mu_0)}L}$, as in (2.9). For $\gamma > 0$, 0 is a strict subsolution to (2.10)–(2.12). The theory of parabolic partial differential equations discussed in [6,12] guarantees that the solution to (2.10)–(2.12) corresponding to zero initial data, say $\underline{u}(x,t)$, converges to the minimal positive equilibrium for (2.10)–(2.12) and that, moreover, any solution to (2.10)–(2.12) with nonegative initial data is at least as large as $\underline{u}(x,t)$ for all $x \in (0,l)$ and $t > 0$. Therefore, should we stop the immigration and should model (2.10) with boundary data (2.8) predict survival of the immigrant species when the initial density is the minimum positive solution of

$$-\mu u_{xx} = f(u) \qquad \text{in } (0,l) \tag{2.13}$$

$$u_x(0) = -\gamma \tag{2.14}$$

$$u_x(l) = 0, \tag{2.15}$$

we can expect the population to persist when immigration ceases. Hence we take the minimum positive solution to (2.13)–(2.15) as the population density at the time immigration is stopped in our second regime.

Immigrant species are described in the theory of island biogeography [1] in terms of their proficiency in dispersal and colonization. The quantity γ in (2.14) indicates how proficient the species is at dispersing from the continent to the island, with an increase in γ indicating an increase in proficiency of dispersal. The parameter dependence of γ is shown in (2.9). Large values of μ_0 correspond to large mean distances traveled per unit time and small values of r_0 correspond to low rates of mortality in transit. Thus for a species with a fixed dispersal rate μ on the island, having a large value of μ_0 and a small value of r_0 is indicative of a good disperser. Note that the ratio of the dispersal rate over the transit corridor to that over the island also affects the flux of the species onto the island. If for example, $\mu_0 = \mu$, which is plausible in say the case of flying insects, then $\gamma = K_c\sqrt{(r_0/\mu_0)}\,e^{-\sqrt{(r_0/\mu_0)}L}$, which does not exceed K_c/eL independent of μ_0 and r_0. (In this case γ achieves the maximum value K_c/eL when $\mu_0 = r_0L^2$. Biologically, this piece of information suggests that the advantage proferred by arriving at the island quickly may be offset if it also results in the immigrant spreading itself out on the island at low densities.) Since we assume that once the immigrant species arrives on the island it remains rather than attempting to return to the continent or disperse off of the island, it is plausible that species such as birds, which can have a large μ_0, may have a considerably smaller μ.

The parameters in the population law (2.6) affect the proficiency of the immigrant species at colonizing. A smaller value of the ratio a/K of the minimum uniform population density to the carrying capacity indicates a better colonizer than a larger value.

In either regime, we view colonization as successful provided the solution $u(x,t)$ to (2.6)–(2.8), having the population density of the immigrant species at the cessation of immigration as initial condition, is asymptotically supported throughout the island. By this last phrase, we mean there is a positive constant c and a time t_0 so that $u(x,t) \geqslant c$ for all $x \in (0,l)$ and for all $t \geqslant t_0$. Certainly u will be asymptotically supported throughout the island if it converges to a positive equilibrium. Moreover, it follows from [13] that for (2.6)–(2.8) any solution either converges to zero or converges to a positive equilibrium (and hence in such case is asymptotically supported throughout the island). However, it is not necessary to establish that u converges to a positive equilibrium to guarantee that it is asymptotically supported throughout the island. In a sense the constant c is arbitrary. However, c should not be too small so as to avoid detrimental stochastic effects. In some cases, depending on the ratio r/μ of growth rate to diffusion rate of the immigrant species on the island, we are able to take $c = a - \varepsilon$ with $\varepsilon > 0$ and arbitrarily small. Indeed, there will be cases in which $c = K - \varepsilon$ is a suitable choice and u tends to the carrying capacity K as $t \to \infty$. We gain further insight into success at colonization by examining $u(x,0)$ from our first regime more closely. Recall that in this case $u(x,0) = K_c e^{-\sqrt{(r_0/\mu_0)}(x+L)}$ for $x \in [0,l]$. If we require this density be above the minimum uniform population density a on the entire island, we need $K_c e^{-\sqrt{(r_0/\mu_0)}(l+L)} \geqslant a$. If l is large relative to the other parameters this requirement is severe. On the other hand, since $u(x,0)$ is decreasing in

x on $(0,l)$, we must have $K_c e^{-\sqrt{(r_0/\mu_0)L}} > a$ or the immigrant species goes extinct. Therefore the case $K_c e^{-\sqrt{(r_0/\mu_0)}(l+L)} < a < K_c e^{-\sqrt{(r_0/\mu_0)L}}$ is of interest. If a is very close to $K_c e^{\sqrt{(r_0/\mu_0)L}}$, the interval over which $u(x,0) > a$ is very small and it is likely that the immigrant species goes extinct. Likewise, if a is very close to $K_c e^{-\sqrt{(r_0/\mu_0)}(l+L)}$, $u(x,0) > a$ over most of the island and it is likely that colonization will be successful. Consequently, we see in the first regime that the immigrant species should be successful at colonizing the island provided that its population density at the cessation of immigration is larger than a on enough of the island. Such is the case in the second regime as well, although in this case we do not know that $u(x^1,0) > a$ implies $u(x,0) > a$ for $0 \leqslant x < x^1$.

Let us now consider the scenario in which the immigrant species competes for resources on the island in a direct way with another species. We envision the immigrant species dispersing from the continent to the island via the same previously described mechanism, while the other species is to some extent established on the island. Let $v(x,t)$ denote the population density of the second species. Once immigration ceases, we subject u and v to the population laws

$$\left.\begin{aligned} u_t &= \mu u_{xx} + f(u,v) \\ v_t &= \nu v_{xx} + g(u,v) \end{aligned}\right. \qquad \text{in}(0,l)\times(0,\infty), \tag{2.16}$$

where $\partial f/\partial v < 0$ and $\partial g/\partial u < 0$ and $t = 0$ denotes the time of cessation of immigration. We assume as before that once the immigrant species reaches the island it remains. Hence we take

$$u_x(0,t) = 0 = u_x(l,t) \qquad \text{for } t > 0. \tag{2.17}$$

Since the other species is to some extent established on the island, it may have evolved on the island in such a way that the transit corridors surrounding the island are now quite inhospitable. Consequently, we allow either

$$v_x(0,t) = 0 = v_x(l,t) \qquad \text{for } t > 0 \tag{2.18}$$

or

$$v(0,t) = 0 = v(l,t) \qquad \text{for } t > 0 \tag{2.19}$$

as the boundary constraint for the second species. We employ (2.3) as the density of the immigrant species at the cessation of immigration.

The density $v(x,0)$ of the second species at the time of cessation of immigration of the first species is somewhat arbitrary and reflects the extent to which the second species is established on the island. If the second species is regarded as well established on the island, then the solution to

$$v_t = \nu v_{xx} + g(0,v)$$

augmented by (2.18) or (2.19) and starting at $v(x,0)$ is asymptotically supported throughout the island. We for the most part assume that the reaction terms exhibit an Allee effect; i.e., $f(u,0)$ and $g(0,v)$ are of the form (2.7). However, for (2.16)–(2.18) it is sometimes possible for the outcome of the interaction to depend upon $u(x,0)$ and $v(x,0)$ when the reaction terms $f(u,0)$ and $g(0,v)$ are purely logistic. We note that such is not the case for (2.6)–(2.8) if (2.7) is replaced with

$$f(u) = ru\left(1 - \frac{u}{K}\right),$$

since then all nonnegative nontrivial initial data propagate to the spatially homogeneous equilibrium K. We note also that there are four basic outcomes to the attempt of the immigrant species to colonize the island in the face of competition from a second and somewhat more established species: coexistence; immigrant displacement of established species; survival of established species and failure of immigrant to colonize; and extinction of both species. In case u and v are both subject to zero Neumann boundary data, we take coexistence to mean that u and v are both asymptotically supported throughout the island in the sense we have previously described. (Should v be subject to zero Dirichlet boundary data, we modify the notion of asymptotically supported in an appropriate manner so as to account for the fact that v vanishes at the edges of the island.) In the case of (2.16)–(2.18) or (2.16)–(2.19), it is no longer true that being asymptotically supported throughout the island is equivalent to convergence to a component-wise positive equilibrium. (See [14], for example.) However, a theory of upper–lower solutions applies to (2.16)–(2.18) and (2.16)–(2.19). This theory can be employed so as to derive lower bounds on solutions from equilibria in a manner similar to that for the single equation (2.6). (See Section 5 for a complete description of this phenomena.)

We have already noted the discussion of Allee dynamics in [10]. We should note as well that Berryman and collaborators [15] use energy budget analysis to arrive at a growth rate curve of the same shape as (2.7). Other discussions of Allee dynamics are found in [8, 9]. The form we take for the population density of the immigrant species at the cessation of immigration in both regimes of our first scenario has been influenced by [7], as previously acknowledged. We also pointed out that the formula for the population density over the transit corridor is essentially given in [3, p. 68]. The approach in [3] is more explicitly probabilistic. Indeed, it is important to recall that diffusion equations may be interpreted as descriptions of the development over time of probability densities.

3. A SINGLE COLONIZING POPULATION—FIRST REGIME

In this section we examine the behavior of the model (2.6)–(2.8) for single-species population dynamics on the island subject to the initial condition (2.3) induced by the dispersal of immigrants from the mainland. Recall that the basic model is

$$\begin{gathered} u_t = \mu u_{xx} + f(u), \qquad 0 < x < l, t > 0 \\ u_x(0,t) = u_x(l,t) = 0 \end{gathered}$$

with $f(u) = ru(u-a)(K-u)$, and that the initial condition is

$$u(x,0) = K_c e^{-\sqrt{r_0/\mu_0}(x+L)}.$$

If $u(x,0) < a$ then the solution to the ordinary differential equation $w_t = f(w)$ with $w(0) = \max u(x,0)$ is a supersolution to (2.6)–(2.8), and $w \to 0$ as $t \to \infty$. Thus, in this scenario, colonization always fails if $u(x,0) < a$ on $(0,l)$, which will be true if $u(0,0) < a$ since the initial density induced by dispersal from the continent is decreasing in x. Thus, colonization always fails if

$$K_c e^{-\sqrt{r_0/\mu_0}L} < a,$$

which will be the case if L or $\sqrt{r_0/\mu_0}$ is too large. Establishing sufficient conditions for successful colonization requires more analysis.

If we define $F(u)$ to be the antiderivative of $f(u)$ with $F(0) = 0$ then the expression

$$E(t) = \int_0^l \left[\frac{\mu u_x^2}{2} - F(u) \right] dx \tag{3.1}$$

is a Lyapunov function for the model in the sense of [13]. Computing $E'(t)$, integrating the first term by parts, and using the model yields

$$E'(t) = -\int_0^l u_t^2 \, dx.$$

It follows as in [13] that all solutions to the model must converge to the set of equilibria. Also, if we compute E for $u \equiv 0$ we obtain $E \equiv 0$; so if substituting the initial data into E yields $E(0) < 0$ then u cannot approach zero as $t \to \infty$ and thus the model will predict successful colonization. (In general it is not clear which equilibrium u approaches if $E(0) \geqslant 0$.) If we label the initial condition as $u_0(x)$ then we have $u_{0x} = -\sqrt{r_0/\mu_0}\,u_0$. Thus, we have

$$\begin{aligned} E(0) &= \int_0^l \left[\frac{\mu u_{0x}^2}{2} - F(u_0) \right] dx \\ &= \int_0^l \left[\frac{-\mu\sqrt{r_0/\mu_0}}{2} u_0 \mu_{0x} + \frac{F(u_0) u_{0x}}{\sqrt{r_0/\mu_0}\, u_0} \right] dx \\ &= \int_{u_0(0)}^{u_0(l)} \left[\frac{-\mu\sqrt{r_0/\mu_0}}{2} u + \frac{F(u)}{\sqrt{r_0/\mu_0}\, u} \right] du. \end{aligned} \tag{3.2}$$

The last integral can and will be explicitly calculated. However, since the form of u_0 is somewhat complicated it is convenient to introduce some notation. Let $z_0 = \sqrt{r_0/\mu_0}$ and $M_0 = K_c e^{-\sqrt{r_0/\mu_0}L} = K_c e^{-z_0 L}$. Then $u_0 = M_0 e^{-z_0 x}$ and computing the last integral in (3.2) yields

$$\begin{aligned} E(0) = \Bigg[\left(\frac{\mu z_0^2 + raK}{4} \right) (1 - e^{-2z_0 l}) &- \frac{r(a+K)}{9} (1 - e^{-3z_0 l}) M_0 \\ &+ \frac{r}{16} (1 - e^{-4z_0 l}) M_0^2 \Bigg] M_0^2 / z_0. \end{aligned} \tag{3.3}$$

The question now is when does (3.3) yield $E(0) < 0$ so that successful colonization is predicted. (The case $E(0) \geqslant 0$ is inconclusive.) Obviously the expression depends on various parameters in complicated ways, so it is useful to consider how the expression varies as the parameters are varied in specific ways. Suppose that the size of the island is large; i.e., $l \to \infty$. Then the sign of $E(0)$ is determined by the sign of

$$\frac{\mu z_0^2 + raK}{4} - \frac{r(a+K)}{9} M_0 + \frac{M_0^2 r}{16}. \tag{3.4}$$

Recall that $M_0 = K_c e^{-\sqrt{r_0/\mu_0}L}$. If we have $K_c = K$ and set $\beta = e^{-\sqrt{r_0/\mu_0}L}$ then $M_0 = K\beta$ with $0 < \beta < 1$, $\beta \to 0$ as $L \to \infty$, $\beta \to 1$ as $L \to 0$. If we have $a = \alpha K$ then the expression in (3.4) may be written as

$$\frac{\mu z_0^2}{4} + rK^2 \left[\frac{\alpha}{4} - \frac{(1+\alpha)\beta}{9} + \frac{\beta^2}{16} \right]. \tag{3.5}$$

Thus, $E(0) < 0$ if rK^2 is large relative to μz_0^2 and

$$\frac{\alpha}{4} - \frac{(1+\alpha)\beta}{9} + \frac{\beta^2}{16} < 0. \tag{3.6}$$

The inequality (3.6) will be satisfied when $\beta \approx 1$ (corresponding to small values of L or $\sqrt{r_0/\mu_0}$) provided $\alpha < 7/20$; so if $K_c = K, r$ is large, and $a < (7/20)K$ then a large island close enough to the continent will be colonized successfully. Also, for any $\beta \in (0,1)$, that is, for any distance from the continent to the island, colonization will succeed if the ratio $\alpha = a/K$ of minimum viable population to carrying capacity is sufficiently small. If the island is small, we would want to examine what happens as $l \to 0$. At $l = 0, E(0) = 0$, but we can calculate $d(E(0))/dl$ at $l = 0$ to be

$$M_0^2\left[\frac{\mu z_0^2 + raK}{2} - \frac{r(a+K)M_0}{3} + \frac{r}{4}M_0^2\right]. \tag{3.7}$$

If we again assume $K_c = K$, and let $a = \alpha K, e^{-\sqrt{r_0/\mu_0}L} = \beta$, we have that the expression in (3.7) is negative for μz_0^2 small or rK^2 large if

$$\frac{\alpha}{2} - \frac{(1+\alpha)}{3}\beta + \frac{\beta^2}{4} < 0 \tag{3.8}$$

The inequality (3.8) will hold for $\beta \approx 1$ if $\alpha < \frac{1}{2}$, and for any fixed $\beta \in (0,1)$ if α is sufficiently small. The condition $\alpha < \frac{1}{2}$ is natural, since $E(0) < 0$ for $u_0(x) \equiv K$ only if $\alpha < \frac{1}{2}$; also, the model (2.6), (2.7) on an infinite interval supports a traveling wavefront going from 0 to K if $\alpha < \frac{1}{2}$ but the wavefront goes from K to 0 if $\alpha > \frac{1}{2}$. If we let $\sqrt{r_0/\mu_0} \to 0$, so that the dispersal ability of our organism becomes arbitrarily good, we have for $K_c = K$ that $M_0 \to K$ and in (3.3) we obtain

$$\begin{aligned}\lim_{z_0 \to 0} E(0) &= rK^2 l\left[\frac{aK}{2} - \frac{(a+K)K}{3} + \frac{K^2}{4}\right]\\ &= rK^4 l\left[\frac{\alpha}{2} - \left(\frac{1+\alpha}{3}\right) + \frac{1}{4}\right],\end{aligned} \tag{3.9}$$

which is negative if $\alpha < \frac{1}{2}$; so a sufficiently good disperser will colonize successfully if $\alpha < \frac{1}{2}$. Finally, we note that if rK^2 is small or μz_0^2 is large then we will never have $E(0) < 0$ for the case $K_c = K$ and meaningful values of the remaining parameters. This does not necessarily imply that colonization fails, but only that the Lyapunov approach is inconclusive.

A different way of determining conditions for successful colonization is based on the observation that if the initial data for our model is a local subsolution to the equilibrium problem then the solution to the time-dependent problem will increase toward the smallest global equilibrium lying above the local subsolution [6, 12, 16–18]. If our initial data lie above such a subsolution then the corresponding solution of the time-dependent problem will be bounded below by something that approaches a global equilibrium. Since all nonzero nonnegative global equilibria are strictly positive by the maximum principle, the interpretation is that colonization is successful. We want to use local subsolutions of (2.6)–(2.8) satisfying

$$\begin{aligned} \mu v_{xx} + f(v) &= 0 \qquad \text{on } (0, l_0) \\ v_x(0) &= 0 \\ v(l_0) &= 0 \end{aligned} \tag{3.10}$$

for some $l_0 \in (0, l)$. (These are strict subsolutions because of the boundary condition at l_0.) In using such subsolutions we need only have our initial data bounded below by v on $(0, l_0)$ to conclude that the equilibrium our solution approaches is positive, and the behavior of the initial data for $l_0 < x < l$ is irrelevant as long as it remains nonnegative. The point is that the density of colonists decays exponentially, so we cannot expect a high density over all of a large island; on the other hand, if a sufficiently high density is induced over part of the island that may be sufficient to cross the threshold for successful colonization. Constructing a suitable local subsolution for $0 < x < l_0$ then allows conclusions to be drawn about colonization of any larger island at the same distance from the continent.

A function v satisfying (3.10) on $(0, l_0)$ and extended to be zero on (l_0, l) will be a subsolution for the model (2.6) with boundary conditions $u_x(0,t) = 0$, $u_x(l,t) + bu(l,t) = 0$ for any $b > 0$, or even $u_x(0,t) = 0$, $u(l,t) = 0$. Thus, a conclusion of successful colonization based on comparison of the density induced by dispersal from the continent with such a function v will remain valid under these less favorable boundary conditions. (The condition $u(l,t) = 0$ describes a situation where any individual crossing the seaward boundary of the island perishes immediately.) Thus, conditions implying colonization on the basis of such a comparison will be robust with respect to the boundary condition at $x = l$. It turns out that solutions to (3.10) with the boundary condition $v(0) = 0$ can also be constructed; however, such a solution will have $v_x(l_0/2) = 0$ and so will require a total interval of support twice as long as that needed under the condition $v_x(0) = 0$. The construction of a solution with $v(0)=v(l_0)=0$ exploits the symmetry of the differential equation in (3.10) with respect to x about $x=l_0/2$ and yields a solution with the same symmetry properties, so that $v_x(l_0/2)=0$. Alternatively, the solution can be constructed by setting $v_x(l_0/2)=0$, $v(l_0/2)=v_0$ and varying v_0 in what amounts to a shooting method to achieve $v(0)=v(l_0)=0$. Such solutions would be relevant if we imposed boundary conditions $u(0,t)=u(l,t)=0$ in (2.6). Such a modification would obviously cause quantitative changes in the conditions for colonization, but the qualitative features would not be changed.

Solutions can be obtained for (3.10) by finding v satisfying the differential equation and the Dirichlet boundary conditions $v(-l_0)=v(l_0)=0$. (This can be seen by letting $w=v'$ and examining the symmetry of the phase portrait.) Such solutions have been studied extensively; see, for example, [6, 19]. It is observed in [6] that Eq. (2.6) (or (3.10)) has the first integral $\mu(v')^2/2+F(v)$ and that if δ is such that $F(\delta)>0$ then there is a solution v_δ to $\mu'' v+f(v)=0$, which is positive on $(-l_0, l_0)$ with maximum δ at $x=0$ (so that in fact v satisfies (3.10)) with

$$l_0(\delta)=\sqrt{\mu/2}\int_0^\delta [F(\delta)-F(s)]^{-1/2}\,ds. \tag{3.11}$$

(There will exist $\delta_0\in(a,K)$ with $F(\delta)>0$ for $\delta\in(\delta_0,K)$ if $K>2a$.) If

$$K_c e^{-\sqrt{r_0/\mu_0}(L+l_0(\delta))}>\delta \tag{3.12}$$

for some δ with $F(\delta)>0$ then $u(x,0)>\delta\geqslant v_\delta(x)$ on $(0,l_0(\delta))$ so that $u(x,0)$ is bounded below by a local subsolution, and thus colonization succeeds if $l>l_0(\delta)$. It is worth noting that $l_0(\delta)=\sqrt{\mu/r}\,l_1(\delta)$, where l_1 depends on δ, a, and K only, so decreasing $\sqrt{\mu/r}$ decreases $l_0(\delta)$. Also, if $K_c=K>2a$ then (3.12) holds if $\sqrt{r_0/\mu_0}$ is small enough. Of course (3.12) is sufficient but not necessary for colonization, and in fact in many cases may impose much too strong a condition. What is really required is that $K_c e^{-\sqrt{r_0/\mu_0}(L+x)}\geqslant v_\delta(x)$ on $[0,l_0(\delta)]$. In some cases sharper conditions may be possible, and we next illustrate one way in which they can sometimes be obtained.

If w satisfies $w(0)=v_\delta(0)=\delta, w'(0)=v_\delta'(0)=0$, and $w''\geqslant v_\delta''$ it is a simple exercise in differential inequalities to show that $w\geqslant v_\delta$. We can find such a w for a given δ if we can construct a function $g(v)\leqslant f(v)$ on $[0,\delta]$ such that if $\mu w''+g(w)=0$ and $w(0)=\delta$, $w'(0)=0$ then $0\leqslant w\leqslant\delta$ on $[0,l_1(\delta)]$ for some $l_1(\delta)>0$. To facilitate our specific construction we assume that

$$a=\alpha K \qquad \text{with } \alpha\leqslant 1/3. \tag{3.13}$$

We can then construct $g(u)$ from the tangent lines to $f(u)$ at $u=0$ and $u=a$ by defining $g(u)$ to be equal to the larger of the two lines at each point. The tangent line at $u=0$ is the graph of $y=-raKu$; that at a is the graph of $y=ra(K-a)(u-a)$. The tangent line at a intersects the graph of $y=f(u)$ at $u=K-a$, and for $0\leqslant u\leqslant K-a$ both lines lie below the graph of $y=f(u)$. They intersect at $u=a(K-a)/(2K-a)$. Thus, we can take

$$g(u)=\begin{cases}-raKu, & 0\leqslant u\leqslant a(K-a)/(2K-a)\\ ra(K-a)(u-a), & a(K-a)/(2K-a)\leqslant u\leqslant K-a.\end{cases} \tag{3.14}$$

If (3.13) holds then the integral of $g(u)$ from 0 to $K-a$ is positive and so is $F(K-a)$, so we can take $\delta=K-a$. (This choice is somewhat arbitrary, but it serves to illustrate the method of estimation.) For our choices of δ and g we have for x near zero

$$\begin{gathered}w''+(r/\mu)a(K-a)w=(r/\mu)a(K-a)a\\ w(0)=K-a\\ w'(0)=0\end{gathered}$$

so that $w(x)=a+(K-2a)\cos(\sqrt{(r/\mu)a(K-a)}\,x)$ until x is large enough that $w(x)=a(K-a)/(2K-a)$, that is, for

$$0\leqslant x\leqslant x_0\equiv\sqrt{\mu/(ra(K-a))}\,\cos^{-1}(-aK/((2K-a)(K-2a))). \tag{3.15}$$

We have $w(x_0)=a(K-a)/(2K-a)$, but to find $w(x)$ for $x>x_0$ we also need $w'(x_0)$. We have

$$w'(x_0)=-(K-2a)\sqrt{(r/\mu)a(K-a)}\,\sin\left(\sqrt{(r/\mu)a(K-a)}\,x_0\right),$$

with

$$\begin{aligned}\sin\left(\sqrt{(r/\mu)a(K-a)}\,x_0\right)&=\sqrt{1-\cos^2\left(\sqrt{(r/\mu)a(K-a)}\,x_0\right)}\\ &=\sqrt{1-\frac{a^2K^2}{(2K-a)^2(K-2a)^2}}\\ &=\frac{2(K-a)\sqrt{K^2-3aK+a^2}}{(2K-a)(K-2a)}.\end{aligned}$$

(By (3.13) $K^2 - 3aK + a^2 > 0$.) Thus,

$$w'(x_0) = -\frac{2(K-a)}{2K-a}\sqrt{(r/\mu)a(K-a)(K^2-3aK+a^2)}\,.$$

Since $w'(x_0) < 0$, w crosses below $a(K-a)/(2K-a)$ so that $\mu w'' - raKw = 0$, and hence

$$\begin{aligned} w(x) = {} & \frac{a(K-a)}{2K-a}\cosh\sqrt{(r/\mu)aK}\,(x-x_0) \\ & - \frac{2(K-a)}{2K-a}\sqrt{(K-a)(K^2-3aK+a^2)/K} \\ & \times \sinh\left(\sqrt{(r/\mu)aK}\,(x-x_0)\right) \end{aligned} \tag{3.16}$$

for $x > x_0$. It follows that $w(x) = 0$ when $x = x_0 + x_1$, i.e., $x - x_0 = x_1$, such that

$$x_1 = \sqrt{\mu/(raK)}\,\tanh^{-1}\left(\frac{a\sqrt{K}}{2\sqrt{(K-a)(K^2-3aK+a^2)}}\right). \tag{3.17}$$

(The expression inside the $\tanh^{-1}$ is less than one by (3.13).) From (3.15), (3.17), and the fact that $v_{K-a}(x) \leqslant w(x)$ we have immediately

$$\begin{aligned} l_0(K-a) & \leqslant x_0 + x_1 \\ & = \sqrt{\mu/(ra)}\left[\frac{1}{\sqrt{K-a}}\cos^{-1}\left(\frac{-aK}{(2K-a)(K-2a)}\right)\right. \\ & \qquad \left. + \frac{1}{\sqrt{K}}\tanh^{-1}\left(\frac{a\sqrt{K}}{2\sqrt{(K-a)(K^2-3aK+a^2)}}\right)\right]. \end{aligned}$$

In fact, by (3.13)

$$0 > \frac{-aK}{(2K-a)(K-2a)} > -\frac{3}{5} \geqslant -\frac{\sqrt{2}}{2}$$

so $x_0 \leqslant 3\pi\sqrt{\mu/(ra(K-a))}\,/4$, and also the terms corresponding to positive exponentials in (3.16) have negative coefficients, so that for $x > x_0$, keeping only the negative exponentials yields

$$\begin{aligned} w(x) \leqslant {} & \frac{(K-a)}{2(2K-a)}\left[a + 2\sqrt{(K-a)(K^2-3aK+a^2)/K}\right] \\ & \times \exp\left[-\sqrt{(r/\mu)aK}\,(x-x_0)\right]. \end{aligned} \tag{3.18}$$

Using these estimates we can give some fairly explicit conditions implying successful colonization. We will have $u(x,0) \geqslant v_{K-a}(x)$ if $u(x,0) \geqslant w(x)$, which will be true if $u(x,0) \geqslant K-a$ on $[0,x_0]$ and $u(x,0)$ is larger than the expression on the right of (3.18) for $x > x_0$. Suppose $K_c = K$ and $e^{\sqrt{r_0/\mu_0}L} = \beta$. Then $u(x,0) \geqslant u(x_0,0) = K\beta e^{-\sqrt{r_0/\mu_0}x_0}$ for $x \in [0,x_0]$ so $u(x,0) \geqslant K-a$ on $[0,x_0]$ provided that $K\beta \geqslant (K-a)\exp\sqrt{r_0/\mu_0}\,x_0$, which will hold if

$$\beta \geqslant (1-\alpha)\exp\left[3\pi\sqrt{r_0\mu/(\mu_0 r\alpha(1-\alpha))}\,/4K\right]. \qquad (3.19)$$

If (3.19) holds then $u(x_0,0) \geqslant K-a$, and for $x > x_0$ $u(x,0) = u(x_0,0)\exp[-\sqrt{r_0/\mu_0}(x-x_0)]$, so $u(x,0) \geqslant w(x) \geqslant v_{K-a}(x)$ for $x > x_0$ if

$$\sqrt{r_0/\mu_0} \leqslant \sqrt{(r/\mu)aK} \qquad (3.20)$$

and

$$1 \geqslant \left[a + 2\sqrt{(K-a)(K^2-3aK+a^2)/K}\right]/[2(2K-a)].$$

The last inequality is equivalent to

$$1 \geqslant \left[\alpha + 2\sqrt{(1-\alpha)(1-3\alpha+\alpha^2)}\right]/2(2-\alpha),$$

which will hold if (3.13) is satisfied, so (3.13), (3.19), and (3.20) imply successful colonization if $K_c = K$.

The conditions just obtained are not intended to be optimal; they are merely representative of explicit conditions that follow from estimation of the subsolution v_δ defined by (3.10).

4. INITIAL ISLAND POPULATION DENSITIES—SECOND REGIME

Recall that in Section 2 we describe two regimes for determining the density $u(x,0)$ of the immigrant species on the island at the cessation of immigration. In the first regime, we obtain the explicit formula

$$u(x,0) = K_c e^{-\sqrt{(r_0/\mu_0)}(x+L)},$$

$x \in [0,l]$, while in the second regime, $u(x,0)$ is the minimal positive solution to the problem

$$-u_{xx} = \tilde{f}(u) \qquad \text{in } (0,l) \tag{4.1}$$

$$u_x(0) = -\gamma \tag{4.2}$$

$$u_x(l) = 0. \tag{4.3}$$

In (4.1)–(4.3), $\gamma > 0$ is given by $\gamma = K_c\sqrt{(r_0\mu_0)}\,/\,\mu e^{-\sqrt{(r_0/\mu_0)}L}$ and $\tilde{f}(u) = (r/\mu)u(u-a)(K-u)$ for $0 \leqslant u \leqslant K$, where $r, \mu > 0$ and $0 < a < K$. In the second regime $u(x,0)$ is a strict upper solution for

$$u_t = \mu u_{xx} + f(u) \qquad \text{in } (0,l)\times(0,\infty) \tag{4.4}$$

$$u_x(0,t) = 0 \qquad \text{on } (0,\infty) \tag{4.5}$$

$$u_x(l,t) = 0 \qquad \text{on } (0,\infty), \tag{4.6}$$

where $f(u) = ru(u-a)(K-u)$. Consequently, the theory of upper and lower solutions for parabolic partial differential equations [6] guarantees that the solution to (4.4)–(4.6) starting at $u(x,0)$ decreases monotonically with time and converges to an equilibrium solution to (4.4)–(4.6) as $t \to \infty$. If the equilibrium in question is nonzero (hence positive throughout the island by the maximum principle), it is reasonable to say that the immigrant species is successful at colonizing the island. Consequently, successful colonization of the island is tantamount to $u(x,0)$ exceeding a nontrivial equilibrium to (4.4)–(4.6). Whether or not $u(x,0)$ exceeds a nontrivial equilibrium to (4.4)–(4.6) depends upon the parameters in (4.1)–(4.3) and (4.4)–(4.6), most especially γ and the ratio r/μ. To address this issue, it is necessary to analyze the structure of the positive solutions to (4.1)–(4.3) in terms of the parameters γ and r/μ.

To do so, we allow γ to range over all of $\mathbb{R}$ and r to be nonnegative, and define f (and hence also $\tilde{f}$) outside the interval $[0,K]$. From a biological viewpoint only nonnegative values of γ are of interest, but we must consider $\gamma < 0$ as well to perform the necessary mathematical analysis. From a modeling standpoint, the crucial features of the population law are maintained whether f is extended in the obvious way (i.e., use the formula (2.7) for all $u \in \mathbb{R}$) or f is extended by

$$f(u) = \begin{cases} -raKu, & u \leqslant 0 \\ ru(u-a)(K-u), & 0 \leqslant u \leqslant K \\ -rK(K-a)(u-K), & u \geqslant K \end{cases} \tag{4.7}$$

(i.e., extend f outside $[0, K]$ linearly and smoothly). However, the mathematical analysis is facilitated if f is extended via (4.7), so that is how we extend f. A complete account of the relevant analysis would likely require journal space sufficient for an entire article and would be of independent mathematical interest. In this article, however, our interest is in the ramifications of the analysis for island colonization. Consequently, we present only an overview of the analysis, with a focus on those aspects most directly relevant to the issue at hand.

Note to begin with that for any $r/\mu \neq 0$, (4.4)–(4.6) has the spatially homogeneous equilibria 0, a, and K. There may or may not be additional, spatially heterogeneous positive equilibria. In case there are no spatially heterogeneous positive equilibria for (4.4)–(4.6), $\gamma > 0$ must be such that $u(x,0) \geqslant a$ throughout the island in order for the immigrant species to succeed at colonization. (Otherwise, 0 is the only nonegative equilibrium below $u(x,0)$.) What we see is that for r/μ small enough, (4.4)–(4.6) admits only homogeneous equilibria and that for such $r/\mu, u(x,0) \geqslant a$ throughout the island for γ sufficiently large. Moreover, we quantify explicitly how small r/μ needs to be (in terms of K and a), and also how large γ needs to be (in terms of K, a and r/μ). As r/μ increases, spatially inhomogeneous equilibria to (4.4)–(4.6) occur and the requirement $u(x,0) \geqslant a$ throughout the island for successful colonization can be relaxed.

Let us now give a summary of facts concerning the minimal positive solutions to (4.1)–(4.3), where now $\tilde{f}(u)$ is defined for all $u \in \mathbb{R}$ via (4.7).

THEOREM 4.1

For any $\gamma > 0$, (4.1)–(4.3) *admits a minimal positive solution, denoted* u_γ *and having the following additional properties*:

(a) *If* $0 < \gamma_1 < \gamma_2$, $u_{\gamma_1} < u_{\gamma_2}$ *on* $(0, l)$.
(b) *For any* $\gamma_1 > 0$, $\lim_{\gamma \to \gamma_1^-} u_\gamma = u_{\gamma_1}$.
(c) *If* $u_\gamma \geqslant a$ *on* $[0, l]$, *then* $u_\gamma \geqslant K$ *on* $(0, l)$.

The existence of a minimal positive solution to (4.1)–(4.3) for $\gamma > 0$ follows from the fact that 0 is a strict lower solution, as noted in Section 2. Property (a) holds since u_{γ_2} is a strict upper solution to (4.1)–(4.3) for $\gamma = \gamma_1$. This property tells us that if the immigrant species is successful in colonizing the island when $\gamma = \gamma_1$, it will be successful when $\gamma = \gamma_2$. Consequently, increasing the diffusion rate μ_0 across the transit corridor or decreasing the diffusion rate μ on the island enhances the prospects for colonization. Property (b) is essentially a consequence of the Ascoli–Arzela theorem. (See, for example, [20, Sect. 1].) The last property, (c), tells us that in our second regime if the population density of the immigrant has been driven above the uniform minimal viable density, it is in fact above the carrying capacity. This fact is a consequence of the inhomogeneous boundary data and the Allee-type dynamics. Observe that $u'_\gamma(0) = -\gamma < 0$, so that $u_\gamma(x) < u_\gamma(0)$ for small values of x. So if $u_\gamma \geqslant a$ on $(0,l)$, $u_\gamma(0) > a$. If $u_\gamma(0) \leqslant K$, $u''_\gamma(x) = -\tilde{f}(u_\gamma(x)) < 0$ for small values of x. Thus u_γ and u'_γ both decrease for small values of x and continue to do so as long as u_γ remains larger than a. If u_γ reaches a for some $x \in [0,l]$, then $u'_\gamma(x) < 0$, so that u_γ fails to satisfy the boundary condition (4.3) if $x = l$ and dips below a if $x < l$, either of which is a contradiction. So $u_\gamma(0) > K$. Either $u_\gamma \geqslant K$ for all $x \in [0,l]$ or there is $x_1 \in [0,l]$ with $u_\gamma(x_1) < K$. In this last case, there must be a largest $x_0 < x_1$ so that $u_\gamma(x_0) = K$. Since $(u_\gamma(x_1) - u_\gamma(x_0))/(x_1 - x_0) < 0$, the mean value theorem guarantees $x_2 \in (x_0, x_1)$ so that $u'_\gamma(x_2) < 0$ and $u_\gamma(x_2) < K$. Then, as before, u_γ and u'_γ decrease for $x > x_2$, forcing u_γ below a or a failure to meet (4.3). The only possibility is that $u_\gamma \geqslant K$ on $[0,l]$.

We next must augment the preceding description of the set of minimal positive solutions to (4.1)–(4.3) for $\gamma > 0$. Let $C^2[0,l]$ denote the Banach space of twice continuously differentiable functions on $[0,l]$ with the usual norm $\| \ \|$, given by

$$\|u\| = \max_{x \in [0,l]} |u(x)| + \max_{x \in [0,l]} |u'(x)| + \max_{x \in [0,l]} |u''(x)|,$$

and fix $r/\mu > 0$.

THEOREM 4.2

Let $\mathscr{C}$ *denote the connected component of* $\{(\gamma,u) \in \mathbb{R} \times C^2[0,l] : (\gamma,u)$ *solves* (4.1)–(4.3) *with* $u \geqslant 0\}$ *containing* (0,0). *Then* $\mathscr{C}$ *has the following properties*:

(a) $(0,K) \in \mathscr{C}$.
(b) *There is a* $u \in C^2[0,l]$ *with* $u \neq K$ *and* $u \neq 0$ *so that* $(0,u) \in \mathscr{C}$.
(c) *There is a* $\gamma_0 < 0$ *so that if* $(\gamma,u) \in \mathscr{C}, \gamma \geqslant \gamma_0$.
(d) *There is a* $\gamma_1 > 0$ *so that* $\mathscr{C}$ *contains the arc* $\tilde{\mathscr{C}}$ *given by*

$$\tilde{\mathscr{C}} = \{(0,0)\} \cup \{(\gamma,u_\gamma) : 0 < \gamma < \gamma_1\}.$$

(e) *There is a* $\gamma_2 < 0$ *so that* $\mathscr{C}$ *contains an arc* $\{(\gamma,\bar{u}(\gamma)) : \gamma > \gamma_2\}$, *where* $\bar{u}(0) \equiv K$ *and* $\bar{u}(\gamma) > K$ *on* $(0,l)$ *for* $\gamma > 0$. *Moreover, there is a* $\gamma_3 > 0$ *so that* $\bar{u}(\gamma) = u_\gamma$ *for* $\gamma > \gamma_3$.

Theorem 4.2 provides a general description of how the two stable homogeneous equilibria to (4.4)–(4.6) (namely $u \equiv 0$ and $u \equiv K$) are linked together through spatially heterogeneous positive solutions of

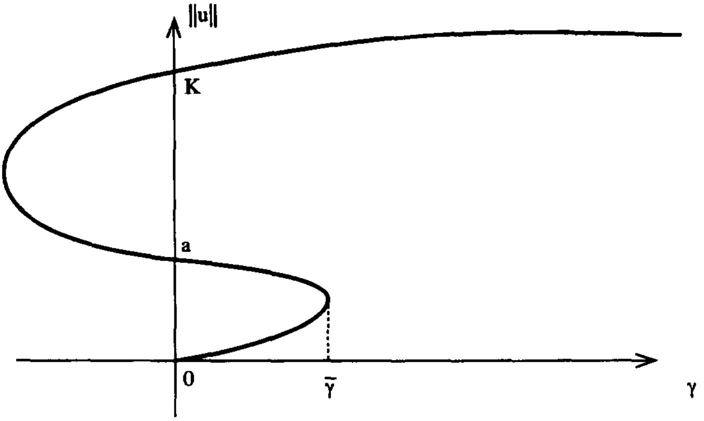


FIG. 4.1. The simplest possible form for the continuum $\mathscr{C}$ of positive solutions corresponding to a positive flux of immigrants into the island is illustrated schematically. In this case colonization fails if $\gamma < \bar{\gamma}$ and succeeds if $\gamma > \bar{\gamma}$. The parameter γ effectively represents the rate at which immigrants arrive at the island, which will naturally depend on biological and geographic factors as described in the text.

(4.1)–(4.3) as the flux parameter subsequently increases and decreases. (See Fig. 4.1.) By increasing γ from 0, the zero equilibrium at $\gamma = 0$ is deformed into the minimal positive solutions for (4.1)–(4.3) (i.e., the population densities of the immigrant species at the cessation of immigration) for some range of γ. For γ sufficiently small, these minimal solutions are necessarily less than a throughout $(0, l)$ and the immigrant species fails to colonize. By (b), (c), and (e), the arc of minimal positive solutions to (4.1)–(4.3) emanating from $(0,0)$ is connected to $(0, K)$ by first passing through a positive solution when $\gamma = 0$ other than 0 or K. It may or may not be the case that this solution is a, the other homogeneous equilibrium at $\gamma = 0$. Note also that the arc emanating from $(0,0)$ is necessarily connected to positive solutions to (4.1)–(4.3), which are not minimal positive solutions. By (e), the equilibrium $u \equiv K$ at $\gamma = 0$ can by increasing γ also be continuously deformed into spatially heterogeneous positive solutions of (4.1)–(4.3), all of which exceed K on $(0, l)$. Moreover, solutions along this arc are for γ large enough the minimal positive ones (i.e., u_γ's).

A ramification of Theorem 4.2 is that there is at least one break in the graph $\{(\gamma, u_\gamma) : \gamma > 0\}$. Indeed, from Theorem 4.1 (b)–(c), there must be a critical value $\bar{\gamma} > 0$ so that $u_{\bar{\gamma}}(x) < a$ for some $x \in [0, l]$ while for $\gamma > \bar{\gamma}, u_\gamma(x) > K$ for all $x \in [0, l]$. Consequently, when the flux parameter γ crosses the threshold value $\bar{\gamma}$, the immigrant species tends to its carrying capacity on the island (i.e., K) after the cessation of immigration. The immigrant species is then clearly successful at colonization. Moreover, if 0, a, and K are the only nonnegative equilibria to (4.4)–(4.6) the threshold valve $\bar{\gamma}$ is the demarcation point between unsuccessful ($\gamma \leqslant \bar{\gamma}$) and successful ($\gamma > \bar{\gamma}$) colonization.

The proof of Theorem 4.2 is somewhat complicated, its essence an appeal to the global implicit function theorem of Alexander and Yorke [21], at the point $(0, K)$. Part (e) guarantees that the continuum $\mathscr{C}$ through $(0, K)$ is unbounded. As a result, it follows from [21] that $\mathscr{C} - (\{(0,K)\} \cup \{(\gamma, \bar{u}(\gamma)) : \gamma > 0\})$ must also be unbounded. The a priori bound given in part (c) and the maximum principle together assert that $\mathscr{C} - (\{(0,K)\} \cup \{(\gamma, \bar{u}(\gamma)) : \gamma > 0\})$ can be unbounded only if $(0,0) \in \mathscr{C}$. Parts (d) and (e) are consequences of the classical (local) implicit function theorem, while the a priori bound in (c) is a consequence of upper and lower solution methods. We prove (c) and (e). The proof of (d) is similar to that of (e) and is omitted.

Proof. (Theorem 4.2(c)). It follows from (4.7) that

$$\tilde{f}(u) \leqslant \frac{rK^2(K-a)}{\mu} - \frac{r}{\mu}K(K-a)u$$

for all $u \in \mathbb{R}$. Consequently, if u is a positive solution to (4.1)–(4.3) for some $\gamma < 0$, then u is a lower solution to

$$\begin{aligned} -w'' &= \frac{rK^2(K-a)}{\mu} - \frac{r}{\mu}K(K-a)w \qquad \text{on } (0,l) \\ w'(0) &= |\gamma| \\ w'(l) &= 0. \end{aligned} \tag{4.8}$$

K or any larger constant is an upper solution to (4.8). Since

$$w = K - |\gamma| \frac{\cosh\left(\sqrt{(r/\mu)(K)(K-a)}\,(l-x)\right)}{\left(\sqrt{(r/\mu)(K)(K-a)}\right)\sinh\left(\sqrt{(r/\mu)(K)(K-a)}\,l\right)}$$

is the unique solution to (4.8), it follows that u can be positive on $(0, l)$ only if w is. When

$$|\gamma| > K\frac{\sqrt{(r/\mu)K(K-a)}\,\sinh\left(\sqrt{(r/\mu)K(K-a)}\,l\right)}{\cosh\left(\sqrt{(r/\mu)K(K-a)}\,l\right)},$$

w ceases to be positive throughout $(0,l)$. So there can be no positive solution (4.1)–(4.3) if

$$\gamma \leqslant \frac{-K\sqrt{(r/\mu)(K)(K-a)}\,\sinh\left(\sqrt{(r/\mu)(K)(K-a)}\,l\right)}{\cosh\left(\sqrt{(r/\mu)K(K-a)}\,l\right)}.$$

Proof. (Theorem 4.2(e)). Let W denote the subspace of $C^2[0,1]$ consisting of those functions w with $w'(0)=0=w'(l)$. Define $F\colon W \times \mathbb{R} \to C[0,l]$ by $F(w,\gamma)=w''+\gamma h''+\tilde{f}(w+\gamma h)$, where $h(x)=\cosh(l-x)/\sinh l$. Note that $h'(0)=-1$ and $h'(l)=0$, so that $F(w,\gamma)=0$ is equivalent to $w+\gamma h$ solving (4.1)–(4.3). Observe that $F(K,0)=\tilde{f}(K)=0$ and that $(\partial F/\partial w)(K,0)v=v''+\tilde{f}'(K)v$. Since $v'(0)=0=v'(l)$ and $\tilde{f}(K)=-(r/\mu)K(K-a)<0$, $(\partial F/\partial w)(K,0)v=0$ implies $v\equiv 0$. As a result, the implicit function theorem implies that there is a smooth function $w(\gamma)$ defined in a neighborhood of $\gamma=0$ with $w(0)=K$ so that the solution set to (4.1)–(4.3) near $(0,K)$ is given by $\{(\gamma, w(\gamma)+\gamma h)\colon \gamma \in(-\delta,\delta)\}$ for some $\delta>0$. It is a simple matter to calculate that for $\gamma\in(-\delta,\delta)$, $z_\gamma=(\partial w/\partial\gamma)$ satisfies

$$z_\gamma''+h''+\tilde{f}'(w(\gamma)+\gamma h)(z_\gamma+h)=0$$

in $(0,l)$ with $(z_\gamma+h)'(0)=-1$ and $(z_\gamma+h)'(l)=0$. When $\gamma=0$, $w(\gamma)+\gamma h=K$. Hence

$$z_0+h=\frac{\cosh\sqrt{(r/\mu)K(K-a)}\,(l-x)}{\sqrt{(r/\mu)K(K-a)}\,\sinh\left(\sqrt{(r/\mu)K(K-a)}\,l\right)},$$

which is positive on $(0,l)$. So there must be $\bar{\delta}<\delta$ so that $z_\gamma+h>0$ on $(0,l)$ for $\gamma\in(0,\bar{\delta})$. Consequently, $w(\gamma)+\gamma h$ is initially increasing with respect to γ, so that $w(\gamma)+\gamma h>K$ for $\gamma\in(0,\delta)$. Then $\tilde{f}'(w(\gamma)+\gamma h)=-(r/\mu)K(K-a)$ for all $x\in(0,l)$ and $\gamma\in(0,\bar{\delta})$, by (4.7). Hence

$$z_\gamma+h=\frac{\cosh\sqrt{(r/\mu)K(K-a)}\,(l-x)}{\sqrt{(r/\mu)K(K-a)}\,\sinh\sqrt{(r/\mu)K(K-a)}\,l}$$

for all $\gamma\in[0,\bar{\delta}]$. It is now easy to see that $\bar{u}(\gamma)=w(\gamma)+\gamma h$ can be extended for all $\gamma>0$ in such a way that $\bar{u}(\gamma)$ is a solution to (4.1)–(4.3) with $\bar{u}(\gamma)>K$ on $(0,l)$, because the foregoing arguments may be repeated arbitrarily.

Suppose now that for some $\gamma > 0$, (4.1)–(4.3) admits two solutions greater than or equal to K on $(0,l)$, and denote them by u_1, and u_2. Then $(u_1 - u_2)'' + \tilde{f}'(\theta(x)u_1(x) + (1-\theta(x))u_2(x))(u_1 - u_2) = 0$ on $(0,l)$ and $(u_1 - u_2)'(0) = 0 = (u_1 - u_2)'(l)$, where $\theta(x) \in [0,1]$. Since $\theta(x)u_1(x) + (1-\theta(x))u_2(x) \geqslant K$, $\tilde{f}'(\theta(x)u_1(x) + (1-\theta(x))u_2(x)) = -(r/\mu)K(K - a) < 0$ hence $u_1 - u_2 \equiv 0$. Consequently, if $u_\gamma \geqslant K$ on $(0,l)$, $u_\gamma = \bar{u}(\gamma)$. We give a lower bound on u_γ in Proposition 4.4, which establishes this last fact and completes the proof of Theorem 4.2.

We can make the ramifications of Theorems 4.1 and 4.2 for immigrant species in the second regime more precise by obtaining some quantitative estimates. The first estimate is on the values of (r/μ) for which (4.4)–(4.6) admits only the spatially homogeneous equilibria 0, a, and K. A condition ruling out spatially inhomogeneous equilibria is obtained by using Sturm–Liouville comparison theory. A condition implying the existence of spatially inhomogeneous equilibria can be obtained from (4.1)–(4.3) when $\gamma = 0$ by making the transformation $z = u - a$ in the dependent variable and using bifurcation theory (along the lines of [22]) to analyze the resulting boundary value problem. So doing, we obtain the following result.

THEOREM 4.3

Consider (4.1)–(4.3) *with* $\gamma = 0$ *and* $r/\mu > 0$. *Then*:

(a) *Equations* (4.1)–(4.3) *admit only the three spatially homogeneous solutions* 0, a, *and* K *provided*

$$\frac{r}{\mu} \leqslant \min\left\{\frac{\pi^2}{a^2 l^2}, \frac{\pi^2}{(K-a)^2 l^2}\right\}.$$

(*b*) *Equations* (4.1)–(4.3) *admit at least* $2n$ *spatially heterogeneous positive solutions when*

$$\frac{r}{\mu} > \frac{n^2\pi^2}{a(K-a)l^2}.$$

The spatially heterogeneous solutions to (4.1)–(4.3) whose existence is asserted in (b) represent nonconstant equilibria for (4.4)–(4.6). Any such solution, say u^*, has the property that u^* oscillates around a a finite number of times on $(0,l)$. Since a is the minimum uniform viable density for the immigrant species, the existence of a u^* allows the possibility of successful colonization when the density of the immigrant species $u(x,0)$ at the cessation of immigration in the second regime fails to exceed a throughout the island. Theorem 4.3 (b) asserts that such solutions are available when the ratio $(r/\mu) > \pi^2/a(K-a)l^2$, but not if $(r/\mu) \leqslant \min\{\pi^2/a^2l^2, \pi^2/(K-a)^2l^2\}$. In general, $\min\{\pi^2/a^2l^2, \pi^2/(K-a)^2l^2\} < \pi^2/a(K-a)l^2$, so there is a gap in the values of r/μ where we can at present determine whether or not (4.4)–(4.6) admits nonconstant equilibria. However, if $K = 2a, \pi^2/a^2l^2 = \pi^2/(K-a)^2l^2 = \pi^2/a(K-a)l^2$ and there is no such gap. Recall from the discussion following the statement of Theorem 4.2 that there is a critical value $\bar{\gamma}$ of γ so that the solution to (4.4)–(4.6) with $u(x,0) = u_\gamma(x)$ tends to the carrying capacity for the immigrant (i.e., K) precisely when $\gamma > \bar{\gamma}$. An important consequence of Theorem 4.3 is that provided $(r/\mu) \leqslant \min\{\pi^2/a^2l^2, \pi^2/(K-a)^2l^2\}$, colonization is successful only when $\gamma > \bar{\gamma}$. (This is because if 0, a, and K are the only equilibria for the homogeneous problem (2.6)–(2.8) then the only initial data u_γ that can avoid tending toward zero as $t \to \infty$ are those with $u_\gamma > a$ and hence $u_\gamma > K$.)

Our second estimate is an upper bound on the critical flux parameter $\bar{\gamma}$. To obtain the estimate we first need the lower bound on u_γ given in the following result.

PROPOSITION 4.4

Let r/μ and $\gamma > 0$ be fixed. Let u_γ denote the minimal positive solution to (4.1)–(4.3). *Let $A = \max\{a, K-a\}$. Then*

$$u_\gamma \geqslant \frac{\gamma \cosh\left(\sqrt{(r/\mu)KA}\,(l-x)\right)}{\sqrt{(r/\mu)KA}\,\sinh\left(\sqrt{(r/\mu)KA}\,l\right)}$$
$$\geqslant \frac{\gamma}{\sqrt{(r/\mu)KA}\,\sinh\left(\sqrt{(r/\mu)KA}\,l\right)}.$$

Proof. Note that $\tilde{f}'(u) \geqslant -(r/\mu)KA$ for all u by (4.7). For any $z > 0, \tilde{f}(z)/z = (\tilde{f}(z) - \tilde{f}(0))/(z-0) = \tilde{f}'(\tilde{z})$, where $0 < \tilde{z} < z$ by the mean value theorem. As a consequence, u_γ is an upper solution for the problem

$$\begin{aligned} -w'' &= -(r/\mu)KAw \qquad \text{on } (0,l) \\ w'(0) &= -\gamma \\ w'(l) &= 0. \end{aligned} \tag{4.9}$$

As 0 is a lower solution to (4.9), the proposition follows from the fact that (4.9) admits a unique solution.

We know from Theorem 4.1 (c) that $u_\gamma \geqslant K$ whenever $u_\gamma \geqslant a$ and in that case the immigrant species tends to K long term following the cessation of immigration. Proposition 4.4 implies

$$u_\gamma \geqslant a \qquad \text{if } \frac{\gamma}{\sqrt{(r/\mu)Ka}\,\sinh\!\left(\sqrt{(r/\mu)Ka}\,l\right)} \geqslant a.$$

Hence $\bar{\gamma} \leqslant a\sqrt{(r/\mu)Ka}\,\sinh\sqrt{(r/\mu)Ka}\,l$. We have the following result.

THEOREM 4.5

Let $A = \max\{a, K-a\}$ *and suppose that*

$$K_c\sqrt{r_0\,\mu_0}\,e^{-\sqrt{(r_0/\mu_0)}L} \geqslant a\sqrt{r\mu KA}\,\sinh\!\left(\sqrt{\frac{r}{\mu}KA}\,l\right).$$

Then if the density of the immigrant species upon cessation of immigration is determined through the second regime, the immigrant species tends to its carrying capacity asymptotically following the cessation of its immigration.

Observe now that the expression

$$\frac{\gamma\cosh\!\left(\sqrt{(r/\mu)K(A)}\,(l-x)\right)}{\sqrt{(r/\mu)KA}\,\sinh\!\left(\sqrt{(r/\mu)KA}\,l\right)}$$

bounding u_γ from below in the statement of Proposition 4.4 is a decreasing function of x on $(0,l)$, as is the expression $K_c e^{-\sqrt{(r_0/\mu_0)}(x+l)}$ for the density of the immigrant species at the cessation of immigration in the first regime. Consequently, if

$$\frac{\gamma}{\sqrt{(r/\mu)KA}\,\sinh\!\left(\sqrt{(r/\mu)KA}\,l\right)} < a < \frac{\gamma\coth\!\left(\sqrt{(r/\mu)KA}\,l\right)}{\sqrt{(r/\mu)KA}},$$

the lower solution approach to successful colonization described in Section 3 is in principle applicable in the context of our second regime. In this setting the condition (3.12) for successful colonization becomes $l_0(\delta) < l$ and

$$\frac{\gamma\cosh\!\left(\sqrt{(r/\mu KA)}\,(l-l_0(\delta))\right)}{\sqrt{(r/\mu)KA}\,\sinh\!\left(\sqrt{(r/\mu)KA}\,l\right)} > \delta, \tag{4.10}$$

where $l_0(\delta)$ is as given in (3.11). We do not pursue this line of inquiry further at this time, but we do believe it worthwhile to point out the availability of such techniques for our second regime in cases in which $u_\gamma(x) < a$ for some but not all values of x.

We know that if $(r/\mu) \leqslant \min\{\pi^2/a^2l^2, \pi^2/(K-a)^2l^2\}$, then the immigrant species will not be successful at colonizing the island if γ is such that (γ, u_γ) lies on the initial arc $\tilde{\mathscr{C}}$ of minimal solutions to (4.1)–(4.3) emanating from the solution (0,0) as described in Theorem 4.2(d). It follows as in our proof of Theorem 4.2(e) that (γ, u_γ) lies on $\tilde{\mathscr{C}}$ as long as $\tilde{f}'(u_\gamma) < 0$. (In this case the local implicit function theorem remains applicable.) Since $\tilde{f}(u) = (r/\mu)u(u-a)(K-a)$ for $u \in [0,K]$, $\tilde{f}'(u) = (r/\mu)(-3u^2 + 2(a+K)u - aK)$. It is now easy to observe that $\tilde{f}'(u)$ is increasing on $[0,(a+K)/3]$, and hence that $\tilde{f}'(u) < 0$ on $[0,a/3]$ since $\tilde{f}'(a/3) = (r/\mu)((a^2/3) - (aK/3)) < 0$. As a consequence, (γ, u_γ) lies on $\tilde{\mathscr{C}}$ and the immigrant's attempt at colonization fails if

$$\frac{r}{\mu} \leqslant \min\left\{\frac{\pi^2}{a^2l^2}, \frac{\pi^2}{(K-a)^2l^2}\right\} \qquad \text{and} \qquad u_\gamma \leqslant a/3.$$

Our third and final estimate is on a value $\tilde{\gamma}$ so that $u_\gamma \leqslant a/3$ provided $0 < \gamma \leqslant \tilde{\gamma}$. Observe that $\tilde{f}''(u_\gamma) \geqslant 0$ for $u_\gamma \leqslant a/3$, so that the graph of $\tilde{f}(u)$ lies below the secant line joining (0,0) to $(a/3, \tilde{f}(a/3))$. Consequently, u_γ is a lower solution for

$$\begin{aligned} -w'' &= \big(\tilde{f}(a/3)/(a/3)\big)w \qquad \text{on } (0,l) \\ w'(0) &= -\gamma \\ w'(l) &= 0. \end{aligned} \tag{4.11}$$

Thus we may make the comparison $u_\gamma \leqslant w \leqslant a/3$, so long as the solution w to (4.11) does not exceed $a/3$. Now

$$\frac{\tilde{f}(a/3)}{a/3} = -\left(\frac{r}{\mu}\right)\left(\frac{2}{9}\right)a(3K-a) = -Q^2. \tag{4.12}$$

Using (4.12) and solving (4.11) for w yields

$$w(x) = \frac{\gamma[e^{Qx} + e^{2Ql}e^{-Qx}]}{Q[e^{2Ql} - 1]}. \tag{4.13}$$

From (4.13),

$$w'(x) = \frac{\gamma[e^{Qx} - e^{Q(2l-x)}]}{e^{2Ql} - 1} < 0 \qquad \text{on } [0,l].$$

Thus

$$w(x) \leqslant w(0) = \frac{\gamma[e^{2Ql} + 1]}{Q[e^{2Ql} - 1]} = \frac{\gamma}{Q\tanh(Ql)}.$$

It follows that $u_\gamma \leqslant a/3$ provided that

$$\begin{aligned}\gamma &\leqslant \frac{a}{3} Q\tanh(Ql)\\ &= \frac{a}{9}\sqrt{\frac{r}{\mu}}\sqrt{2a(3K-a)}\tanh\left(\frac{1}{3}\sqrt{\left(\frac{r}{\mu}\right)}\sqrt{2a(3K-a)}\,l\right). \qquad (4.14)\end{aligned}$$

Hence if $r/\mu \leqslant \min\{\pi^2/a^2l^2, \pi^2/(K-a)^2l^2\}$ and γ satisfies (4.14), the immigrant species fails to colonize the island in our second regime.

5. COLONIZATION WITH COMPETITION

We have so far considered conditions that ensure that a single immigrant species from a continent will successfully colonize an island. What happens, however, if there are other species already established on the island, as is likely to be the case in the formation of island communities? There are obviously fundamental questions to be asked: Will the invasion lead to coexistence, or to the elimination of an established species, or perhaps to the failure of the invading species to establish itself? In the case of two competing species the method of sub- and supersolutions may be used to draw some interesting conclusions. Recall that the model for this situation is (2.16),

$$\begin{aligned}u_t &= \mu u_{xx} + f(u,v)\\ v_t &= \nu v_{xx} + g(u,v)\end{aligned}$$

with f, g competitive interaction terms, that is, with $\partial f/\partial v$, $\partial g/\partial u < 0$ for $u, v \geqslant 0$. As before, the variable u denotes the density of the invading species, and v denotes the density of the previously established species. We assume $f(0,v) = 0$ and $g(u,0) = 0$. The method of sub- and supersolutions can be applied to models for two competing species in much the same way as for a single species, but does not extend simply or directly to models with more than two competitors present. For two competitors, the appropriate sort of comparison principle uses a sub-/supersolution pair. Let B_u define the boundary condition on u and B_v that on v; these may be either of Dirichlet or Neumann type, i.e., $B_u[w] = w$ or $B_u[w] = \partial w/\partial n$ with n the outward pointing normal. A sub-/supersolution pair in the classical sense is a pair of smooth functions $(\underline{u}, \bar{v})$ satisfying

$$\begin{aligned} &\underline{u}_t \leqslant \mu \underline{u}_{xx} + f(\underline{u}, \bar{v}) \qquad && \text{on } (0,l) \times (0,\infty) \\ &\bar{v}_t \geqslant \nu \bar{v}_{xx} + g(\underline{u}, \bar{v}) && \\ &B_u[\underline{u}] \leqslant 0, \qquad B_v[\bar{v}] \geqslant 0 && \text{for } x = 0, l. \end{aligned} \tag{5.1}$$

The key result, stated in the form most convenient for the present purposes, is as follows:

THEOREM 5.1

Suppose that (u, v) *satisfy* (2.16) *with boundary conditions* $B_u[u] = 0$, $B_v[v] = 0$ *at* $x = 0, l$ *as in* (2.17) *and* (2.18) *or* (2.19), *and that* $(\underline{u}, \bar{v})$ *satisfy* (5.1). *If*

$$\underline{u}(x,0) \leqslant u(x,0) \quad \text{and} \quad \bar{v}(x,0) \geqslant v(x,0) \tag{5.2}$$

then

$$\underline{u}(x,t) \leqslant u(x,t) \quad \text{and} \quad \bar{v}(x,t) \geqslant v(x,t) \tag{5.3}$$

for all $t > 0$. *A corresponding result holds with the inequalities* (5.1)–(5.3) *reversed.*

The classical formulation of Theorem 5.1 is given in [23,24] and was used to study a Lotka–Volterra system in [25]. The condition that $\underline{u}$ and $\bar{v}$ should be smooth may be removed, giving a considerable increase in the power of the technique. In a biological context a convenient reference is [16,17] and a description of the use of weak sub-/supersolutions is given in [18]. The rough idea is that the local maximum of two smooth subsolutions together with the local minimum of two smooth supersolutions is again a sub-/supersolution pair. For a full description the reader may consult the above references. This idea is used freely in what follows.

In our discussion of competition between immigrant and resident species we usually suppose that the resident species with density v has become established on the island and that the immigrant species with density u diffuses from the mainland. We imagine that the distribution of u, obtained for example from (2.3), gives the initial distribution for u

in the model (2.16) and that boundary conditions (2.17) and (2.18) or (2.19) are satisfied. This is obviously an oversimplification and it may be unrealistic to suppose as in (2.17) that once the migratory species arrives on the island it remains there. However, these assumptions permit a reasonably simple analysis and focus attention on the ability of the invading species to survive. The more complex assumption that there is a continuous stream of immigrants interacting with the environment and the established species via an inhomogeneous boundary condition could perhaps be treated as in the single-species model discussed in Section 4, but only at the expense of extra technical difficulties. Similarly, the Neumann boundary condition $u_x(0,t)=u_x(l,t)=0$ in (2.17) could be replaced with a Dirichlet condition or something more general, but again that would complicate the analysis, and if we use homogeneous boundary conditions it is not obvious which sort is the most realistic.

The four possible outcomes are that the immigrant species will displace the resident species, that it will be unable to invade, that coexistence between the two species will develop (possibly but not necessarily in a stationary state), or that both will become extinct (a possibility only if Allee effects are present, and generally the least plausible of the possibilities). If we enquire which of these will come about, the answer will clearly depend in general on several factors: the nature of the interactions f and g, the diffusion coefficients μ and ν, the size of the island, and the boundary conditions, as well as the initial distribution, which at least in the case of the migrant species may itself depend on several factors as in (2.3). Thus, although in some situations results of interest may be obtained in which some of these factors do not play a role, in general simple results cannot be expected.

The simplest type of result, applicable only when both species satisfy zero Neumann boundary conditions, uses solutions of the reaction system (i.e., the corresponding system of ordinary differential equations) as comparison functions. Note that this class of result does not depend on μ, ν, or l. Let $p(\xi,\eta,t), q(\xi,\eta,t)$ be the solution of the system

$$\begin{aligned} \frac{dp}{dt} &= f(p,q) \\ \frac{dq}{dt} &= g(p,q) \end{aligned} \tag{5.4}$$

with $p(\xi,\eta,0)=\xi, q(\xi,\eta,0)=\eta$. Then a direct application of Theorem 5.1 yields the following result:

THEOREM 5.2

Suppose that (u,v) *satisfy* (2.16)–(2.18). *Assume that there are nonnegative constants* a,b,c,d *such that* $a \leqslant u(x,0) \leqslant c$ *and* $d \leqslant v(x,0) \leqslant b$. *Then for* $t > 0$,

$$\begin{aligned} p(a,b,t) \leqslant u(x,t) \leqslant p(c,d,t) \\ q(c,d,t) \leqslant v(x,t) \leqslant q(a,b,t). \end{aligned} \tag{5.5}$$

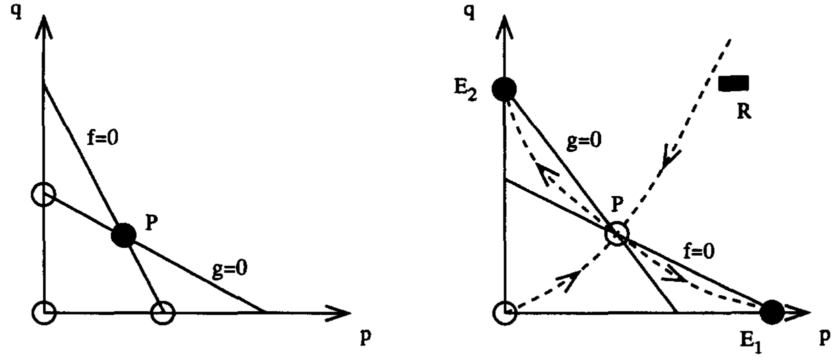
The lower bound on u and upper bound on v follow from Theorem 5.1 with $\underline{u} = p(a,b,t), \bar{v} = q(a,b,t)$; similarly $\bar{u} = p(c,d,t)$ and $\underline{v} = q(c,d,t)$ yield the upper bound on u and lower bound on v.

When applicable this result provides rather simple answers, for the solutions of (4.1) are often well known qualitatively and of course the actual orbits are easy to compute numerically. We start for illustration with a relatively easy case and assume that the interactions are of Lotka–Volterra type, that is,

$$\begin{aligned} f(u,v) &= r_1(1 - u/K_1 - \alpha_1 v/K_1)u \qquad \text{and} \\ g(u,v) &= r_2(1 - \alpha_2 u/K_2 - v/K_2)v, \end{aligned}$$

as described in Fig. 5.1.

If the system (5.4) has a unique equilibrium P, which is a global attractor for solutions that are initially positive in both components, then all nonzero nonnegative initial distributions in the diffusive model (2.16)–(2.18) will eventually lead to constant distributions with values at the equilibrium. This follows from Theorem 5.2 after using the maximum principle to show that any nonzero nonnegative initial distribution is strictly positive for $t > 0$. (The case where there is a stable coexistence equilibrium is shown in Fig. 5.1a.) In this situation, the details of geography and history are irrelevant to the outcome of the interaction. In the bistable case (Fig. 5.1b), the equilibria $E_1 = (K_1, 0)$ and $E_2 = (0, K_2)$ are both locally stable and the final state of the system depends on the initial conditions and hence on accidents of geography and history. If neither species is present initially, then either can successfully colonize the island in the absence of the other from a continent at any distance, since if only one species is present it will satisfy a diffusive logistic equation for which all solutions with nonzero nonnegative initial data eventually approach the carrying capacity. On the other hand, if the island is distant from the source populations of both species then the initial densities induced via immigration as in (2.3) will be quite small, so that if either species is present at carrying capacity then the other cannot successfully invade. Finally, if the continental source of



(a) (b)

FIG. 5.1. The reaction phase planes for two classes of Lotka–Volterra interactions are shown. The solid (respectively open) circles represent stable (respectively unstable) equilibria. (a) All orbits starting in the interior of the positive quadrant approach P as t approaches infinity. (b) The bistable case with two stable states E_1 and E_2, P being unstable. The stable and unstable manifolds of P are shown schematically as broken lines; all orbits starting above (respectively below) the stable manifold approach E_1 (respectively E_2) as t approaches infinity. If the resident species is at or near its carrying capacity and the initial density of the colonizing species is sufficiently high then it may be possible for the colonist to displace the resident. That scenario would occur in the case of the system shown in (b) if the initial data for the system were to lie in the shaded rectangle R.

one species is close to the island, then it may sometimes be possible for that species to displace the resident species. In particular, if the resident species v is at equilibrium E_2 we may take $b = d = K_2$, and the immigrating species u will displace the resident v if the minimum $K_1 e^{-\sqrt{r_0/\mu_0}(L+l)}$ of $u(x,0)$ is to the right of the point where a horizontal line through E_2 cuts the stable manifold of the unstable equilibrium P with both species present (see Fig. 5.1b). Thus, in the bistable case, history and/or geography may play a role in the outcome of the interaction.

In practice the assumption that the interactions are of Lotka–Volterra type is likely to be a gross oversimplification. Once advantage of arguments based on comparisons with the ordinary differential equations (5.4) is that they may readily be applied when more elaborate assumptions are made. If both species experience on Allee effect [8–10] as was assumed in the single species case one possible configuration of the phase plane is shown in Fig. 5.2.

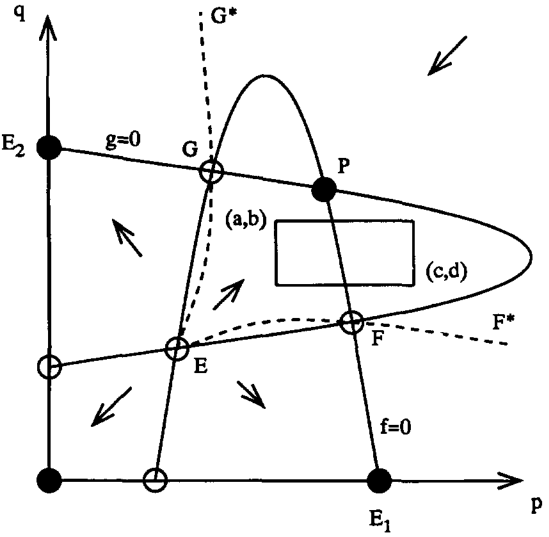


FIG. 5.2. The reaction phase plane when there is an Allee effect in both species is shown. There are several equilibria, the convention regarding stability being the same as in Fig. 1. Orbits starting in the sector bounded by the manifolds EFF^* and EGG^* will approach P. Thus, if the initial data are in the rectangle with corners (a,b) and (c,d) then the corresponding solutions will approach P.

Orbits of (5.4) starting in the sector with sides $EFF^* - EGG^*$ will tend toward the stable equilibrium P. With a, b, c, d as shown in the figure, indicating immigration from a continent relatively close to the island, Theorem 5.2 implies that the initial densities will approach the equilibrium P and coexistence will ensue. However, the situation is different from the case of Lotka–Volterra interactions with a stable coexistence equilibrium, since the equilibria 0, E_1, and E_2 in Fig. 5.2 are all now locally stable. For colonization to succeed the initial density of the immigrating species must therefore be sufficiently large. Hence, even though stable coexistence is possible the presence of Allee effects means that either or both species may fail to successfully colonize the island if the source populations are too far away from the island. Thus, with Allee effects, the geography and history of the system may play a role in determining the eventual outcome even if the competitors can coexist.

The conditions under which Theorem 5.2 is applicable are rather restrictive. First, the boundary conditions on both species must be of no-migration type. Second, the sub-/supersolution pairs must be spatially constant and lie below/above the initial distributions. If the immigrating species has initial density $u(x,0)$ given by (2.3) then for any given constant a there will be values of x with $u(x,0) < a$ if the island is sufficiently large, and Theorem 5.2 is not applicable. Also, if the dynamics are as in Fig. 5.1b and the rectangle $[a,c]\times[d,b]$ crosses the stable manifold of P then Theorem 5.2 is vacuous. Our next aim will be to find criteria leading to coexistence in the presence of Allee effects as in Fig. 5.2. Our approach will be in the spirit of the subsolution arguments used for the single-species case in Section 3.

One plausible scenario (from the many possibilities) is that a resident species may have evolved reduced dispersal abilities. This possibility is described by Darwin in *The Origin of the Species*, Chapter 5 (The Laws of Variation) with regard to beetles inhabiting the island of Madeira and appears to be a not uncommon feature of island species [3, Chap. 2]. In our models such a scenario could be interpreted as reducing the diffusion rate and making the sea surrounding the island lethal to the resident population. Thus we assume that the resident species satisfies the homogeneous Dirichlet boundary condition (2.19) but that its diffusion rate is small enough relative to the size of the island that it can persist in the absence of the other species. (The necessity for a sufficiently small diffusion rate and/or sufficiently large island under Dirichlet boundary conditions is well known; see [7] for example. It is sometimes call the KISS phenomenon after Kierstead and Slobodkin [26] and Skellam [27] who originated the observation in the ecological context.) The immigrating species is still assumed to satisfy the zero Neumann condition (2.17) after its initial density has been induced by dispersal as in (2.3), but that assumption is not crucial and could be replaced with a Dirichlet condition.

Suppose that (a,b) and (c,d) are as shown in Fig. 5.3, so that $f(a,b) > 0$ and $g(c,d) > 0$, and that

$$\int_0^a f(s,b)\,ds > 0, \qquad \int_0^d g(c,s)\,ds > 0. \tag{5.6}$$

Condition (5.6) permits the construction of local subsolutions as in Section 3, which can be used to construct irregular subsolutions for sub-/supersolution pairs. Let $\phi(x), \psi(x)$ be solutions of the following:

$$\begin{aligned} \mu\phi_{xx} + f(\phi,b) &= 0 \\ \phi(0) &= a, \\ \phi_x(0) &= 0, \end{aligned} \tag{5.7}$$

$$\begin{aligned} \nu\psi_{xx} + g(c,\psi) &= 0, \\ \psi(0) &= d, \\ \psi_x(0) &= 0. \end{aligned} \tag{5.8}$$

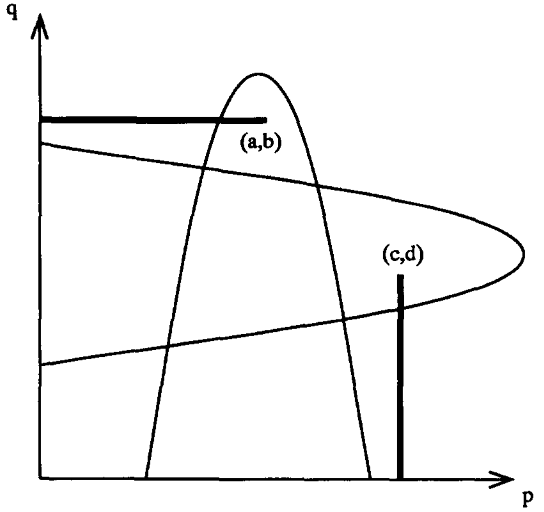


FIG. 5.3. A stage in the construction of the sub-/supersolutions for the system with an Allee effect. The integrals in (5.6) are best visualized as being along the heavy straight lines.

Conditions (5.6) ensure that ϕ and ψ decrease to zero as $|x|$ increases. Also, the distance required for ϕ or ψ to decrease to zero is proportional to $\sqrt{\mu}$ or $\sqrt{\nu}$ respectively; see formula (3.11). If we assume that ν is small enough that the distance required for ψ to decrease to zero is less that $l/2$ then for at least some choices of $l_1 \in (0,l)$ the function $\psi(x-l_1)$ satisfies the differential equation in (5.8) and decreases to zero inside the interval $(0,l)$ as x moves away from l_1 in either direction. Such a situation is shown schematically in Fig. 5.4. Taking the maximum of $\psi(x-l_1)$ and zero yields the function $\underline{v}$, which will be a subsolution in the super-/subsolution pair $(c,\underline{v})$. The condition that ν be small enough that $\psi(x-l_1)$ becomes negative inside $(0,l)$ is needed because of the Dirichlet boundary condition on v. No such condition need be imposed on ϕ, so taking $\underline{u}$ to be the maximum of $\phi(x-l_2)$ and zero for any $l_2 \in (0,l)$ yields a sub-/supersolution pair $(\underline{u},b)$. A possible form for $\underline{u}$ and $\underline{v}$ is shown in Fig. 5.4. We have by Theorem 5.1:

THEOREM 5.3

Suppose that u and v satisfy (2.16), (2.17), *and* (2.19) *and that $\underline{u},\underline{v}$ are as described above. If*

$$\underline{u}(x) \leqslant u(x,0) \leqslant c \quad \textit{and} \quad \underline{v}(x) \leqslant v(x,0) \leqslant b \tag{5.9}$$

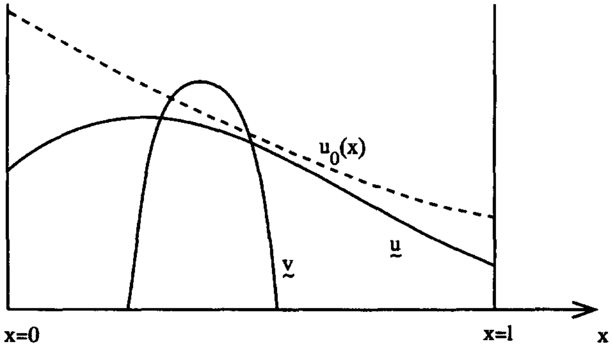


FIG. 5.4. The subsolutions of two sub-/supersolution pairs are shown. If u_0, v_0 lie above $\underset{\sim}{u}, \underset{\sim}{v}$ then the situation leads to coexistence. Note that u_0 may be fairly small over part of the interval. This may be important if we imagine a large island with the mainland on the left.

then for $t > 0$,

$$\underset{\sim}{u}(x) \leqslant u(x,t) \leqslant c \quad \text{and} \quad \underset{\sim}{v}(x) \leqslant v(x,t) \leqslant b.$$

This result raises several points. Observe first that the theorem guarantees coexistence in the sense that both species persist in the long term. However, it is not clear that there is a unique equilibrium that $(u(x,t), v(x,t))$ approaches as $t \to \infty$. The possibility of time periodic solutions has not been ruled out for (2.16) with boundary conditions (2.17) and (2.19), although by using the theory of monotone semiflows developed by Hirsch and others [14] it can be shown that any such solution would be unstable and thus would generally not be seen in practice. A complete description of the ω-limit set of (2.16) under boundary conditions (2.17) and (2.19) is not available at the moment. However, if both species satisfy zero Neumann boundary conditions (2.17), (2.18) then solutions as in Theorem 5.3 will indeed tend to the constant stationary state P.

Note next that in contrast to the results of Theorem 5.2 the results of Theorem 5.3 depend crucially on the diffusion rates μ and ν and on the size of the island l. Broadly, as is to be expected, the smaller μ and ν and the larger l, the easier it will be for coexistence to be established relative to any given initial distributions. We have already observed that the condition that the support of $\underset{\sim}{v}$ lie inside $(0, l)$ can always be met if ν is sufficiently small, and as μ and ν become smaller the size of the region over which the initial distributions must be bounded away from zero to satisfy (5.9) becomes smaller as well. If the resident species is long established and ν is small then the initial distribution of v will be near the carrying capacity of the environment except in boundary layers and thus will lie above $\underline{v}$ and so satisfy the required lower bound. As in the case of a single species, once l is large enough to permit the construction of $\underline{u}$ and $\underline{v}$, any further increase in l imposes no additional restrictions on the initial data. This is important if the initial density of the immigrant species is taken to be a decaying exponential as in (2.3). Thus the condition on the lower bound in Theorem 5.3 is significantly weaker than that required in Theorem 5.2; see Fig. 5.4 for an illustration of this point. If we assumed a specific form for $f(u,v)$ such as $f(u,v) = ru[(K-u)(u-a) - \alpha v]$ and similarly for $g(u,v)$ so that $f(u,b)$ and $g(c,v)$ would have the cubic form used in Section 3 then the quantitative estimates obtained in that section could be extended in a straightforward manner to $\underline{u}$ and $\underline{v}$ and so the above discussion could be made quantitative. We leave the details to the interested reader.

The qualitative structure shown in Fig. 5.2 represents only one of the possible arrangements of the isoclines of f and g. If the isoclines never cross, as shown in Fig. 5.5, then coexistence is not possible in the nondiffusive system (5.4). In this case there is a range of initial data where the resident species is at its carrying capacity and the immigrating species is near its carrying capacity and for which the populations of both species approach zero as $t \to \infty$. If the initial distribution of v is identically equal to the carrying capacity for v and the initial distribution of u falls in that range then both species can be expected to become extinct as a result of the attempt at colonization. This phenomenon requires fairly restrictive conditions on the interactions and initial data, so it is unclear whether it will actually occur in natural systems. A more likely outcome in this situation is that one species will prevail and the other will become extinct, with the winner depending on the initial conditions and hence on the historical and/or geographical details of the system.

6. CONCLUSIONS

Our simple models for population dynamics with dispersal capture some of the effects that have been observed empircally or predicted on the basis of other theoretical considerations. What is new in our approach is that it is based on models that are spatially explicit and incorporate dispersal in a mechanistic (if greatly simplified) way. One of the effects displayed by our models is the distance effect, whereby a colonizing species must originate sufficiently close to the island being colonized and have sufficiently rapid dispersal and sufficiently low

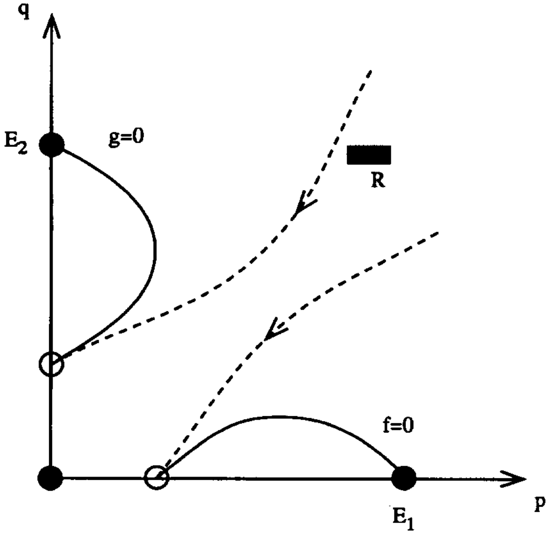


FIG. 5.5. In this case there is an Allee effect for both species with no coexistence state. The stable manifolds of the unstable equilibria are shown schematically as broken lines. If the initial data lie between the stable manifolds, for example, as indicated by the shaded rectangle *R*, then the populations of both species will decline toward extinction.

mortality in transit for colonization to succeed. In fact, our models give criteria for successful colonization in terms of parameters such as dispersal rates, population growth rates and/or mortality rates, minimum viable populations (or more precisely population densities), and carrying capacities, which can in principle be measured; see for example [15,28,29] or the discussion in [11]. Some of our results characterizing a good colonizer roughly (and not surprisingly) agree with those obtained by MacArthur and Wilson [1, Chap. 4] via different modeling considerations. Their explicit criteria include a low mortality rate and a large carrying capacity. They also remark [1, p. 78] that "If colonists disperse rapidly they will not find mates and *r* will not even be positive, let alone large. Hence cohesiveness of the propagule is essential." Our models do not incorporate separate birth and mortality rates, but our criteria for a good colonizer typically include a high maximum rate of increase, a high ratio of carrying capacity to minimum viable population, and a low dispersal rate on the island (as opposed to the high dispersal rate over the transit corridor between the island and the continental source population). In fact, if the dispersal rates are the same over the transit corridor and on the island then in one of our models there is an optimal dispersal rate with higher or lower rates being less favorable to colonization. The observation that some island species have evolved lower dispersal rates was made by Darwin in his discussion of the laws of variation in *The Origin of the Species* and has been supported by more recent studies (see [3, Chap. 2]). The predictions of our models agree with that observation to the extent that the models suggest that once a colonizing species has arrived on an island a reduced dispersal rate is likely to be of adaptive value. In the context of a species attempting to colonize in the presence of a competitor our models suggest that there are some conditions under which history and geography are crucial to the outcome and other where they are not. If there are no Allee effects present, the only case where history and geography seem to be critical corresponds to situations of strong competition where the outcome in the spatially homogeneous case depends on initial conditions. On the other hand, if Allee effects are present, then geography is always relevant and history may be, even if competition is weak.

There are many questions that deserve further attention. The models studied here only allow one space dimension and do not incorporate spatial heterogeneity or boundary conditions leading to strong size and shape effects as in [2,7,25–27,30–33]. It would be of obvious interest to consider models combining distance and area effects. It would also be of interest to consider situations with more competitors or more trophic levels in the community. In another direction of inquiry, it would be of interest to fit some of the parameters in our models to data as in [26,28,29]. In principal it should be possible to address these questions, but in practice there are many difficult technicalities to be overcome.

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