

SHOULD A PARK BE AN ISLAND?*

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Abstract. The object of this article is to study the interaction of interspecies competition and environmental heterogeneity in the context of refuge or preserve design. Specifically, situations in which the primary preserve is surrounded by partially disrupted secondary successional environments are compared to those in which the surroundings of the preserve are completely disrupted and hence inhospitable to both primary and secondary biomes. The somewhat surprising conclusion is reached (suggested in the ecological literature) that in some cases complete disruption of surroundings is preferable to partial disruption if the partially disrupted "buffer zones" benefit some species more than their competitors. The modelling approach is based on reaction-diffusion equations with variable coefficients, and the analysis relies on finding criteria for coexistence or extinction in terms of elliptic eigenvalue problems and then estimating the eigenvalues in terms of environmental parameters.

Key words. interspecies competition, environmental heterogeneity, refuge design, reaction-diffusion equations, eigenvalue problems, parametrically determined persistence and extinction

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1. Introduction. The object of this article is to study the interaction of interspecies competition and environmental heterogeneity in the context of refuge or preserve design. Our work is motivated by Janzen's discussion of "the eternal external threat" [15] to nature preserves posed by the presence of partially disrupted habitats surrounding them. In [14] and [15], Janzen describes a wide range of different types of environmental interference that may occur; we focus on fairly direct competitive effects in situations where a conserved region of, for example, pristine forest may be surrounded either by areas of secondary successional habitat or by closely cultivated regions, depending on the choice of resource management policies. Our approach is based on a class of diffusive Lotka-Volterra competition models with spatially varying coefficients. Obviously, such models can reflect only a greatly simplified picture of the true biological interactions, but they provide a means of assessing the qualitative effects of external interference on a preserve. The main conclusion suggested by the analysis is that for certain parameter ranges the sort of effects described in [14], [15] are predicted by the models.

The mathematical techniques used here represent a synthesis of those used in [2], [7], [8], [10] to study diffusive competition models with constant coefficients and those used in [4]-[6], [20] to study diffusive logistic equations with spatially varying coefficients. (For background, see [9], [16], [18], [22].) The basic methodology is to reduce questions about the dynamics of the reaction-diffusion model (specifically, whether the two populations being considered can coexist in the long term) to questions about the principal eigenvalues of associated linear elliptic problems. The reduction is effected via methods of nonlinear analysis. We then estimate the relevant eigenvalues in terms of parameters describing habitat quality and arrangement, diffusion rates, and the strength of competition. The eigenvalue estimates enable us to identify certain parameter ranges for which coexistence is assured and others for which one of the

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populations is driven to extinction by its competitor. We observe that, in some cases, changing the parameter describing the habitat surrounding a preserve while leaving other parameters fixed can shift the predictions of the model from persistence to extinction for the population we wish to preserve. Specifically, if the growth rates of both competitors remain high within a preserve but the growth rate of one is kept low in the surrounding region while the growth rate of the other is increased to the same level as within the preserve, then the second competitor can drive the first to extinction, even within the preserve. It is in this sense that our models support the discussion in [14], [15]. Note that, for such an effect to occur, the presence of diffusion or some sort of dispersal mechanism is crucial, since otherwise conditions outside the preserve could not affect events inside. This is a major theme of [15]. At this point, a caveat is in order: our conclusions do not describe all species in all situations. The effects described by Janzen in [15] were observed in tropical regions. They are interesting partly because they contrast with the usual orderly succession typically observed in temperate regions where the climax forest may eventually competitively exclude "pioneer" or secondary successional species rather than vice versa. These data suggest that the phenomenon we wish to model depends on specific characteristics of the competitors, such as their relative growth and dispersal rates and competitive abilities. Thus, our analysis should only describe some effects occurring in some situations. As is noted in [6], any effort at refuge design must be based on detailed biological knowledge of the specific situation. Our models merely support the view that the sort of effects described in [15] can sometimes occur if there is an appropriate relation between the growth rates of the species involved and their competitive interactions and hence should be seriously considered when management policies are being developed. Some ideas related to those discussed here are treated in [17] and [21]. In [17] some very general existence results and associated eigenvalue estimates are derived; they do not, however, apply to the specific problems discussed here. The models in [21] have spatially constant growth rates but variable interaction coefficients or carrying capacities and are designed to describe somewhat different phenomena. Much of the mathematical analysis in [21] is numerical, but the biological discussion is detailed, and numerous references are given to the ecological literature.

Our main objectives in this article are to give a qualitative analysis of the simplest models that capture the essential features of the phenomenon described by Janzen and to develop the mathematical machinery needed for later quantitative analysis. To keep things simple, we have introduced spatial variation in only two of the parameters of the model system. Our methods extend to cases where other parameters also vary with location, but to treat those cases would involve a moderate increase in the complexity of various conditions that are already fairly complicated in the simplest case. The problem with such cases is not so much in the mathematical analysis but in the interpretation of the analysis in biological terms. Some more general models for a single population are discussed in [5]. We hope eventually to treat cases combining some of the spatial effects discussed there and in [4], [6], [21] with those described here, but we anticipate that the mathematical analysis will be more involved, as well as more difficult to interpret biologically. Most of the analytic methods we use in this article were developed during the 1980s or early 1990s by various researchers, including ourselves. There are some technical refinements in this article that are new. It is also our intention to explore the quantitative aspects of our models in more detail in future work. We plan to collaborate with ecologists in trying to determine appropriate parameter ranges for real situations and to perform numerical computations with the models using those parameter ranges. The mathematical analysis of the present article

provides the framework for numerical computation, but a thorough examination of the quantitative aspects of the models would require at least another article of comparable length, so we have deferred it for now.

The models we consider are all derived from Lotka-Volterra competition models with diffusion. In taking such a modelling approach, we make the implicit assumption that the spatial and temporal scales under consideration are large enough that continuous models are appropriate. The classical Lotka-Volterra model for two competing species is a pair of ordinary differential equations describing the dynamics of their total populations P and Q . It may be written as

$$\frac{dP}{dt} = (R_1 - BP - CQ)P, \quad \frac{dQ}{dt} = (R_2 - EP - FQ)Q,$$

where $R_1, R_2, B, C, E,$ and F are positive constants. This type of model is closely related to the logistic equation for a single population. Thus, any effects of age structure in the populations or in their competitive interactions are lumped into the overall average reproduction rates, competition parameters, and so on, that are represented by $R_1, R_2, B, C, E,$ and F . In the absence of the second competitor, the first satisfies a logistic equation $dP/dt = (R_1 - BP)P = r_1(1 - P/K_1)P$ where the intrinsic growth rate (i.e., the per capita rate of increase in population at low density) is described by $r_1 = R_1$ and the carrying capacity of the environment (i.e., the stable positive equilibrium population) is given by $K_1 = R_1/B$. The corresponding constants for the second competitor are $r_2 = R_2$ and $K_2 = R_2/F$. Thus, B and F quantify the strength of "density-dependent" self limitation in the two competitors. The coefficients C and E describe the strength of competition between the two populations; specifically, C describes the impact that Q has upon P , and E describes the impact of P on Q . If we were to rewrite the original system as $dP/dt = r_1(1 - P/K_1 - \alpha_1 Q)P$, $dQ/dt = r_2(1 - Q/K_2 - \alpha_2 P)Q$, then $C = \alpha_1 r_1$ and $E = \alpha_2 r_2$. If $C = E = 0$, then the two populations do not compete, and each increases according to a logistic growth law. We may rescale the system by taking $p = BP$ and $q = FQ$; the system then becomes

$$\frac{dp}{dt} = (R_1 - p - cq)p, \quad \frac{dq}{dt} = (R_2 - ep - q)q,$$

where $c = C/F$ and $e = E/B$. In terms of the formulation of the model as a pair of logistic equations with competitive interaction described by α_1 and α_2 , we have $c = \alpha_1 K_2$ and $e = \alpha_2 K_1$. Thus, c and e represent the product of the carrying capacity K for each population times a coefficient α measuring its impact on its competitor. In that sense, c and e characterize the effects of competition, and we refer to them as *competition coefficients*.

When the model is formulated in terms of $R_1, R_2, c,$ and e , the condition for coexistence becomes especially simple. The model predicts coexistence if $R_1 - cR_2 > 0$ and $R_2 - eR_1 > 0$, which is true, in particular, if the strength of competition as measured by the size of the competition coefficients c and e is small enough. (In this case, there is coexistence in the sense that there is a globally stable positive equilibrium state (p^*, q^*) . In our more general models, we only show that there is coexistence in the sense that both populations are bounded away from zero in the long term.) If $R_1 - cR_2 > 0$ and $R_2 - eR_1 < 0$, then the first species excludes the second, and, if $R_2 - eR_1 > 0$ but $R_1 - cR_2 < 0$, the second excludes the first. The case where $R_1 - cR_2 < 0, R_2 - eR_1 < 0$ is more complicated. There is an unstable equilibrium (p^*, q^*) , but generically one species excludes the other with the winner and loser in the competition determined by the initial conditions.

We wish to consider the effects of dispersal and spatial variation, so we must consider the geometry of our environment and work with population densities rather than populations. Let Ω be a bounded domain in \mathbb{R}^2 with smooth boundary and let Ω_1 be a subdomain of Ω ; Ω represents the total environment under consideration, and Ω_1 the part of Ω we wish to consider as a refuge or preserve. Let $U(x, t)$ and $V(x, t)$ represent the population densities of two competitors at location $x \in \Omega$ and time t . If we add the dispersal mechanism of diffusion to the basic Lotka-Volterra model, we obtain

$$\frac{\partial U}{\partial t} = d_1 \Delta U + (R_1 - BU - CV)U,$$

$$\frac{\partial V}{\partial t} = d_2 \Delta V + (R_2 - EU - FV)V,$$

where d_1 and d_2 are positive constants that measure the rates of diffusion of the competing populations. (The derivation and interpretation of reaction-diffusion models for the dispersal, growth, and interaction of populations are discussed at length in [16], and to some extent in [4]-[6], [9], [18], [20]-[22].) The parameters R_1 , R_2 , B , C , E , and F have the same interpretations in our model as in the classical spatially homogeneous model. In principle, R_1 , R_2 , B , C , E , and F might all depend on both x and t , but, for our present purposes, it suffices to allow R_1 and R_2 to depend on x , but the other coefficients to remain constant. A fairly simple model is adequate because we want to describe the simplest sort of mechanism by which one competitor can gain an advantage on $\Omega - \Omega_1$ which leads to exclusion of the other competitor on all of Ω . If we assume that $R_2(x)$ is large on all of Ω but $R_1(x)$ is large on Ω_1 but small on $\Omega - \Omega_1$, then we see that the second competitor may be able to increase in numbers on $\Omega - \Omega_1$ to the point where it excludes the first on all of Ω via diffusion from $\Omega - \Omega_1$, even if the competitors could coexist if both R_1 and R_2 were kept small on $\Omega - \Omega_1$. We refer to a situation where the first population thrives only in a pristine forest habitat (Ω_1), but the second can also inhabit (or perhaps constitute) secondary successional habitats such as irregularly cleared brushy areas ($\Omega - \Omega_1$). If the second competitor attains a high density on $\Omega - \Omega_1$, it may disperse into Ω_1 and thus gain the advantage in the competition there. This is the essence of the effects described in [14], [15]. There are other mechanisms that might produce similar effects. It is plausible that, if R_1 and R_2 were constants but the competition coefficients C and E varied in a way that gave one competitor an advantage in competition on part of Ω , then the results would be similar. However, we believe that the mechanism we have proposed is a more accurate mathematical depiction of the processes described verbally in [15]. The Lotka-Volterra system may be rescaled to eliminate parameters. We may divide the first equation by d_1 and the second by d_2 and then rescale the time variable t to $d_2 t$ so that equations take the form (in the new time variable)

$$(d_2/d_1)U_t = \Delta U + [(R_1/d_1) - (B/d_1)U - (C/d_1)V]U,$$

$$V_t = \Delta V + [(R_2/d_2) - (E/d_2)U - (F/d_2)V]V.$$

We can then use $u = (B/d_1)U$, $v = (F/d_2)V$, $c = Cd_2/Fd_1$, $e = Ed_1/Bd_2$, and $\tilde{R}_i = R_i/d_i$ for $i = 1, 2$, and, as in the classical case, we obtain

$$(1/d)u_t = \Delta u + (\tilde{R}_1 - u - cv)u, \quad v_t = \Delta v + (\tilde{R}_2 - eu - v)v,$$

where $d = d_1/d_2$ is the rescaled diffusion rate of the first competitor. If $d > 1$, then the first competitor disperses more rapidly than the second; if $d < 1$, the second competitor

disperses more rapidly. We are especially interested in the case where R_1 and R_2 are both constant on Ω_1 and on $\Omega - \Omega_1$, with $R_1 = 0$ on $\Omega - \Omega_1$ and with R_2 having a constant value on $\Omega - \Omega_1$ greater than or equal to zero but less than or equal to its value on Ω_1 . Our analysis of this case proves to be robust, so that our conclusions remain valid if R_1 is positive but small on $\Omega - \Omega_1$.

To perform the detailed analysis of our model system, it is convenient to write it in the form

$$(1.1) \quad \begin{aligned} (1/d)u_t &= \Delta u + u[r_1\chi_{\Omega_1}(x) - u - cv], \\ v_t &= \Delta v + v[r_2(\chi_{\Omega_1}(x) + l\chi_{\Omega - \Omega_1}(x)) - eu - v] \quad \text{in } \Omega \times (0, \infty), \end{aligned}$$

where r_1 and r_2 are positive constants, $l \in [0, 1]$, and, as usual, χ_{Ω_1} and $\chi_{\Omega - \Omega_1}$ are the characteristic functions of Ω_1 and $\Omega - \Omega_1$; i.e., $\chi_{\Omega_1}(x) = 0$ if $x \notin \Omega_1$ and $\chi_{\Omega_1}(x) = 1$ if $x \in \Omega_1$, and correspondingly for $\chi_{\Omega - \Omega_1}$. We assume that the exterior of Ω is totally hostile to both populations; that assumption is reflected in the Dirichlet boundary condition

$$(1.2) \quad u = v = 0 \quad \text{on } \partial\Omega \times (0, \infty).$$

A similar analysis could be carried out if the exterior region is only somewhat hostile; then (1.2) would be replaced with a mixed (or Robin) boundary condition, but the qualitative features of the analysis would not be greatly affected.

The crucial parameter in our analysis of the effects discussed in [14], [15] is l . When $l = 0$, the growth rates of both populations are positive on Ω_1 and zero outside Ω_1 . As $l \uparrow 1$, the growth rate of the second population on the region $\Omega - \Omega_1$ rises to equal its growth rate on Ω_1 . The case where $l = 0$ corresponds to a situation where the habitat $\Omega - \Omega_1$ surrounding Ω_1 is made unsuitable for either population, for example, by systematic clearing or close cultivation; the case where $l = 1$ corresponds to a situation where the first population cannot increase in numbers, even at low densities, on $\Omega - \Omega_1$, but the second can. This type of situation could occur if the first population were systematically removed from $\Omega - \Omega_1$ by the direct or indirect effects of some type of harvesting, such as logging, that does not significantly affect the second population. Our fundamental conclusion is that there are values of the parameters c , e , r_1 , and r_2 for which (1.1) predicts coexistence when $l = 0$ but extinction for the first population when $l = 1$. That conclusion remains valid if the term $r_1\chi_{\Omega_1}(x)$ in the first equation of (1.1) is replaced by $r_1(\chi_{\Omega_1}(x) + \varepsilon l\chi_{\Omega - \Omega_1}(x))$ for ε small. The last observation implies that moving l from zero to one improves the overall quality of the total environment Ω for either population in the absence of the other, but can result in the extinction of the first in the presence of the second. That is, even if both competitors can increase their numbers in $\Omega - \Omega_1$, the second may still exclude the first if it enjoys a sufficient advantage in growth rate and carrying capacity on $\Omega - \Omega_1$.

Before we perform our detailed analysis of the parameter dependence of (1.1) in §§ 3 and 4, we make a qualitative analysis of the more general model

$$(1.3) \quad \begin{aligned} u_t &= d_1\Delta u + u[R_1(x) - u - cv], \\ v_t &= d_2\Delta v + v[R_2(x) - eu - v], \end{aligned}$$

with boundary condition (1.2). We do not treat the question of global existence of positive solutions for the time-dependent problem (1.2)–(1.3); that follows readily via the methods discussed in [1], [13], [22]. We focus on finding criteria for the existence or nonexistence of equilibria with both densities positive and on the persistence or extinction of the populations. The criteria we obtain involve eigenvalue problems

incorporating the coefficients of (1.3). The use of eigenvalues to characterize the dynamics of dispersing populations is pervasive; see [2], [4]–[10], [18], [20], [21], among many others. To illustrate the idea in a simple case, let us suppose that a population has constant growth and diffusion rates r and d on a region Ω with hostile exterior. If we ignore self-limitation, then the population density can be modeled by $w(x, t)$ satisfying $w_t = d\Delta w + rw$ on Ω , $w = 0$ on $\partial\Omega$. It follows from elementary results on partial differential equations that the density will increase in time if $r - d\lambda_1 > 0$ and decrease if $r - d\lambda_1 < 0$, where λ_1 is the principal eigenvalue of $-\Delta\phi = \lambda\phi$ on Ω with $\phi = 0$ on $\partial\Omega$. Another way to state the condition for population growth that generalizes nicely to models with spatially varying coefficients is $\lambda_1^* = d\lambda_1/r < 1$. The quantity λ_1^* is the principal eigenvalue for the problem $-\Delta\phi = \lambda(r/d)\phi$ on Ω , $\phi = 0$ on $\partial\Omega$. The conditions we obtain for exclusion or coexistence in (1.3) are, in some sense, analogous to the conditions $R_1 - eR_2 > 0$ and $R_2 - cR_1 > 0$ for the nondiffusive model, but they are cast in terms of the eigenvalues of moderately complicated differential operators. We then obtain a picture of the ranges of parameters (r_1, r_2) that admit coexistence in (1.1) by piecing together a number of parameter-dependent eigenvalue estimates based partly on our results for (1.3). Finally, we observe that those estimates imply the existence of regions in the r_1, r_2 plane where changing the parameter l from zero to one changes the prediction of the model from coexistence to exclusion. That observation is a mathematical formulation of the type of effect discussed in [14], [15].

2. Qualitative features of the model. In this section, we consider the reaction-diffusion system

$$(2.1) \quad \begin{aligned} u_t &= d_1\Delta u + u[R_1(x) - u - cv], \\ v_t &= d_2\Delta v + v[R_2(x) - eu - v] \end{aligned}$$

in $\Omega \times (0, \infty)$, subject to the boundary condition

$$(2.2) \quad u = v = 0 \quad \text{on } \partial\Omega \times (0, \infty).$$

Here Ω is a bounded smooth domain in \mathbb{R}^N , e, c, d_1, d_2 are positive parameters, and for $i = 1, 2$, $R_i \in L^\infty(\Omega)$ with $\{x \in \Omega: R_i(x) > 0\}$ having positive Lebesgue measure. The steady-state solutions to (2.1)–(2.2) are the solutions to the corresponding elliptic system

$$(2.3) \quad \begin{aligned} -d_1\Delta u &= u[R_1(x) - u - cv] \\ -d_2\Delta v &= v[R_2(x) - eu - v] \end{aligned} \quad \text{in } \Omega,$$

$$(2.4) \quad u = 0 = v \quad \text{on } \partial\Omega.$$

Solutions to (2.3)–(2.4) where both u and v are positive in Ω are referred to as coexistence states of (2.1)–(2.2), while solutions to (2.3)–(2.4) with one positive component and one component identically zero are called extinction states to (2.1)–(2.2). We are interested in solutions that are positive on Ω but zero on $\partial\Omega$; that is, nonnegative but not identically zero on $\bar{\Omega}$. We use the symbol $> \neq 0$ to denote such functions.

It was shown in [4] that the related single-equation problem

$$(2.5) \quad w_t = d_i\Delta w + w[R_i(x) - w] \quad \text{in } \Omega \times (0, \infty),$$

$$(2.6) \quad w = 0 \quad \text{on } \partial\Omega \times (0, \infty)$$

admits a unique positive steady-state, which we denote $\theta(d_i, R_i)$ precisely when $\lambda_1(R_i/d_i) < 1$, $i = 1, 2$, where $\lambda_1(m)$ denotes the principal positive eigenvalue of

$$(2.7) \quad -\Delta z = \lambda m z \quad \text{in } \Omega,$$

$$(2.8) \quad z = 0 \quad \text{on } \partial\Omega.$$

In general, m may change sign on Ω as long as $m > 0$ on a set of positive measure. The steady-state $\theta(d_i, R_i)$ is asymptotically stable with respect to nontrivial nonnegative initial data, while the eigenfunction corresponding to $\lambda_1(m)$ in (2.7)–(2.8) is unique up to a scale factor and may be chosen positive in Ω . That $\lambda_1(R_i/d_i)$ exists follows from [19], since $\{x \in \Omega: R_i(x) > 0\}$ has positive Lebesgue measure. Additionally, $\lambda_1(m)$ is continuous as a function from $L^{N/2}(\Omega)$ into \mathbb{R} and has the monotonicity property that $m \leq m'$, $m < m'$ on a set of positive Lebesgue measure and the existence of $\lambda_1(m)$ imply the existence of $\lambda_1(m')$ and the inequality $\lambda_1(m') < \lambda_1(m)$ (see [4], [11]).

Suppose now that problem (2.3)–(2.4) admits a componentwise positive solution. Since λ_1 is characterized by having a positive eigenfunction, it follows that

$$\lambda_1\left(\frac{R_1(x) - cv - u}{d_1}\right) \quad \text{and} \quad \lambda_1\left(\frac{R_2(x) - eu - v}{d_2}\right)$$

both exist and are equal to 1. Consequently, the monotonicity of $\lambda_1(m)$ allows us to assert that $\lambda_1(R_i(x)/d_i) < 1$, $i = 1, 2$ is a necessary condition for the existence of a coexistence state for (2.1)–(2.2). Note that

$$\lambda_1\left(\frac{R_i(x)}{d_i}\right) = d_i \lambda_1(R_i(x))$$

and so $\lambda_1(R_i(x)/d_i) < 1$ is equivalent to $d_i < \lambda_1(R_i(x))^{-1}$. Note also that $d_i \rightarrow \theta(d_i, R_i)$ is a continuous map from $(0, \lambda_1(R_i(x))^{-1})$ into $C_0^{1+\alpha}(\bar{\Omega})$ (see [4], for example). Suppose that c and e in (2.1)–(2.2) are held fixed and that the d_i , $i = 1, 2$ are allowed to vary. Then a bifurcation from extinction states to coexistence states occurs. In particular, there is a transition from the state $(d_1, d_2, \theta(d_1, R_1), 0)$ to a coexistence state (d_1, d_2, u, v) across the curve

$$\lambda_1\left(\frac{R_2(x) - e\theta(d_1, R_1)}{d_2}\right) = 1$$

in $\{(d_1, d_2): d_1 < \lambda_1(R_1(x))^{-1}, d_2 < \lambda_1(R_2(x))^{-1}\}$, as well as a transition from the state $(d_1, d_2, 0, \theta(d_2, R_2))$ to a coexistence state (d_1, d_2, u, v) across the corresponding curve

$$\lambda_1\left(\frac{R_1(x) - c\theta(d_2, R_2)}{d_1}\right) = 1.$$

That these bifurcations occur as indicated can be argued as in [2], [7], where the special case of R_1 and R_2 positive constants is treated. Moreover, the fact that there are no coexistence states to (2.1)–(2.2) when $d_1 \geq \lambda_1(R_1)^{-1}$ or $d_2 \geq \lambda_1(R_2)^{-1}$ allows us to conclude as in [3] the existence of a single continuum of coexistence states (d_1, d_2, u_1, u_2) to (2.1)–(2.2), which is of dimension at least two at every point and which meets the extinction states of the form $(d_1, d_2, \theta(d_1, R_1), 0)$ at parameter values along

$$\lambda_1\left(\frac{R_2(x) - e\theta(d_1, R_1)}{d_2}\right) = 1$$

and those of the form $(d_1, d_2, 0, \theta(d_2, R_2))$ at parameter values along

$$\lambda_1\left(\frac{R_1(x) - c\theta(d_2, R_2)}{d_1}\right) = 1.$$

In particular, we know there is a coexistence state associated with every parameter pair (d_1, d_2) located between the curves

$$\lambda_1\left(\frac{R_2(x) - e\theta(d_1, R_1)}{d_2}\right) = 1 \quad \text{and} \quad \lambda_1\left(\frac{R_1(x) - c\theta(d_2, R_2)}{d_1}\right) = 1.$$

Note that when c and e are both equal to zero (an extreme case that reduces essentially to (2.5)-(2.6)), the curves in question are the rays $\{(d_1, d_2): d_1 < \lambda_1(R_1)^{-1}, d_2 = \lambda_1(R_2)^{-1}\}$ and $\{(d_1, d_2): d_1 = \lambda_1(R_1)^{-1}, d_2 < \lambda_1(R_2)^{-1}\}$, and the region between them is $\{(d_1, d_2): d_1 < \lambda_1(R_1)^{-1}, d_2 < \lambda_1(R_2)^{-1}\}$. The biological meaning of this observation is that when two species do not compete (i.e., $c = e = 0$), then the condition for coexistence is simply that each species by itself can sustain a positive population density on Ω . (In the special case where $R_1(x) = r_1\chi_{\Omega_1}(x)$, $R_2 = r_2[\chi_{\Omega_1}(x) + \chi_{\Omega - \Omega_1}(x)]$, the condition for the i th species to sustain a population on Ω is simply that, for any fixed value of $r_i > 0$, d_i is sufficiently small, or, alternatively, for fixed $d_i > 0$, that r_i is sufficiently large. This can be viewed as a requirement that population increase on Ω overbalances dispersal out of Ω through $\partial\Omega$.) The important mathematical observation is that the set of values (d_1, d_2) admitting coexistence lies between the curves defined by $\lambda_i(R_i(x)/d_i) = 1$ (equivalently, $\lambda_i(R_i)^{-1} = d_i$) for $i = 1, 2$. The continuity of $\lambda_i(m)$ suggests that it is reasonable to expect that, for c and e small, the region between the two curves

$$\lambda_1\left(\frac{R_1(x) - c\theta(d_2, R_2)}{d_1}\right) = 1 \quad \text{and} \quad \lambda_1\left(\frac{R_2(x) - e\theta(d_1, R_1)}{d_2}\right) = 1$$

should correspond to the subset of $\{(d_1, d_2): d_1 < \lambda_1(R_1)^{-1}, d_2 < \lambda_1(R_2)^{-1}\}$ such that

$$(2.9) \quad \lambda_1\left(\frac{R_2(x) - c\theta(d_2, R_2)}{d_1}\right) < 1$$

and

$$(2.10) \quad \lambda_1\left(\frac{R_2(x) - e\theta(d_1, R_1)}{d_2}\right) < 1.$$

In fact, we have the following result. (Note that (2.9) and (2.10) are equivalent to $d_1 < \lambda_1(R_1(x) - c\theta(d_2, R_2))^{-1}$ and $d_2 < \lambda_1(R_2(x) - e\theta(d_1, R_1))^{-1}$, respectively.)

THEOREM 2.1. *Suppose that (2.9) and (2.10) hold. Then problem (2.1)-(2.2) has a coexistence state. In particular, if $R_1 = R_2$, $c < 1$ and $e < 1$, then the region in $\{(d_1, d_2): d_1 < \lambda_1(R_1)^{-1}, d_2 < \lambda_1(R_2)^{-1}\}$ between the curves*

$$\lambda_1\left(\frac{R_1(x) - c\theta(d_2, R_2)}{d_1}\right) = 1 \quad \text{and} \quad \lambda_1\left(\frac{R_2(x) - e\theta(d_1, R_1)}{d_2}\right) = 1$$

is precisely the set of points (d_1, d_2) for which (2.9) and (2.10) hold.

Proof. If

$$\lambda_1\left(\frac{R_1 - c\theta(d_2, R_2)}{d_1}\right) < 1 \quad \text{and} \quad \lambda_1\left(\frac{R_2 - e\theta(d_1, R_1)}{d_2}\right) < 1,$$

then $\sigma_1 < 0$ and $\sigma_2 < 0$, where σ_1 and σ_2 are the unique real numbers so that

$$-d_1\Delta\phi_1 + [c\theta(d_2, R_2) - R_1]\phi_1 = \sigma_1\phi_1 \quad \text{in } \Omega,$$

$$\phi_1 = 0 \quad \text{on } \partial\Omega$$

and

$$\begin{aligned} -d_2\Delta\phi_2 + [e\theta(d_1, R_1) - R_2]\phi_2 &= \sigma_2\phi_2 \quad \text{in } \Omega, \\ \phi_2 &= 0 \quad \text{on } \partial\Omega \end{aligned}$$

admit positive solutions ϕ_1 and ϕ_2 , as can be deduced from, say, [9, Thm. 6]. Consequently, for $\varepsilon > 0$ and sufficiently small, $\tau_{1\varepsilon} > 0$ and $\tau_{2\varepsilon} > 0$, where $\tau_{1\varepsilon}$ and $\tau_{2\varepsilon}$ are the unique real numbers so that

$$\begin{aligned} d_1\Delta\phi_{1\varepsilon} + [R_1 - c(1+\varepsilon)\theta(d_2, R_2)]\phi_{1\varepsilon} &= \tau_{1\varepsilon}\phi_{1\varepsilon} \quad \text{in } \Omega, \\ \phi_{1\varepsilon} &= 0 \quad \text{on } \partial\Omega \end{aligned}$$

and

$$\begin{aligned} d_2\Delta\phi_{2\varepsilon} + [R_2 - e(1+\varepsilon)\theta(d_1, R_1)]\phi_{2\varepsilon} &= \tau_{2\varepsilon}\phi_{2\varepsilon} \quad \text{in } \Omega, \\ \phi_{2\varepsilon} &= 0 \quad \text{on } \partial\Omega \end{aligned}$$

admit positive solutions $\phi_{1\varepsilon}$ and $\phi_{2\varepsilon}$. Let $u = \delta\phi_{1\varepsilon}$ and $v = (1+\varepsilon)\theta(d_2, R_2)$. Then

$$\begin{aligned} d_1\Delta u + [R_1 - u - cv]u & \\ = \delta\phi_{1\varepsilon}[\tau_{1\varepsilon} - R_1 + c(1+\varepsilon)\theta(d_2, R_2) + R_1 - \delta\phi_{1\varepsilon} - c(1+\varepsilon)\theta(d_2, R_2)] & \\ = \delta\phi_{1\varepsilon}[\tau_{1\varepsilon} - \delta\phi_{1\varepsilon}] & \\ > 0 & \end{aligned}$$

for $\delta > 0$ sufficiently small. Also,

$$\begin{aligned} d_2\Delta v + [R_2 - eu - v]v & \\ = (1+\varepsilon)\theta(d_2, R_2)[\theta(d_2, R_2) - R_2 + R_2 - e\delta\phi_{1\varepsilon} - (1+\varepsilon)\theta(d_2, R_2)] & \\ = (1+\varepsilon)\theta(d_2, R_2)[-e\delta\phi_{1\varepsilon} - \varepsilon\theta(d_2, R_2)] & \\ < 0. & \end{aligned}$$

So (u, v) satisfies

$$\begin{aligned} -d_1\Delta u &\leq [R_1 - u - cv]u \quad \text{in } \Omega, \\ -d_2\Delta v &\geq [R_2 - eu - v]v \end{aligned}$$

Similarly, if $\bar{u} = (1+\varepsilon)\theta(d_1, R_1)$ and $\bar{v} = \delta\phi_{2\varepsilon}$, then (\bar{u}, \bar{v}) satisfies

$$\begin{aligned} -d_1\Delta \bar{u} &\geq [R_1 - \bar{u} - c\bar{v}]\bar{u} \quad \text{in } \Omega, \\ -d_2\Delta \bar{v} &\leq [R_2 - e\bar{u} - \bar{v}]\bar{v} \end{aligned}$$

Since the Hopf maximum principle [12] guarantees that $u < \bar{u}$ and $v < \bar{v}$ for $\delta > 0$ sufficiently small, the existence of a coexistence state follows from the method of upper and lower solutions for systems, as in [10].

Suppose now that $R_1 = R_2$. When $c = e = 1$, (2.3)-(2.4) can have a componentwise positive solution only if

$$\lambda_1\left(\frac{R_1 - u - v}{d_1}\right) = 1 = \lambda_1\left(\frac{R_1 - u - v}{d_2}\right),$$

whence $d_1 = d_2$. It follows from bifurcation theoretic considerations that

$$\lambda_1\left(\frac{R_1(x) - \theta(d_1, R_1)}{d_1}\right) = 1 \quad \text{for all } d_1 < \lambda_1(R_1)^{-1}.$$

Now suppose that $c < 1$ and $e < 1$. Then

$$\frac{R_1(x) - c\theta(d_2, R_1)}{d_2} > \frac{R_1(x) - \theta(d_2, R_1)}{d_2} \quad \text{for } x \in \Omega,$$

so

$$\lambda_1\left(\frac{R_1(x) - c\theta(d_2, R_1)}{d_2}\right) < 1.$$

Now, however,

$$\lambda_1\left(\frac{R_1(x) - c\theta(d_2, R_1)}{d}\right) = d\lambda_1(R_1(x) - c\theta(d_2, R_1)).$$

Consequently, if

$$\lambda_1\left(\frac{R_1(x) - c\theta(d_2, R_1)}{d_1}\right) = 1,$$

then $d_1 > d_2$. Similarly, if

$$\lambda_1\left(\frac{R_1(x) - e\theta(d_1, R_1)}{d_2}\right) = 1,$$

then $d_1 < d_2$. The result now follows from the observation that

$$\lambda_1\left(\frac{R_1(x) - c\theta(d_2, R_2)}{d_1}\right)$$

decreases as d_1 decreases and

$$\lambda_1\left(\frac{R_1(x) - e\theta(d_1, R_1)}{d_2}\right)$$

decreases as d_2 decreases.

So, indeed, it is the case that when $R_1 = R_2$, $c < 1$ and $e < 1$, the region in $\{(d_1, d_2): d_1 < \lambda_1(R_1)^{-1}, d_2 < \lambda_1(R_2)^{-1}\}$ between the curves

$$\lambda_1\left(\frac{R_1(x) - c\theta(d_2, R_2)}{d_1}\right) = 1 \quad \text{and} \quad \lambda_1\left(\frac{R_2(x) - e\theta(d_1, R_1)}{d_2}\right) = 1,$$

where coexistence states are guaranteed by the methods of global bifurcation theory corresponds precisely to the set of parameters (d_1, d_2) satisfying an analytic condition sufficient for the existence of a coexistence state, namely, (2.9) and (2.10). Note now that

$$\lambda_1\left(\frac{R_1(x) - c\theta(d_2, R_2)}{d_1}\right)$$

decreases as d_1 decreases, and also that

$$\lambda_1\left(\frac{R_2(x) - e\theta(d_1, R_1)}{d_2}\right)$$

decreases as d_2 decreases, independent of whether $R_1 = R_2$. Hence the question of whether the region in (d_1, d_2) parameter space wherein coexistence states are guaranteed to exist by global bifurcation theory corresponds to the set of parameter values for

which (2.9) and (2.10) are simultaneously satisfied is really a question about the relative locus in parameter space of the boundary curves

$$\lambda_1 \left(\frac{R_1(x) - c\theta(d_2, R_2)}{d_1} \right) = 1 \quad \text{and} \quad \lambda_1 \left(\frac{R_2(x) - e\theta(d_1, R_1)}{d_2} \right) = 1.$$

Determining such when $R_1 \neq R_2$ is, in general, a difficult problem. The most general statement that can be made is that, for any (\bar{d}_1, \bar{d}_2) with $\bar{d}_1 < \lambda_1(R_1)^{-1}$ and $\bar{d}_2 < \lambda_1(R_2)^{-1}$, there are sufficiently small \bar{c} and \bar{e} so that (2.9) and (2.10) hold for (\bar{d}_1, \bar{d}_2) , and hence (\bar{d}_1, \bar{d}_2) lie in the region bounded by the curves

$$\lambda_1 \left(\frac{R_1(x) - \bar{c}\theta(d_2, R_2)}{d_1} \right) = 1 \quad \text{and} \quad \lambda_1 \left(\frac{R_2(x) - \bar{e}\theta(d_1, R_1)}{d_2} \right) = 1.$$

However, from the point of view of applications, such a result is unsatisfactory for two reasons. First, it does not guarantee that the curves

$$\lambda_1 \left(\frac{R_1(x) - \bar{c}\theta(d_2, R_2)}{d_1} \right) = 1 \quad \text{and} \quad \lambda_1 \left(\frac{R_2(x) - \bar{e}\theta(d_1, R_1)}{d_2} \right) = 1$$

meet only at the limiting point $(\lambda_1(R_1)^{-1}, \lambda_1(R_2)^{-1})$, and second, and perhaps more important, it does not quantify explicitly how small \bar{c} and \bar{e} must be. Fortunately, in the models we consider in this article, we are able to determine that a region in an appropriate parameter space wherein coexistence states are assured by global bifurcation theoretic methods does correspond to the region wherein appropriate analogues to (2.9) and (2.10) are simultaneously satisfied, for ranges of the competition parameters that can be explicitly determined.

In the situations just described, we have an "envelope" in (d_1, d_2) parameter space described by (2.9) and (2.10) wherein coexistence states to (2.1)-(2.2) are guaranteed to exist. This "envelope" has the following important property regarding the persistence of the time-dependent solutions to (2.1)-(2.2).

THEOREM 2.2. *Suppose that (2.9) and (2.10) hold. Then, if $(u(x, t), v(x, t))$ is a solution to (2.1)-(2.2) with $u(x, 0) > \neq 0$, $v(x, 0) > \neq 0$, then there are functions w_1 and w_2 , both positive for $x \in \Omega$ and $T > 0$ so that $u(x, t) \geq w_1(x)$ and $v(x, t) \geq w_2(x)$ for all $x \in \bar{\Omega}$ and $t \geq T$.*

Proof. Suppose that $(u(x, t), v(x, t))$ solves (2.1)-(2.2) with $u(x, 0) > \neq 0$, $v(x, 0) > \neq 0$ and that (2.9) and (2.10) hold. Since $u(x, t) > 0$ for $x \in \Omega$ and $t > 0$, v is a lower solution to

$$(2.11) \quad p_t = d_2 \Delta p + (R_2 - p)p \quad \text{in } \Omega \times (0, \infty),$$

$$(2.12) \quad p = 0 \quad \text{on } \partial\Omega \times (0, \infty).$$

From (2.10), we have that $\lambda_1(R_2/d_2) < 1$, and, consequently, $\theta(d_2, R_2)$ is a global attractor (with respect to nontrivial nonnegative initial data) for (2.11)-(2.12). Consequently, given $\varepsilon > 0$, there is a $T_\varepsilon > 0$ so that $v(x, t) < (1 + \varepsilon)\theta(d_2, R_2)(x)$ for all $t \geq T_\varepsilon$. Then $u_t = d_1 \Delta u + [R_1(x) - c(1 + \varepsilon)\theta(d_2, R_2) - u]u + [c(1 + \varepsilon)\theta(d_2, R_2) - cv]u$, and hence u is an upper solution to

$$(2.13) \quad w_t = d_1 \Delta w + [R_1 - c(1 + \varepsilon)\theta(d_2, R_2) - w]w \quad \text{in } \Omega \times (T_\varepsilon, \infty),$$

$$(2.14) \quad w = 0 \quad \text{on } \partial\Omega \times (T_\varepsilon, \infty),$$

where $w(x, T_\varepsilon) = u(x, T_\varepsilon) > 0$ in Ω . Now, however, (2.9) implies that

$$\lambda_1 \left(\frac{R_1(x) - c(1 + \varepsilon)\theta(d_2, R_2)}{d_1} \right) < 1 \quad \text{for } \varepsilon > 0 \text{ sufficiently small.}$$

$\theta(d_1, R_1(x) - c(1 + \varepsilon)\theta(d_2, R_2))$ is then a global attractor (with respect to nontrivial nonnegative initial data), so there is $T'_\varepsilon > T_\varepsilon$ so that $w(x, t) \geq \frac{1}{2}\theta(d_1, R_1(x) - c(1 + \varepsilon)\theta(d_2, R_2))(x)$ for $t > T'_\varepsilon$. Since $u(x, t) \geq w(x, t)$ for $t > T_\varepsilon$, we may take $w_1 = \frac{1}{2}\theta(d_1, R_1(x) - c(1 + \varepsilon)\theta(d_2, R_2))$ for any sufficiently small ε . A similar argument holds for v .

Thus far, we have determined conditions on the parameters (d_1, d_2) , which are sufficient for (2.1)–(2.2) to admit a coexistence state, and we have observed that in a number of instances (including the models under consideration in the article) these sufficient conditions correspond to (2.9) and (2.10) and, moreover, that (2.9) and (2.10) imply persistence in (2.1)–(2.2). Since the conditions on (d_1, d_2) were obtained via global bifurcation theory applied to (2.3)–(2.4), it is not evident that the conditions are also necessary. However, as we now demonstrate, we can obtain (again for fixed small c and e) a slightly larger “envelope” of parameter values (d_1, d_2) outside of which problem (2.1)–(2.2) does not possess coexistence states (see also [7]).

Consider (2.3)–(2.4) and suppose that (u, v) solve (2.3)–(2.4) with $u > 0$ and $v > 0$ in Ω . Then v is a lower solution to

$$\begin{aligned} -d_2\Delta z &= [R_2(x) - z]z & \text{in } \Omega, \\ z &= 0 & \text{on } \partial\Omega. \end{aligned}$$

Since any sufficiently large constant is an upper solution, it follows that there is a solution larger than v . Since the solution $\theta(d_2, R_2)$ is unique and exists only for $\lambda_1(R_2(x)/d_2) < 1$, we have $\lambda_1(R_2(x)/d_2) < 1$ with $v \leq \theta(d_2, R_2)$. Hence

$$-d_1\Delta u \geq [R_1(x) - c\theta(d_2, R_2) - u]u \quad \text{in } \Omega.$$

It follows that $u \geq \theta(d_1, R_1(x) - c\theta(d_2, R_2))$, where $\theta(d_1, R_1(x) - c\theta(d_2, R_2))$ is the unique positive solution to

$$\begin{aligned} -d_1\Delta w &= [R_1(x) - c\theta(d_2, R_2) - w]w & \text{in } \Omega, \\ w &= 0 & \text{on } \partial\Omega, \end{aligned}$$

when it exists, and zero otherwise. Thus

$$-d_2\Delta v \leq [R_2(x) - e\theta(d_1, R_1(x) - c\theta(d_2, R_2)) - v]v$$

in Ω , and, as a consequence,

$$\lambda_1\left(\frac{R_2(x) - e\theta(d_1, R_1(x) - c\theta(d_2, R_2))}{d_2}\right) < 1.$$

We have established the following result.

THEOREM 2.3. *Suppose that problem (2.1)–(2.2) admits a coexistence state. Then*

$$(2.15) \quad \lambda_1\left(\frac{R_1(x) - c\theta(d_2, R_2(x) - e\theta(d_1, R_1))}{d_1}\right) < 1$$

and

$$(2.16) \quad \lambda_1\left(\frac{R_2(x) - e\theta(d_1, R_1(x) - c\theta(d_2, R_2))}{d_2}\right) < 1.$$

It follows from the method of upper and lower solutions that $\theta(d_i, R_i)$ is increasing in R_i . From this observation, it is easy to verify that (2.9) implies (2.15) and that (2.10) implies (2.16), as indeed must be the case. Let us now demonstrate that if

$$\lambda_1\left(\frac{R_1(x) - c\theta(d_2, R_2(x) - e\theta(d_1, R_1))}{d_1}\right) > 1$$

or

$$\lambda_1 \left(\frac{R_2(x) - e\theta(d_1, R_1(x) - c\theta(d_2, R_2))}{d_2} \right) > 1,$$

at least one component of any positive time-dependent solution to (2.1)-(2.2) is driven to extinction as time increases. In our proof, we make the convention that if $m \leq 0$ almost everywhere on Ω (in which case, problem (2.7)-(2.8) does not admit a positive solution for $\lambda \geq 0$), then $\lambda_1(m) = +\infty$. We have the following theorem.

THEOREM 2.4. Assume that $d_i < \lambda_1(R_i)^{-1}$, for $i = 1, 2$. Suppose that $(u(x, t), v(x, t))$ is a solution to (2.1)-(2.2) with $u(x, 0) > \neq 0$, $v(x, 0) > \neq 0$. If

$$\lambda_1 \left(\frac{R_1(x) - c\theta(d_2, R_2(x) - e\theta(d_1, R_1))}{d_1} \right) > 1,$$

then $\lim_{t \rightarrow \infty} u(x, t) = 0$, and, if

$$\lambda_1 \left(\frac{R_2(x) - e\theta(d_1, R_1(x) - c\theta(d_2, R_2))}{d_2} \right) > 1,$$

then $\lim_{t \rightarrow \infty} v(x, t) = 0$, the limits being uniform for $x \in \bar{\Omega}$.

Proof. We give the proof of the second assertion of the theorem; the first is proved analogously. Suppose that $(u(x, t), v(x, t))$ solves (2.1)-(2.2) with $u(x, 0) > \neq 0$, $v(x, 0) > \neq 0$ and that

$$\lambda_1 \left(\frac{R_2(x) - e\theta(d_1, R_1(x) - c\theta(d_2, R_2))}{d_2} \right) > 1.$$

Since $u(x, t) > 0$ for $x \in \Omega$ and $t > 0$, v is a lower solution to (2.11)-(2.12), as in the proof of Theorem 2.2. Again, $\theta(d_2, R_2)$ is a global attractor (with respect to nontrivial nonnegative initial data) for (2.11)-(2.12). Hence, for any $\varepsilon > 0$, there is a T_ε so that $v(x, t) < (1 + \varepsilon)\theta(d_2, R_2)(x)$ for all $t \geq T_\varepsilon$. u is then an upper solution to (2.13)-(2.14), where $w(x, T_\varepsilon) = u(x, T_\varepsilon) > 0$ in Ω . If

$$\lambda_1 \left(\frac{R_1(x) - c(1 + \varepsilon)\theta(d_2, R_2)}{d_1} \right) < 1,$$

$\theta(d_1, R_1(x) - c(1 + \varepsilon)\theta(d_2, R_2))$ is positive on Ω and is a global attractor (with respect to nonnegative initial data). If

$$\lambda_1 \left(\frac{R_1(x) - c(1 + \varepsilon)\theta(d_2, R_2)}{d_1} \right) \geq 1,$$

then $\theta(d_1, R_1(x) - c(1 + \varepsilon)\theta(d_2, R_2)) \equiv 0$. In either case, there is $T'_\varepsilon > T_\varepsilon$, so that $u(x, t) > (1 - \varepsilon)\theta(d_1, R_1(x) - c(1 + \varepsilon)\theta(d_2, R_2))(x)$ for $t > T'_\varepsilon$. As a consequence, v is a lower solution to

$$(2.17) \quad \begin{aligned} y_t &= d_2 \Delta y + [R_2(x) - e(1 - \varepsilon)\theta(d_1, R_1(x) \\ &\quad - c(1 + \varepsilon)\theta(d_2, R_2)) - y]y \quad \text{in } \Omega \times (T'_\varepsilon, \infty), \\ y &= 0 \quad \text{in } \partial\Omega \times (T'_\varepsilon, \infty), \end{aligned}$$

where $y(x, T'_\varepsilon) = v(x, T'_\varepsilon)$. Since

$$\lambda_1 \left(\frac{R_2(x) - e\theta(d_1, R_1(x) - c\theta(d_2, R_2))}{d_2} \right) > 1,$$

then

$$\lambda_1 \left(\frac{R_2(x) - e(1-\varepsilon)\theta(d_1, R_1(x) - c(1+\varepsilon)\theta(d_2, R_2))}{d_2} \right) > 1$$

for $\varepsilon > 0$ and sufficiently small. Consequently, $\lim_{t \rightarrow \infty} y(x, t) = 0$, uniformly for $x \in \bar{\Omega}$. Since $v(x, t) \leq y(x, t)$ for $x \in \bar{\Omega}$ and $t > T'_\varepsilon$, the result is established.

Thus far in this section, we have considered the question of existence of coexistence states for (2.1)–(2.2) and consequences thereof, in the case where $R_1(x)$ and $R_2(x)$ are appropriate fixed L^∞ functions on Ω and the interaction parameters c and e are fixed constants, while the diffusion coefficients d_1 and d_2 are considered as varying over appropriate ranges. The information we have obtained has been expressed in terms of inequalities involving the principal eigenvalue $\lambda_1(m)$ of the weighted elliptic eigenvalue problem (2.7)–(2.8), where m depends on R_1, R_2, c, e, d_1 , and d_2 , as in Theorems 2.1–2.4. Our models view $R_1(x)$ and $R_2(x)$ as representing parametric families of such functions. Specifically, we set

$$R_1(x) = r_1[\chi_{\Omega_1} + \varepsilon l \chi_{\Omega - \Omega_1}], \quad R_2(x) = r_2[\chi_{\Omega_1} + l \chi_{\Omega - \Omega_1}],$$

where $\bar{\Omega}_1 \subset \Omega$, r_1, r_2 are positive, $l \in [0, 1]$, and $0 \leq \varepsilon \ll 1$, where the physical interpretation of $R_1(x)$ and $R_2(x)$ is as discussed in the previous section. The inequalities involved in Theorems 2.1–2.4 can now be interpreted as depending on the parameters d_1, d_2, r_1, r_2, l , and ε , as well as the constants c and e .

The most relevant parameter in terms of reflecting change in the nature of the habitat is l . We express the change in the predictions of the model as l is varied in terms of the other parameters. Specifically, we track how parametric “envelopes” where coexistence states are guaranteed and parametric “envelopes” outside of which coexistence states fail to exist change as l varies from zero to one. In the following, these “envelopes” are expressed in terms of the modified intrinsic growth rates r_1/d_1 and r_2/d_2 , instead of d_1 and d_2 , the parameters used when R_1 and R_2 were considered fixed. Note that, in the parametric representations of our model, these ratios arise naturally. For instance, say $\varepsilon = 0$ and consider $\lambda_1(R_1(x)/d_1) = \lambda_1(r_1 \chi_{\Omega_1}/d_1)$. Since $\lambda_1(r_1 \chi_{\Omega_1}/d_1) = d_1/r_1 \lambda_1(\chi_{\Omega_1})$, the basic inequality $\lambda_1(R_1(x)/d_1) < 1$ is equivalent to $r_1/d_1 > \lambda_1(\chi_{\Omega_1})$. Recall that the rescaling process discussed in detail in the Introduction allows us to subsume the diffusion rates d_1 and d_2 into the growth rates so that a system of the form

$$U_t = d_1 \Delta U + [\bar{r}_1 \chi_{\Omega_1} - BU - CV]U,$$

$$V_t = d_2 \Delta V + [\bar{r}_2[\chi_{\Omega_1} + l \chi_{\Omega - \Omega_1}] - EU - FV]V$$

may be rescaled to

$$(2.18) \quad \left(\frac{1}{d} \right) u_t = \Delta u + u[r_1 \chi_{\Omega_1} - u - cv],$$

$$v_t = \Delta v + v[r_2(\chi_{\Omega_1} + l \chi_{\Omega - \Omega_1}) - eu - v] \quad \text{in } \Omega \times (0, \infty),$$

where we maintain the boundary condition

$$(2.19) \quad u = 0 = v \quad \text{on } \partial\Omega \times (0, \infty).$$

In (2.18) the rescaled diffusion rate $d = d_1/d_2$ measures the dispersal rate of the first competitor relative to that of the second, and the growth rate coefficients $r_i = \bar{r}_i/d_i$, $i = 1, 2$, describe the effective rates of growth of the two populations in favorable habitats (e.g., in Ω_1) when dispersal is considered. (Recall also that it is the quantity

\bar{r}_i/d_i rather than simply \bar{r}_i that determines whether solutions to the simple linear model $w_t = d_i \Delta w + \bar{r}_i w$ in $\Omega \times (0, \infty)$, $w = 0$ on $\partial\Omega \times (0, \infty)$ will increase or decrease with time.) The competition coefficients $c = Cd_2/Fd_1$ and $e = Ed_1/Bd_2$ describe the strength of competitive interactions between two species; if $c = e = 0$, then the species do not compete. Sometimes we may replace the term $r_1 \chi_{\Omega_1}$ with $r_1[\chi_{\Omega_1} + \varepsilon l \chi_{\Omega - \Omega_1}]$ where $0 < \varepsilon \ll 1$. That corresponds to assuming a low, but nonzero, intrinsic population growth rate for the first competitor on $\Omega - \Omega_1$.

The equilibrium system corresponding to (2.18)-(2.19) is

$$(2.20) \quad \begin{aligned} -\Delta u &= u[r_1 \chi_{\Omega_1} - u - cv], \\ -\Delta v &= v[r_2(\chi_{\Omega_1} + l \chi_{\Omega - \Omega_1}) - eu - v] \end{aligned} \quad \text{in } \Omega,$$

$$(2.21) \quad u = 0 = v \quad \text{on } \partial\Omega.$$

Of course, unless $d_1 = d_2$, the time derivative of u in (2.18) will carry a scaling constant $1/d$. However, any conclusions concerning the existence or nonexistence of coexistent steady states or about long-time coexistence versus extinction, for example, are left unchanged. As a simple illustration, consider

$$\begin{aligned} u_t &= d \Delta u + [r - u]u \quad \text{in } \Omega \times (0, \infty), \\ u &= 0 \quad \text{on } \partial\Omega \times (0, \infty). \end{aligned}$$

If we divide through by d , we can rewrite the equation as

$$\frac{1}{d} w_t = \Delta w + [R - w]w,$$

where $R = r_1/d$ and $w = (1/d)u$. However, in either case, persistence or extinction is determined by the same condition on the size of $\lambda_1(R) = \lambda_1(r/d)$ (see [4]).

The results in Theorems 2.1-2.4 have analogues for (2.18)-(2.19), which we summarize in Corollary 2.5. (Recall that $\theta(f(x))$ denotes the unique (see [4]) positive solution of

$$\begin{aligned} -\Delta w &= w[f(x) - w] \quad \text{in } \Omega, \\ w &= 0 \quad \text{on } \partial\Omega, \end{aligned}$$

should one exist, and denotes zero otherwise.)

COROLLARY 2.5. Consider (2.18)-(2.19). Let $l=0$ or 1 and assume that $r_1 > \lambda_1(\chi_{\Omega_1})$, $r_2 > \lambda_1(\chi_{\Omega_1} + l \chi_{\Omega - \Omega_1})$. Then the following hold:

(i) For appropriate quantifiable ranges of c and e (see Theorem 3.5 when $l=1$), if r_1 and r_2 satisfy

$$(2.22) \quad \lambda_1(r_1 \chi_{\Omega_1} - c\theta(r_2(\chi_{\Omega_1} + l \chi_{\Omega - \Omega_1}))) < 1$$

and

$$(2.23) \quad \lambda_1(r_2(\chi_{\Omega_1} + l \chi_{\Omega - \Omega_1}) - e\theta(r_1 \chi_{\Omega_1})) < 1,$$

then problem (2.18)-(2.19) admits a coexistence state, and, for any solution $(u(x, t), v(x, t))$ of (2.18)-(2.19) with $u(x, 0) > \neq 0$, $v(x, 0) > \neq 0$, there are functions w_1 and w_2 , positive for $x \in \Omega$, and $T > 0$ so that $u(x, t) \geq w_1(x)$ and $v(x, t) \geq w_2(x)$ for all $x \in \bar{\Omega}$ and $t \geq T$.

(ii) If problem (2.18)-(2.19) admits a coexistence state, then r_1 and r_2 must satisfy

$$(2.24) \quad \lambda_1(r_1 \chi_{\Omega_1} - c\theta(r_2(\chi_{\Omega_1} + l \chi_{\Omega - \Omega_1}) - e\theta(r_1 \chi_{\Omega_1}))) < 1$$

and

$$(2.25) \quad \lambda_1(r_2(\chi_{\Omega_1} + l\chi_{\Omega-\Omega_1}) - e\theta(r_1\chi_{\Omega_1} - c\theta(r_2(\chi_{\Omega_1} + l\chi_{\Omega-\Omega_1})))) < 1.$$

(iii) If

$$(2.26) \quad \lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2(\chi_{\Omega_1} + l\chi_{\Omega-\Omega_1}) - e\theta(r_1\chi_{\Omega_1}))) > 1,$$

then $\lim_{t \rightarrow \infty} u(x, t) = 0$, and, if

$$(2.27) \quad \lambda_1(r_2(\chi_{\Omega_1} + l\chi_{\Omega-\Omega_1}) - e\theta(r_1\chi_{\Omega_1} - c\theta(r_2(\chi_{\Omega_1} + l\chi_{\Omega-\Omega_1})))) > 1,$$

then $\lim_{t \rightarrow \infty} v(x, t) = 0$, for any solution $(u(x, t), v(x, t))$ of (2.18)-(2.19) with $u(x, 0) > \neq 0$, $v(x, 0) > \neq 0$, the limits being uniform for $x \in \Omega$.

3. Eigenvalue estimation. Corollary 2.5 summarizes the predictions regarding long-time coexistence versus extinction from our qualitative analysis of (1.1), measured in terms of the modified intrinsic growth rates r_1 and r_2 , the "competition coefficients" c and e , and the "environmental" parameter l . Our chief objective is to understand the changes in these predictions as l moves from zero to one, i.e., as we change from a situation where both species are allowed to reproduce only in the preserve Ω_1 to a situation where species u is still allowed to reproduce only in the preserve Ω_1 , while species v is allowed to reproduce equally well throughout the entire habitat Ω . To achieve our objective, we first make here a detailed analysis of the locus of the sets described by the simultaneous inequalities (2.22)-(2.23) and (2.24)-(2.25) for $l=0$ and for $l=1$. This process is one of eigenvalue estimation for weighted linear elliptic Dirichlet boundary value problems, with the results expressed in terms of r_1 and r_2 (and also c and e). Many of the results are in the spirit of [4] or [7].

We begin with the region described by (2.22)-(2.23) when $l=0$. Recall that for $c, e \in (0, 1)$, the positive solutions to (2.18)-(2.19) are long-term persistent in the sense of Corollary 2.5(i) for all (r_1, r_2) satisfying (2.22)-(2.23). We obtain outer bounds on this region as follows. Observe that $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2\chi_{\Omega_1})) = 1$ is equivalent to $r_1 = \lambda^1(c\theta(r_2\chi_{\Omega_1}); \chi_{\Omega_1})$, where $\lambda^1(c\theta(r_2\chi_{\Omega_1}); \chi_{\Omega_1})$ denotes the principal eigenvalue of

$$(3.1) \quad \begin{aligned} -\Delta z + c\theta(r_2\chi_{\Omega_1})z &= \lambda\chi_{\Omega_1}z \quad \text{in } \Omega, \\ z &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

It follows as in [7, Lemma 1.2] that the eigenvalue $\lambda^1(c) = \lambda^1(c\theta(r_2\chi_{\Omega_1}); \chi_{\Omega_1})$ is smooth in c for $r_2 > \lambda_1(\chi_{\Omega_1})$ fixed, as is the positive eigenfunction z , provided that we make the normalization $\int_{\Omega} z^2 = 1$. Let us denote this z by ψ_c . Now fix $c^* \in (0, 1)$ and compare (3.1) with

$$(3.2) \quad -\Delta\psi_{c^*} + c^*\theta(r_2\chi_{\Omega_1})\psi_{c^*} = \lambda^1(c^*)\chi_{\Omega_1}\psi_{c^*}$$

in Ω . Multiplying (3.1) by ψ_{c^*} and (3.2) by ψ_c and integrating by parts yields

$$\lambda^1(c^*) - \lambda^1(c) = (c^* - c) \frac{\int_{\Omega} \theta(r_2\chi_{\Omega_1})\psi_c\psi_{c^*}}{\int_{\Omega} \chi_{\Omega_1}\psi_c\psi_{c^*}},$$

from which we obtain that

$$(3.3) \quad \lambda^1(c^*) = \frac{\int_{\Omega} \theta(r_2\chi_{\Omega_1})\psi_{c^*}^2}{\int_{\Omega} \chi_{\Omega_1}\psi_{c^*}^2}.$$

Returning to (3.2), multiplying by ψ_{c^*} , and then integrating by parts, we obtain

$$\int_{\Omega} |\nabla\psi_{c^*}|^2 + c^* \int_{\Omega} \theta(r_2\chi_{\Omega_1})\psi_{c^*}^2 = \lambda^1(c^*) \int_{\Omega} \chi_{\Omega_1}\psi_{c^*}^2.$$

It follows from (3.3) that

$$-\lambda^1(c^*) + c^* \lambda^{1'}(c^*) = -\frac{\int_{\Omega} |\nabla \psi_{c^*}|^2}{\int_{\Omega} \chi_{\Omega_1} \psi_{c^*}^2}.$$

However,

$$\frac{\int_{\Omega} |\nabla \psi_{c^*}|^2}{\int_{\Omega} \chi_{\Omega_1} \psi_{c^*}^2} \geq \lambda_1(\chi_{\Omega_1}).$$

Hence

$$(3.4) \quad \left[\frac{\lambda^1(c^*)}{c^*} \right]' \leq \frac{-\lambda_1(\chi_{\Omega_1})}{(c^*)^2}.$$

Integrating (3.4) between c and 1, we obtain

$$(3.5) \quad \lambda^1(1) - \frac{\lambda^1(c)}{c} \leq \lambda_1(\chi_{\Omega_1}) \left(1 - \frac{1}{c}\right).$$

Since $\theta(r_2 \chi_{\Omega_1}) > 0$ satisfies $[-\Delta + \theta(r_2 \chi_{\Omega_1})]z = r_2 \chi_{\Omega_1} z$ in Ω , $\lambda^1(1) = r_2$, so (3.5) yields

$$(3.6) \quad r_1 = \lambda^1(c) \geq cr_2 + (1-c)\lambda_1(\chi_{\Omega_1}).$$

Repeating the preceding analysis for the equation $\lambda_1(r_2 \chi_{\Omega_1} - e\theta(r_1 \chi_{\Omega_1})) = 1$ when $e \in (0, 1)$, we obtain the following theorem.

THEOREM 3.1. *Suppose that $c, e \in (0, 1)$ and that (r_1, r_2) satisfies (2.22)–(2.23) for $l = 0$. Then (r_1, r_2) must satisfy (3.6) and*

$$(3.7) \quad r_2 \geq er_1 + (1-e)\lambda_1(\chi_{\Omega_1}).$$

Remark. Theorem 3.1 guarantees that the region in (r_1, r_2) parameter space described by (2.22)–(2.23), where long-term coexistence of the solutions to (1.1) is assured when $l = 0$ is contained within the wedge in (r_1, r_2) parameter space with vertex at $(\lambda_1(\chi_{\Omega_1}), \lambda_1(\chi_{\Omega_1}))$ bounded by the half lines $r_2 = er_1 + (1-e)\lambda_1(\chi_{\Omega_1})$ and $r_1 = cr_2 + (1-c)\lambda_1(\chi_{\Omega_1})$. See Fig. 3.1.

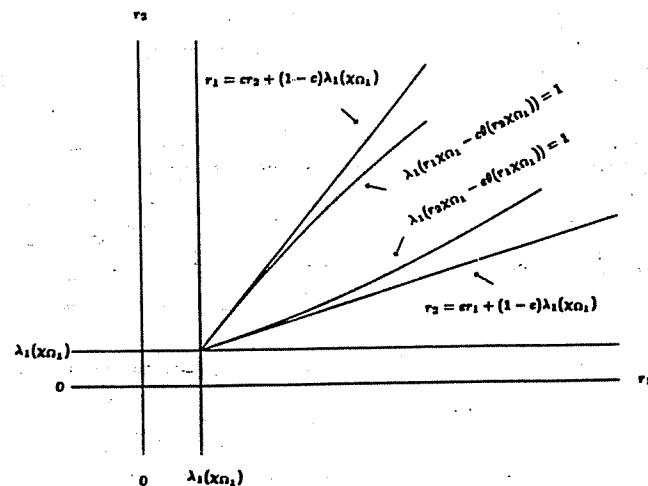


FIG. 3.1. Outside bounds for the region described by (2.22)–(2.23) in which coexistence is guaranteed when $l = 0$ and $c, e \in (0, 1)$.

Using Theorem 3.1, we may obtain outer bounds on the region described by (2.24)–(2.25) outside of which a coexistence state to (1.1) is not possible when $l=0$. So consider $\lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1} - c\theta(r_2\chi_{\Omega_1}))) = 1$. Since $r_1\chi_{\Omega_1} - c\theta(r_2\chi_{\Omega_1}) \leq r_1\chi_{\Omega_1}$, then $\theta(r_1\chi_{\Omega_1} - c\theta(r_2\chi_{\Omega_1})) \leq \theta(r_1\chi_{\Omega_1})$, and hence

$$r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1} - c\theta(r_2\chi_{\Omega_1})) \geq r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1}).$$

The monotonicity of λ_1 guarantees that

$$1 = \lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1} - c\theta(r_2\chi_{\Omega_1}))) < \lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1})).$$

Since $\lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1}))$ decreases as r_2 increases and $\lambda_1(r_1\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1})) < \lambda_1(r_1\chi_{\Omega_1} - \theta(r_1\chi_{\Omega_1})) = 1$, then $r_1 \geq r_2$. Hence $\theta(r_2\chi_{\Omega_1}) \leq \theta(r_1\chi_{\Omega_1})$, so that

$$\theta(r_1\chi_{\Omega_1} - c\theta(r_2\chi_{\Omega_1})) \geq \theta(r_1\chi_{\Omega_1} - c\theta(r_1\chi_{\Omega_1})).$$

It is easy to argue as in [7] that $\theta(r_1\chi_{\Omega_1} - c\theta(r_1\chi_{\Omega_1})) = (1-c)\theta(r_1\chi_{\Omega_1})$. So, if $\lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1} - c\theta(r_2\chi_{\Omega_1}))) = 1$, it follows that $r_2 \geq \delta$, where δ is such that there is a $y > 0$ in Ω so that

$$\begin{aligned} -\Delta y + e(1-c)\theta(r_1\chi_{\Omega_1})y &= \delta\chi_{\Omega_1}y \quad \text{in } \Omega, \\ y &= 0 \quad \text{on } \partial\Omega; \end{aligned}$$

i.e., $\delta = \lambda^1(e(1-c)\theta(r_1\chi_{\Omega_1}); \chi_{\Omega_1})$. The arguments leading to Theorem 3.1 imply that

$$\delta \geq e(1-c)r_1 + (1-e(1-c))\lambda_1(\chi_{\Omega_1}),$$

and hence

$$(3.8) \quad r_2 \geq e(1-c)r_1 + (1-e(1-c))\lambda_1(\chi_{\Omega_1}).$$

We now have the following result.

THEOREM 3.2. *Suppose that $c, e \in (0, 1)$ and that (r_1, r_2) satisfies (2.24)–(2.25) for $l=0$. Then (r_1, r_2) must satisfy (3.8) and*

$$(3.9) \quad r_1 \geq c(1-e)r_2 + (1-c(1-e))\lambda_1(\chi_{\Omega_1}).$$

Remark. It is evident that the wedge in (r_1, r_2) parameter space given by (3.8) and (3.9) contains the wedge determined by (3.6) and (3.7).

Later, we will need interior estimates on the boundary curves of the region described by (2.22)–(2.23) when $l=0$. We have two distinct methods of obtaining such estimates. The two results are markedly different from each other, and, moreover, each serves a different purpose later in our analysis. Consequently, we include both results, the first of which we treat next. The second result follows Theorem 3.5, which is proved in a like manner. We begin our treatment of the first of the two results with the following observation.

PROPOSITION 3.3. *Suppose that $\lambda_1(\Omega)$ and $\lambda_1(\Omega_1)$ denote the principal eigenvalues of $-\Delta$ subject to zero Dirichlet boundary data for Ω and Ω_1 , respectively. Then $\lambda_1(\Omega) < \lambda_1(\chi_{\Omega_1}) < \lambda_1(\Omega_1)$.*

Proof. Choose w and z positive on Ω and y positive on Ω_1 so that

$$(3.10) \quad \begin{aligned} -\Delta w &= \lambda_1(\chi_{\Omega_1})\chi_{\Omega_1}w \quad \text{in } \Omega, \\ w &= 0 \quad \text{on } \partial\Omega, \end{aligned}$$

$$(3.11) \quad \begin{aligned} -\Delta z &= \lambda_1(\Omega)z \quad \text{in } \Omega, \\ z &= 0 \quad \text{on } \partial\Omega; \end{aligned}$$

and

$$(3.12) \quad \begin{aligned} -\Delta y &= \lambda_1(\Omega_1)y \quad \text{in } \Omega_1, \\ y &= 0 \quad \text{on } \partial\Omega_1. \end{aligned}$$

Multiplying (3.10) by z and (3.11) by w and integrating by parts yields that $\lambda_1(\Omega) \int_{\Omega} zw = \lambda_1(\chi_{\Omega_1}) \int_{\Omega} \chi_{\Omega_1} zw < \lambda_1(\chi_{\Omega_1}) \int_{\Omega} zw$, and hence $\lambda_1(\Omega) < \lambda_1(\chi_{\Omega_1})$. Since $\partial y / \partial \nu < 0$ on $\partial\Omega_1$, by the Hopf maximum principle [12], we have from (3.10) and (3.12) that

$$\begin{aligned} 0 &> \int_{\partial\Omega_1} w \frac{\partial y}{\partial \nu} \\ &= \int_{\partial\Omega_1} w \frac{\partial y}{\partial \nu} - y \frac{\partial w}{\partial \nu} \\ &= \int_{\Omega_1} [(-\Delta w)y - (-\Delta y)w] \\ &= \int_{\Omega_1} \lambda_1(\chi_{\Omega_1}) \chi_{\Omega_1} wy - \lambda_1(\Omega_1) yw \\ &= (\lambda_1(\chi_{\Omega_1}) - \lambda_1(\Omega_1)) \int_{\Omega_1} wy. \end{aligned}$$

Hence $\lambda_1(\chi_{\Omega_1}) < \lambda_1(\Omega_1)$, as required.

So now consider $\lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1})) = 1$. Let $\phi > 0$ in Ω_1 satisfy

$$\begin{aligned} -\Delta \phi &= \lambda_1(\Omega_1)\phi \quad \text{in } \Omega_1, \\ \phi &= 0 \quad \text{on } \partial\Omega_1, \end{aligned}$$

and let

$$\tilde{\phi} = \begin{cases} \phi & \text{in } \Omega_1, \\ 0 & \text{in } \Omega \setminus \Omega_1. \end{cases}$$

Then $\tilde{\phi} \in W_0^{1,2}(\Omega)$. Since $\lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1})) = 1$, there is a $w > 0$ in Ω so that

$$\begin{aligned} -\Delta w + e\theta(r_1\chi_{\Omega_1})w &= r_2\chi_{\Omega_1}w \quad \text{in } \Omega, \\ w &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

Since $\tilde{\phi} \in W_0^{1,2}(\Omega)$ and $\tilde{\phi} > 0$ on Ω_1 , the variational characterization of eigenvalues implies that

$$(3.13) \quad \int_{\Omega} |\nabla \tilde{\phi}|^2 + e \int_{\Omega} \theta(r_1\chi_{\Omega_1}) \tilde{\phi}^2 \geq r_2 \int_{\Omega_1} \tilde{\phi}^2.$$

Now, however, $\int_{\Omega} |\nabla \tilde{\phi}|^2 = \int_{\Omega_1} |\nabla \phi|^2 = \lambda_1(\Omega_1) \int_{\Omega_1} \phi^2 = \lambda_1(\Omega_1) \int_{\Omega} \tilde{\phi}^2$ and also $\int_{\Omega} \tilde{\phi}^2 = \int_{\Omega_1} \phi^2$. Hence (3.13) yields

$$(3.14) \quad \lambda_1(\Omega_1) \int_{\Omega} \tilde{\phi}^2 + e \int_{\Omega} \theta(r_1\chi_{\Omega_1}) \tilde{\phi}^2 \geq r_2 \int_{\Omega} \tilde{\phi}^2.$$

The maximum principle guarantees that $\theta(r_1\chi_{\Omega_1}) \leq r_1$, so we obtain from (3.14) that $\lambda_1(\Omega_1) + er_1 \geq r_2$, or $r_2 \leq er_1 + \lambda_1(\Omega_1)$. Proceeding analogously, we obtain that if $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2\chi_{\Omega_1})) = 1$, then $\lambda_1(\Omega_1) + cr_2 \geq r_1$ or $r_2 \geq (1/c)r_1 - (1/c)\lambda_1(\Omega_1)$. We have proved the following theorem.

THEOREM 3.4. Suppose that $c, e \in (0, 1)$ and that (r_1, r_2) satisfies

$$(3.15) \quad r_2 \geq er_1 + \lambda_1(\Omega_1)$$

and

$$(3.16) \quad r_2 \leq \frac{1}{c} r_1 - \frac{1}{c} \lambda_1(\Omega_1).$$

Then, for $l=0$, (r_1, r_2) satisfies (2.22)–(2.23).

Remark. Theorem 3.4 guarantees that the wedge described by (3.15) and (3.16) is contained within the region in (r_1, r_2) parameter space, where, for $l=0$, long-time coexistence of positive solutions to (1.1) is assured (see Fig. 3.2).

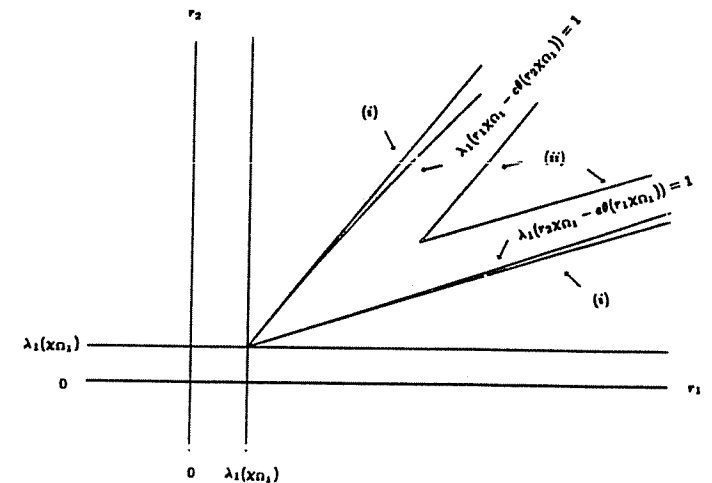


FIG. 3.2. Outside and inside bounds on the boundary curves of the region described by (2.22) and (2.23) when $l=0$ and $c, e \in (0, 1)$. The outside bounds (i) are given by (3.6) and (3.7), while the inside bounds (ii) are given by (3.15) and (3.16).

We now turn our attention to the case when $l=1$. The first issue we address is that of obtaining a quantifiable range of the parameters c and e for which part (i) of Corollary 2.5 is valid. We have the following result.

THEOREM 3.5. Let ψ_0 denote the unique positive solution to (3.10) satisfying $\int_{\Omega} \psi_0^2 = 1$, and let ρ_0 denote the unique positive solution to (3.11) satisfying $\int_{\Omega} \rho_0^2 = 1$. Let

$$K_1 = \frac{(\int_{\Omega} \psi_0^4)^{1/2}}{\int_{\Omega} |\nabla \psi_0|^2}$$

and let $K_2 = (\int_{\Omega} \rho_0^4)^{1/2}$. Then if

$$ce < \frac{1}{\lambda_1(\chi_{\Omega_1}) |\Omega| K_1 K_2},$$

part (i) of Corollary 2.5 holds for $l=1$.

(The condition on ce is not needed for parts (ii) and (iii) of Corollary 2.5.)

Proof. Consider $\lambda_1(r_1 \chi_{\Omega_1} - c \theta(r_2)) = 1$. Fix $r_2 > \lambda_1(\Omega)$ and consider c as varying. Let $\psi = \psi_c = \psi(c)$ be the unique positive solution to

$$(3.17) \quad \begin{aligned} -\Delta w + c \theta(r_2) w &= r_1(c) \chi_{\Omega_1} w & \text{in } \Omega, \\ w &= 0 & \text{on } \partial \Omega, \end{aligned}$$

satisfying $\int_{\Omega} \psi^2 = 1$. Then, as in the proof of Theorem 3.1, ψ is smooth in c as is r_1 , and, if $' = d/dc$,

$$(3.18) \quad -\Delta\psi' + c\theta(r_2)\psi' + \theta(r_2)\psi = r_1x_{\Omega_1}\psi' + r_1'\chi_{\Omega_1}\psi$$

in Ω . Multiplying (3.18) by ψ , integrating by parts, and applying (3.17) yield

$$(3.19) \quad \int_{\Omega} \theta(r_2)\psi_c^2 = r_1'(c) \int_{\Omega_1} \psi_c^2.$$

Now

$$\int_{\Omega} \theta(r_2)\psi_c^2 = \frac{1}{c} \left[r_1(c) \int_{\Omega_1} \psi_c^2 - \int_{\Omega} |\nabla\psi_c|^2 \right] \leq \frac{1}{c} (r_1(c) - \lambda_1(\chi_{\Omega_1})) \int_{\Omega_1} \psi_c^2.$$

Hence

$$r_1'(c) \int_{\Omega_1} \psi_c^2 \leq \frac{1}{c} (r_1(c) - \lambda_1(\chi_{\Omega_1})) \int_{\Omega_1} \psi_c^2,$$

so

$$\left(\frac{r_1(c)}{c} \right)' \leq \frac{-\lambda_1(\chi_{\Omega_1})}{c^2},$$

implying that

$$\frac{r_1(c)}{c} - \frac{r_1(c_0)}{c_0} \leq \frac{\lambda_1(\chi_{\Omega_1})}{c} - \frac{\lambda_1(\chi_{\Omega_1})}{c_0},$$

wherever $c_0 \leq c$. This last is equivalent to

$$(3.20) \quad \frac{r_1(c)}{c} \leq \frac{\lambda_1(\chi_{\Omega_1})}{c} + \frac{r_1(c_0) - \lambda_1(\chi_{\Omega_1})}{c_0}.$$

Since $\lambda_1(\chi_{\Omega_1}) = r_1(0)$, (3.20) in turn implies that

$$(3.21) \quad \frac{r_1(c)}{c} \leq \frac{\lambda_1(\chi_{\Omega_1})}{c} + r_1'(0).$$

Now consider

$$r_1'(0) = \frac{\int_{\Omega} \theta(r_2)\psi_0^2}{\int_{\Omega_1} \psi_0^2},$$

as given by (3.19). Let $\theta \equiv \theta(r_2)$. As $-\Delta\theta + \theta^2 = r_2\theta$ in Ω , we have

$$\int_{\Omega} |\nabla\theta|^2 + \int_{\Omega} \theta^3 = r_2 \int_{\Omega} \theta^2.$$

Since $\int_{\Omega} |\nabla\theta|^2 \geq \lambda_1(\Omega) \int_{\Omega} \theta^2$, it follows that

$$(3.22) \quad \int_{\Omega} \theta^3 \leq (r_2 - \lambda_1(\Omega)) \int_{\Omega} \theta^2.$$

Hölder's inequality implies that

$$\int_{\Omega} \theta^2 \leq \left[\int_{\Omega} (\theta^2)^{3/2} \right]^{2/3} \left[\int_{\Omega} 1^3 \right]^{1/3} = \left(\int_{\Omega} \theta^3 \right)^{2/3} |\Omega|^{1/3}.$$

Hence

$$(3.23) \quad |\Omega|^{-1/2} \left(\int_{\Omega} \theta^2 \right)^{3/2} \leq \int_{\Omega} \theta^3.$$

Combining (3.22) and (3.23), we have

$$(3.24) \quad \left(\int_{\Omega} \theta^2 \right)^{1/2} \leq (r_2 - \lambda_1(\Omega)) |\Omega|^{1/2}.$$

The Cauchy-Schwarz inequality implies that

$$(3.25) \quad \int_{\Omega} \theta \psi_0^2 \leq \left(\int_{\Omega} \theta^2 \right)^{1/2} \left(\int_{\Omega} \psi_0^4 \right)^{1/2}.$$

Combining (3.21), (3.24), and (3.25), we obtain

$$(3.26) \quad \frac{r_1(c)}{c} \leq \frac{\lambda_1(\chi_{\Omega_1})}{c} + (r_2 - \lambda_1(\Omega)) |\Omega|^{1/2} \frac{\left(\int_{\Omega} \psi_0^4 \right)^{1/2}}{\int_{\Omega_1} \psi_0^2}.$$

Since

$$\frac{\lambda_1(\chi_{\Omega_1})}{\int_{\Omega} |\nabla \psi_0|^2} = \frac{1}{\int_{\Omega_1} \psi_0^2},$$

(3.26) is equivalent to

$$\frac{r_1(c)}{c} \leq \frac{\lambda_1(\chi_{\Omega_1})}{c} + (r_2 - \lambda_1(\Omega)) \lambda_1(\chi_{\Omega_1}) |\Omega|^{1/2} \frac{\left(\int_{\Omega} \psi_0^4 \right)^{1/2}}{\int_{\Omega} |\nabla \psi_0|^2}.$$

It follows that, if $\lambda_1(r_1 \chi_{\Omega_1} - c \theta(r_2)) = 1$, then $r_1 \leq \lambda_1(\chi_{\Omega_1}) + c \lambda_1(\chi_{\Omega_1}) |\Omega|^{1/2} K_1 (r_2 - \lambda_1(\Omega))$, or, equivalently,

$$(3.27) \quad r_2 - \lambda_1(\Omega) \geq \frac{1}{c \lambda_1(\chi_{\Omega_1}) |\Omega|^{1/2} K_1} (r_1 - \lambda_1(\chi_{\Omega_1})).$$

An analogous argument shows that, if $\lambda_1(r_2 - e \theta(r_1 \chi_{\Omega_1})) = 1$, then

$$(3.28) \quad r_2 - \lambda_1(\Omega) \leq e |\Omega|^{1/2} K_2 (r_1 - \lambda_1(\chi_{\Omega_1})).$$

It follows that the curve $\lambda_1(r_1 \chi_{\Omega_1} - c \theta(r_2)) = 1$ lies above the curve $\lambda_1(r_2 - e \theta(r_1 \chi_{\Omega_1})) = 1$, and that the region in (r_1, r_2) parameter space determined by (2.22)–(2.23) contains the wedge given by reversing the inequalities in (3.27) and (3.28), provided that $e |\Omega|^{1/2} K_2 < 1 / c \lambda_1(\chi_{\Omega_1}) |\Omega|^{1/2} K_1$, or, equivalently, $ce < 1 / \lambda_1(\chi_{\Omega_1}) |\Omega| K_1 K_2$. As this last is our hypothesis, the result is established.

Proceeding in an analogous manner in the case where $l = 0$, we obtain the following result.

THEOREM 3.6. *Suppose that $ce < 1 / \lambda_1^2(\chi_{\Omega_1}) |\Omega| K_1^2$. Then the region in (r_1, r_2) parameter space determined by (2.22)–(2.23) for $l = 0$ contains the wedge given by*

$$(3.29) \quad r_2 - \lambda_1(\chi_{\Omega_1}) \leq \frac{1}{c \lambda_1(\chi_{\Omega_1}) |\Omega|^{1/2} K_1} (r_1 - \lambda_1(\chi_{\Omega_1}))$$

and

$$(3.30) \quad r_2 - \lambda_1(\chi_{\Omega_1}) \geq e \lambda_1(\chi_{\Omega_1}) |\Omega|^{1/2} K_1 (r_1 - \lambda_1(\chi_{\Omega_1})).$$

Remarks. (i) K_1 and K_2 are “geometric constants” depending only on Ω and Ω_1 .

(ii) It is natural to compare the result of Theorem 3.6 with that of Theorem 3.4. To this end, observe that (3.6) and (3.7) imply that the region in (r_1, r_2) space satisfying (2.22)–(2.23) for $l = 0$ is contained in the wedge emanating from $(\lambda_1(\chi_{\Omega_1}), \lambda_1(\chi_{\Omega_1}))$ given by the inequalities

$$e(r_1 - \lambda_1(\chi_{\Omega_1})) \leq r_2 - \lambda_1(\chi_{\Omega_1}) \leq \frac{1}{c} (r_1 - \lambda_1(\chi_{\Omega_1})).$$

Since Theorem 3.6 guarantees that the wedge given by

$$e\lambda_1(\chi_{\Omega_1})|\Omega|^{1/2}K_1(r_1 - \lambda_1(\chi_{\Omega_1})) \leq r_2 - \lambda_1(\chi_{\Omega_1})$$

$$\leq \frac{1}{c\lambda_1(\chi_{\Omega_1})|\Omega|^{1/2}K_1}(r_1 - \lambda_1(\chi_{\Omega_1}))$$

emanating from $(\lambda_1(\chi_{\Omega_1}), \lambda_1(\chi_{\Omega_1}))$ is contained within the region described by (2.22) and (2.23) for $l=0$, it follows that

$$\frac{1}{c\lambda_1(\chi_{\Omega_1})|\Omega|^{1/2}K_2} < \frac{1}{c}$$

and that $e < e\lambda_1(\chi_{\Omega_1})|\Omega|^{1/2}K_1$; i.e., $\lambda_1(\chi_{\Omega_1})|\Omega|^{1/2}K_1 > 1$. So, in Theorem 3.6, by "relaxing" the slopes of the boundary curves, we obtain a wedge in the interior of the region described by (2.22) and (2.23) for $l=0$ having the same vertex, namely, $(\lambda_1(\chi_{\Omega_1}), \lambda_1(\chi_{\Omega_1}))$, as the wedge (given in Theorem 3.1) containing the region described by (2.22) and (2.23) for $l=0$. Such is not the case for the "interior" wedge given by Theorem 3.4. However, the slopes of the boundary lines to the wedge given in Theorem 3.4 are the same as those of the boundary lines to the wedge given in Theorem 3.1. Consequently, the result of Theorem 3.6 is much better suited for an analysis involving parameter values (r_1, r_2) near the "critical" point $(\lambda_1(\chi_{\Omega_1}), \lambda_1(\chi_{\Omega_1}))$ than is the result of Theorem 3.4. However, the wedge of Theorem 3.4 subsumes the wedge of Theorem 3.6 for values of (r_1, r_2) sufficiently far removed from $(\lambda_1(\chi_{\Omega_1}), \lambda_1(\chi_{\Omega_1}))$ (see Fig. 3.3).

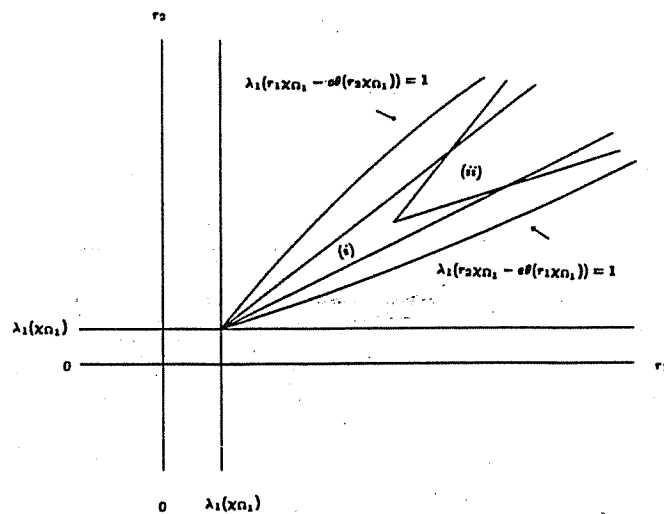


FIG. 3.3. Comparison of the wedges interior to the region given by (2.22)–(2.23) when $l=0$ and $c, e \in (0, 1)$. Wedge (i) is given by Theorem 3.6; wedge (ii) is given by Theorem 3.4.

Before comparing the changes in the predictions of the model as l changes from zero to one, we require one additional estimate: namely, an upper (or "outside") bound on the upper boundary $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2 - e\theta(r_1\chi_{\Omega_1}))) = 1$ of the region determined by (2.24)–(2.25) when $l=1$. Another caveat is in order at this point. Throughout this paper, we have implicitly assumed that Ω_1 is a preserve within the larger habitat Ω ; i.e., $\Omega_1 \subset \Omega$. However, all the preceding results obtain under the weaker assumptions that $\Omega_1 \subset \Omega$ and $\Omega - \Omega_1 \neq \emptyset$. However, in the following result, we must assume that $\Omega_1 \subset \Omega$.

So now assume that $\bar{\Omega}_1 \subset \Omega$ and consider $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2 - e\theta(r_1\chi_{\Omega_1}))) = 1$. Let ψ_0 now denote the unique positive solution to (3.10) satisfying $\max_{x \in \bar{\Omega}} \psi_0 = 1$ and choose $K_3 \in (0, 1)$ so that $K_3\chi_{\Omega_1} \leq \psi_0$. Note that K_3 is a "geometric constant" depending only on Ω and Ω_1 . Since $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2 - e\theta(r_1\chi_{\Omega_1}))) = 1$, there is a $\varphi > 0$ in Ω so that

$$(3.31) \quad \begin{aligned} -\Delta\varphi + c\theta(r_2 - e\theta(r_1\chi_{\Omega_1}))\varphi &= r_1\chi_{\Omega_1}\varphi \quad \text{in } \Omega, \\ \varphi &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

Let us first consider $\theta(r_1\chi_{\Omega_1})$. Let $\bar{\theta} = \gamma\psi_0$, where γ is a positive constant. Observe that

$$\begin{aligned} -\Delta\bar{\theta} &= \lambda_1(\chi_{\Omega_1})\chi_{\Omega_1}\bar{\theta} \\ &= r_1\chi_{\Omega_1}\bar{\theta} + (\lambda_1(\chi_{\Omega_1}) - r_1)\chi_{\Omega_1}\bar{\theta} - \bar{\theta}^2 + \bar{\theta}^2 \\ &= r_1\chi_{\Omega_1}\bar{\theta} - \bar{\theta}^2 + \bar{\theta}[\gamma\psi_0 + (\lambda_1(\chi_{\Omega_1}) - r_1)\chi_{\Omega_1}] \\ &\geq r_1\chi_{\Omega_1}\bar{\theta} - \bar{\theta}^2 + \bar{\theta}\chi_{\Omega_1}(\gamma K_3 + (\lambda_1(\chi_{\Omega_1}) - r_1)) \\ &\geq r_1\chi_{\Omega_1}\bar{\theta} - \bar{\theta}^2, \end{aligned}$$

provided that $\gamma \geq r_1 - \lambda_1(\chi_{\Omega_1})/K_3$. Since $\lim_{r \rightarrow \lambda_1(\chi_{\Omega_1})^+} \theta(r\chi_{\Omega_1}) = 0$ in $C_0^{1+\alpha}(\bar{\Omega})$, there is an $r \in (\lambda_1(\chi_{\Omega_1}), r_1)$ so that

$$\bar{\theta} = \theta(r\chi_{\Omega_1}) < \left(\frac{r_1 - \lambda_1(\chi_{\Omega_1})}{K_3} \right) \psi_0 \quad \text{in } \Omega.$$

Since $-\Delta\bar{\theta} \leq r_1\chi_{\Omega_1}\bar{\theta} - \bar{\theta}^2$, it follows from the method of upper and lower solutions and the uniqueness of $\theta(r_1\chi_{\Omega_1})$ that

$$(3.32) \quad \bar{\theta}(r_1\chi_{\Omega_1}) \leq \left(\frac{r_1 - \lambda_1(\chi_{\Omega_1})}{K_3} \right) \psi_0.$$

It follows from (3.32) and the choice of ψ_0 that

$$\theta(r_2 - e\theta(r_1\chi_{\Omega_1})) \geq \theta(r_2 - [e(r_1 - \lambda_1(\chi_{\Omega_1}))/K_3]).$$

Hence, if $\phi > 0$ in Ω and $\lambda^* > 0$ are such that

$$(3.33) \quad \begin{aligned} -\Delta\phi + c\theta(r_2 - [e(r_1 - \lambda_1(\chi_{\Omega_1}))/K_3])\phi &= \lambda^*\chi_{\Omega_1}\phi \quad \text{in } \Omega, \\ \phi &= 0 \quad \text{on } \partial\Omega, \end{aligned}$$

comparison with (3.31) shows that $r_1 \geq \lambda^*$.

Let us now consider (3.33). Let z_0 now denote the unique solution to (3.11) satisfying $\max_{x \in \bar{\Omega}} z_0 = 1$. Then $z_0 \geq K_4\chi_{\Omega_1}$, for some constant $K_4 \in (0, 1)$ depending only on Ω and Ω_1 . It is easy to observe that, if $s > \lambda_1(\Omega)$, then $(s - \lambda_1(\Omega))z_0$ is a lower solution to

$$(3.34) \quad \begin{aligned} -\Delta w &= sw - w^2 \quad \text{in } \Omega, \\ w &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

Since any large enough constant is an upper solution to (3.34), $(s - \lambda_1(\Omega))z_0 \leq \theta(s)$, and hence, $K_4(s - \lambda_1(\Omega))\chi_{\Omega_1} \leq \theta(s)$ for any $s > \lambda_1(\Omega)$. Since $\theta(s) = 0$ for $s \leq \lambda_1(\Omega)$, it is immediate that $\theta(s) \geq K_4(s - \lambda_1(\Omega))\chi_{\Omega_1}$ for all $s \in \mathbb{R}$. Now compare (3.33) with the eigenvalue problem

$$(3.35) \quad \begin{aligned} -\Delta y + c\{r_2 - [e(r_1 - \lambda_1(\chi_{\Omega_1}))/K_3] - \lambda_1(\Omega)\}K_4\chi_{\Omega_1}y &= \mu\chi_{\Omega_1}y \quad \text{in } \Omega, \\ y &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

A simple integration by parts argument guarantees that if (3.35) admits a positive solution, $\lambda^* > \mu$. Notice that there is such a y when

$$\mu - c\{r_2 - [e(r_1 - \lambda_1(\chi_{\Omega_1})) / K_3] - \lambda_1(\Omega)\}K_4 = \lambda_1(\chi_{\Omega_1}).$$

Since $r_1 \geq \lambda^*$, if $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2 - e\theta(r_1\chi_{\Omega_1}))) = 1$, it follows that

$$r_1 \geq \lambda_1(\chi_{\Omega_1}) + c\{r_2 - [e(r_1 - \lambda_1(\chi_{\Omega_1})) / K_3] - \lambda_1(\Omega)\}K_4$$

or, equivalently,

$$(3.36) \quad r_2 - \lambda_1(\Omega) \leq \left(\frac{K_3 + ceK_4}{cK_3K_4} \right) (r_1 - \lambda_1(\chi_{\Omega_1})).$$

We have established the following result.

THEOREM 3.7. Assume that $\bar{\Omega}_1 \subset \Omega$. Let ψ_0 (respectively, z_0) denote the unique positive solution to (3.10) (respectively, (3.11)) satisfying $\max_{x \in \bar{\Omega}} \psi_0 = 1$ (respectively, $\max_{x \in \bar{\Omega}} z_0 = 1$). Let $K_3, K_4 \in (0, 1)$ be such that

$$\psi_0 \geq K_3\chi_{\Omega_1} \quad \text{and} \quad z_0 \geq K_4\chi_{\Omega_1}.$$

If $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2 - e\theta(r_1\chi_{\Omega_1}))) \leq 1$, then (3.36) holds. In particular, (3.36) holds if (2.24) is satisfied, and, if (3.36) not satisfied, (2.26) holds so that $\lim_{t \rightarrow \infty} u(x, t) = 0$.

Remark. The conditions implying that there is coexistence for some (r_1, r_2) in the case where $l = 1$, namely, $ce < 1/\lambda_1(\Omega_1)|\Omega|K_1K_2$ and (2.22)–(2.23), can only hold if r_1 and r_2 satisfy (3.36).

4. Comparisons and conclusions. We may now establish that, if $c, e \in (0, 1)$, the model (1.1) admits the behavior suggested by Janzen in [14], [15]. Namely, we show that there are values (r_1, r_2) so that, when $l = 0$, long-time persistence of positive solutions to (1.1) is assured, as in Corollary 2.5(i), but, when $l = 1$, species u can be expected to go extinct. (Recall that r_1, r_2, c , and e are obtained by rescaling the original Lotka-Volterra system and hence depend not just on R_1, R_2, C , and E , but also on d_1, d_2, B , and F .)

To establish this, our main result, we show that, if $c, e \in (0, 1)$, then the curves $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2)) = 1$ and $\lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1})) = 1$ intersect for some value $r_1 > \lambda_1(\chi_{\Omega_1})$. Why does this establish the result? We know that for parameter values (r_1, r_2) lying above $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2 - e\theta(r_1\chi_{\Omega_1}))) = 1$, the u component of any positive solution to (1.1) tends to zero as time tends to infinity, for $l = 1$. We also know that this curve lies above the curve $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2)) = 1$ for $r_1 > \lambda_1(\chi_{\Omega_1})$. For $l = 0$, the curve $\lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1})) = 1$ is the lower boundary of the region in which long-term persistence of positive solutions to (1.1) is assured. Consequently, we see that the main result of the paper follows from demonstrating that $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2)) = 1$ and $\lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1})) = 1$ intersect, since the curves $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2)) = 1$ and $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2 - e\theta(r_1\chi_{\Omega_1}))) = 1$ emanate from $(\lambda_1(\chi_{\Omega_1}), \lambda_1(\Omega))$, the curve $\lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1})) = 1$ emanates from $(\lambda_1(\chi_{\Omega_1}), \lambda_1(\chi_{\Omega_1}))$, and $\lambda_1(\Omega) < \lambda_1(\chi_{\Omega_1})$ (by Proposition 3.3). Recall from Theorem 3.5 that if, in addition,

$$ce < \frac{1}{\lambda_1(\chi_{\Omega_1})|\Omega|K_1K_2},$$

then $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2)) = 1$ is the upper boundary of the region in (r_1, r_2) parameter space for which we know long-term persistence obtains for positive solutions to (1.1) in the case of $l = 1$.

Before establishing the intersection of the two designated curves, three remarks are in order. First, the result shows that there is an open set in (r_1, r_2) parameter space where for $l=0$, positive solutions to (1.1) are long-term coexistent, but, for $l=1$, the u component of any positive solution to (1.1) is driven to extinction as time tends to infinity. For such values of (r_1, r_2) , this property continues to obtain if $r_1\chi_{\Omega_1}$ in the first equation is replaced by $r_1(\chi_{\Omega_1} + \varepsilon l\chi_{\Omega - \Omega_1})$ for $0 < \varepsilon \ll 1$ and dependent on (r_1, r_2) . *Second, the result also simultaneously shows that at least for $ce < 1/\lambda_1(\chi_{\Omega_1})|\Omega|K_1K_2$, there are values (r_1, r_2) for which the model predicts long-term persistence of positive solutions to (1.1) for both $l=0$ and $l=1$.* Our initial caveat is not diminished: The models predict the behavior suggested by Janzen *only sometimes*, and effective refuge design must be based on detailed biological knowledge of a specific situation. Third, it follows from the result that all values of the parameters (r_1, r_2) for which long-term persistence of positive solutions to (1.1) is assured when $l=0$ and which are sufficiently close to the "critical value" $(\lambda_1(\chi_{\Omega_1}), \lambda_1(\chi_{\Omega_1}))$ are also such that the u -component of any positive solution to (1.1) when $l=1$ tends to zero as time tends to infinity. The estimates of § 3 enable us to quantify in some sense the size of this region, and we do so once we establish that $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2)) = 1$ and $\lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1})) = 1$ intersect if $c, e \in (0, 1)$.

THEOREM 4.1. *For $c, e \in (0, 1)$, the curves $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2)) = 1$ and $\lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1})) = 1$ intersect for some $\bar{r}_1 > \lambda_1(\chi_{\Omega_1})$.*

Proof. Consider the continuous map $r_1 \rightarrow \lambda_1(r_1\chi_{\Omega_1} - c\theta(r_1))$, where $r_1 \geq \lambda_1(\chi_{\Omega_1})$. Since $\lambda_1(\chi_{\Omega_1}) > \lambda_1(\Omega)$ by Proposition 3.3, it follows that $\theta(\lambda_1(\chi_{\Omega_1})) > 0$ in Ω . Hence $\lambda_1(\chi_{\Omega_1})\chi_{\Omega_1} - c\theta(\lambda_1(\chi_{\Omega_1})) < \lambda_1(\chi_{\Omega_1})\chi_{\Omega_1}$ on Ω , so that $\lambda_1(\lambda_1(\chi_{\Omega_1})\chi_{\Omega_1} - c\theta(\lambda_1(\chi_{\Omega_1}))) > \lambda_1(\lambda_1(\chi_{\Omega_1})\chi_{\Omega_1}) = 1$. Now, however, $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_1)) < \lambda_1(r_1\chi_{\Omega_1} - cr_1)$ for $r_1 \geq \lambda_1(\chi_{\Omega_1})$, as $\theta(r_1) < r_1$. Since $c \in (0, 1)$, then $\lambda_1(\chi_{\Omega_1} - c) > 0$ necessarily exists and

$$\lambda_1(r_1\chi_{\Omega_1} - cr_1) = \frac{1}{r_1} \lambda_1(\chi_{\Omega_1} - c) \rightarrow 0 \quad \text{as } r_1 \rightarrow \infty.$$

Consequently, there is a smallest $\bar{r}_1 > \lambda_1(\chi_{\Omega_1})$ for which $\lambda_1(\bar{r}_1\chi_{\Omega_1} - c\theta(\bar{r}_1)) = 1$; i.e., (\bar{r}_1, \bar{r}_1) lies on the curve $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2)) = 1$. Since we know that, for any $e \in (0, 1)$ the curve $\lambda_1(r_2\chi_{\Omega_1} - e\theta(r_1\chi_{\Omega_1})) = 1$ lies below the line $r_2 = r_1$, the result follows immediately (see Fig. 4.1).

As indicated, as a corollary to Theorem 4.1, we have the following theorem, our main result.

THEOREM 4.2. *Suppose that $c, e \in (0, 1)$. Then there are values (r_1, r_2) of the modified growth rate parameters so that the following hold:*

(i) *If $l=0$ and $(u(x, t), v(x, t))$ is a solution to (1.1) with $u(x, 0) > \neq 0$ and $v(x, 0) > \neq 0$ for $x \in \Omega$, then there are functions w_1 and w_2 , positive for $x \in \Omega$, and $T > 0$ so that $u(x, t) \geq w_1(x)$ and $v(x, t) \geq w_2(x)$ for all $x \in \bar{\Omega}$ and $t \geq T$;*

(ii) *If $l=1$ and $(u(x, t), v(x, t))$ is a solution to (1.1) with $u(x, 0) > \neq 0$ and $v(x, 0) > \neq 0$ for $x \in \Omega$, then $\lim_{t \rightarrow \infty} u(x, t) = 0$, the limit being uniform for all $x \in \bar{\Omega}$.*

If, in addition, $ce < 1/\lambda_1(\chi_{\Omega_1})|\Omega|K_1K_2$, where K_1 and K_2 are as in the statement of Theorem 3.5, then there are also other values of the parameters (r_1, r_2) so that:

(iii) *If $l=1$ and $(u(x, t), v(x, t))$ is a solution to (1.1) with $u(x, 0) > \neq 0$ and $v(x, 0) > \neq 0$ then there are functions \bar{w}_1 and \bar{w}_2 , positive for $x \in \Omega$, and $T > 0$ so that $u(x, t) \geq \bar{w}_1(x)$ and $v(x, t) \geq \bar{w}_2(x)$ for all $x \in \bar{\Omega}$ and $t \geq T$.*

The condition $c, e \in (0, 1)$ is simply what is needed to ensure that the competition between species is weak enough that coexistence is possible when $l=0$; that is, when both species can increase in numbers only on Ω_1 . The biological significance of Theorem

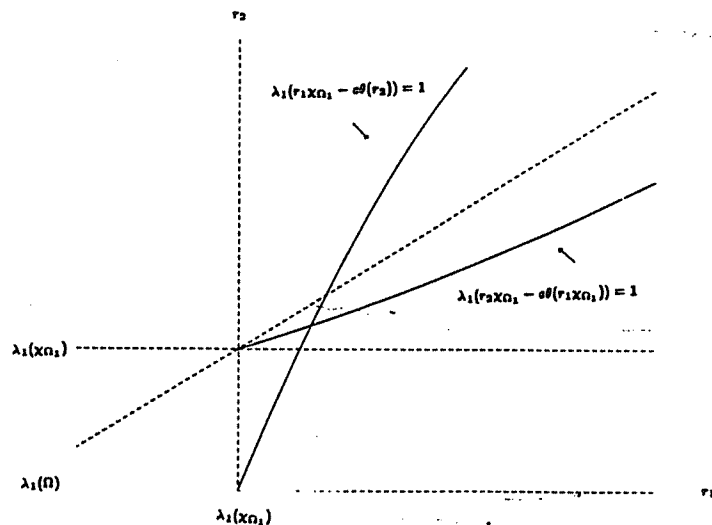


FIG. 4.1. Intersection of the curves $\lambda_1(r_1 x_{\Omega_1} - c\theta(r_2)) = 1$ and $\lambda_1(r_2 x_{\Omega_1} - e\theta(r_1 x_{\Omega_1})) = 1$ as demonstrated in Theorem 4.1. The curve $\lambda_1(r_2 x_{\Omega_1} - e\theta(r_1 x_{\Omega_1})) = 1$ is the lower boundary of the region where coexistence is guaranteed for $l=0$; the curve $\lambda_1(r_1 x_{\Omega_1} - c\theta(r_2)) = 1$ lies below the upper boundary of the region where u is excluded by v when $l=1$. Thus, points (r_1, r_2) lying above both curves but not too far above the curve $\lambda_1(r_2 x_{\Omega_1} - e\theta(r_1 x_{\Omega_1})) = 1$ correspond to parameter values for which coexistence is predicted for $l=0$ (i.e., neither can reproduce itself $\Omega - \Omega_1$), but exclusion of the first competitor is predicted when $l=1$ (i.e., the second competitor can reproduce itself in $\Omega - \Omega_1$).

4.2 is that it shows the qualitative aspects of Janzen's observations in [14], [15] can be reproduced by simple reaction-diffusion models for at least some parameter values. To proceed further, we must obtain more explicit quantitative information about the locations of the curves $\lambda_1(r_1 x_{\Omega_1} - c\theta(r_2 x_{\Omega_1})) = 1$, $\lambda_1(r_2 x_{\Omega_1} - e\theta(r_1 x_{\Omega_1})) = 1$ and the other curves bounding regions of coexistence or exclusion. To the extent that it is possible, we try to make our quantitative estimates in the same spirit as in [7], [8], that is, in forms that separate the coefficients r_1, r_2, c , and e from geometric quantities such as $\lambda_1(x_{\Omega_1})$.

Suppose now, in addition to the hypotheses of Theorem 4.2, that $\bar{\Omega}_1 \subset \Omega$. It follows from Theorem 3.7 that, if $\lambda_1(r_1 x_{\Omega_1} - c\theta(r_2 - e\theta(r_1 x_{\Omega_1}))) = 1$, then

$$r_2 \cong \lambda_1(\Omega) + \left(\frac{K_3 + ceK_4}{cK_3K_4} \right) (r_1 - \lambda_1(x_{\Omega_1})).$$

On the other hand, from Theorem 3.1, if $\lambda_1(r_2 x_{\Omega_1} - e\theta(r_1 x_{\Omega_1})) = 1$,

$$r_2 \cong er_1 + (1-e)\lambda_1(x_{\Omega_1}).$$

So the two curves $\lambda_1(r_1 x_{\Omega_1} - c\theta(r_2 - e\theta(r_1 x_{\Omega_1}))) = 1$ and $\lambda_1(r_2 x_{\Omega_1} - e\theta(r_1 x_{\Omega_1})) = 1$ cannot meet prior to the intersection of the lines

$$(4.1) \quad r_2 = \lambda_1(\Omega) + \left(\frac{K_3 + ceK_4}{cK_3K_4} \right) (r_1 - \lambda_1(x_{\Omega_1}))$$

and

$$(4.2) \quad r_2 = er_1 + (1-e)\lambda_1(x_{\Omega_1}).$$

It is a simple matter to calculate that (4.1) and (4.2) intersect when

$$(4.3) \quad r_1 = r_1^* = \lambda_1(\chi_{\Omega_1}) + \frac{cK_3K_4}{K_3 + ce(1-K_3)K_4} (\lambda_1(\chi_{\Omega_1}) - \lambda_1(\Omega)).$$

Since $K_3 \in (0, 1)$ and $\lambda_1(\chi_{\Omega_1}) > \lambda_1(\Omega)$, $r_1^* > \lambda_1(\chi_{\Omega_1})$. It follows that, if (r_1, r_2) is such that (2.22)–(2.23) hold for $l=0$ and $r_1 < r_1^*$, then the conclusions of Theorem 4.2 parts (i) and (ii) obtain.

Now consider $\lambda_1(r_1\chi_{\Omega_1} - c\theta(r_2\chi_{\Omega_1})) = 1$, the upper boundary of the region in (r_1, r_2) parameter space, where long-term persistence of positive solutions to (1.1) is assured when $l=0$. Make a final additional assumption that

$$ce < \frac{1}{\lambda_1^2(\chi_{\Omega_1})|\Omega|K_1^2}.$$

Then the ray

$$(4.4) \quad r_2 = \lambda_1(\chi_{\Omega_1}) + \frac{1}{c\lambda_1(\chi_{\Omega_1})|\Omega|^{1/2}K_1} (r_1 - \lambda_1(\chi_{\Omega_1})),$$

$r_1 \geq \lambda_1(\chi_{\Omega_1})$, (given in Theorem 3.6) lies within the region in (r_1, r_2) parameter space, where long-term persistence of positive solutions to (1.1) is assured when $l=0$. The lines (4.1) and (4.4) meet when $r_1 = r_1^{**}$, where

$$(4.5) \quad r_1^{**} = \lambda_1(\chi_{\Omega_1}) + c \left[\frac{K_1K_3K_4\lambda_1(\chi_{\Omega_1})|\Omega|^{1/2}}{(K_3 + ceK_4)(\lambda_1(\chi_{\Omega_1})|\Omega|^{1/2}K_1) - (K_3K_4)} \right] (\lambda_1(\chi_{\Omega_1}) - \lambda_1(\Omega)).$$

That r_1^{**} in (4.5) is greater than $\lambda_1(\chi_{\Omega_1})$ follows, since

$$\frac{1}{\lambda_1(\chi_{\Omega_1})|\Omega|^{1/2}K_1} < 1$$

(see remark (ii) following Theorem 3.6) and

$$\frac{K_3 + ceK_4}{K_3K_4} > \frac{1}{K_4} > 1.$$

That, in fact, $r_1^{**} > r_1^*$ follows, since

$$ce < \frac{1}{\lambda_1^2(\chi_{\Omega_1})|\Omega|K_1^2}.$$

Consequently, as long as $r_1 \in (\lambda_1(\chi_{\Omega_1}), r_1^{**})$, there will be parameter values (r_1, r_2) so that the results of Theorem 4.2 parts (i) and (ii) hold. We summarize as follows (see Fig. 4.2).

THEOREM 4.3. Suppose that the assumptions of Theorem 4.2 hold. Suppose additionally that $\bar{\Omega} \subset \Omega$. Let r_1^* be given by (4.3). Then $\lambda_1(\chi_{\Omega_1}) < r_1^*$ and, moreover:

(i) If (r_1, r_2) is such that (2.22)–(2.23) hold for $l=0$ and $r_1 \in (\lambda_1(\chi_{\Omega_1}), r_1^*)$, then the conclusions of Theorem 4.2 parts (i) and (ii) hold.

Suppose further that

$$ce < \frac{1}{\lambda_1^2(\chi_{\Omega_1})|\Omega|K_1^2}.$$

Let r_1^{**} be given by (4.5). Then $r_1^* < r_1^{**}$ and, moreover:

(ii) If (r_1, r_2) is such that (2.22)–(2.23) hold for $l=0$, $r_1 \in (r_1^*, r_1^{**})$, then the

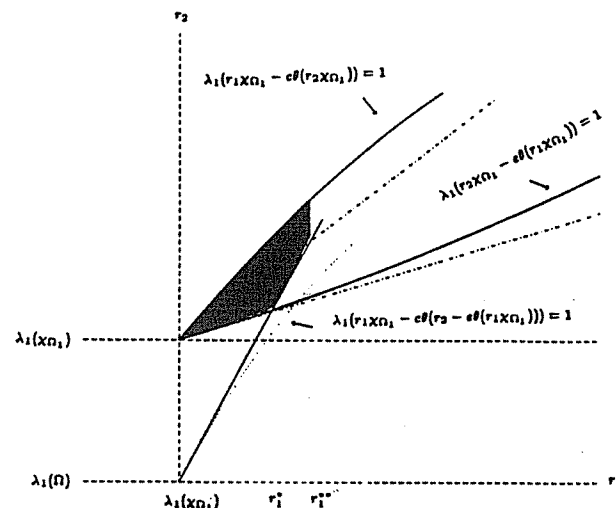


FIG. 4.2. The shaded region is described by Theorem 4.3. If $c, e \in (0, 1)$, then the competition between species is weak enough that, for $l=0$, that is, when the part of Ω favoring the increase in numbers of both species is Ω_1 , there are values of (r_1, r_2) for which coexistence is assured. Those values lie between the curves $\lambda_1(r_1 x_{\Omega_1} - c\theta(r_2 x_{\Omega_1})) = 1$ and $\lambda_1(r_2 x_{\Omega_1} - e\theta(r_1 x_{\Omega_1})) = 1$. In the region of the (r_1, r_2) plane lying above the curve $\lambda_1(r_1 x_{\Omega_1} - c\theta(r_2 - e\theta(r_1 x_{\Omega_1}))) = 1$, the second competitor excludes the first when $l=1$, that is, when the favorable habitat for the first is only Ω_1 but for the second is all of Ω . The mechanism of exclusion is that described by Janzen: The second competitor increases in numbers on $\Omega - \Omega_1$ to an extent that, by dispersal into Ω_1 , it tips the balance of competition. The line whose equation is given in (4.1) is an upper bound for the curve $\lambda_1(r_1 x_{\Omega_1} - c\theta(r_2 - e\theta(r_1 x_{\Omega_1}))) = 1$, so, for values of (r_1, r_2) above that line but between the curves $\lambda_1(r_1 x_{\Omega_1} - c\theta(r_2 x_{\Omega_1})) = 1$ and $\lambda_1(r_2 x_{\Omega_1} - e\theta(r_1 x_{\Omega_1})) = 1$, the effects described by Janzen are predicted by our models. That region is the shaded region in the figure. In fact, the region where the effects are predicted may extend further upward and to the right than is shown by shading, but we do not have estimates to quantify how far. The shaded region includes all points (r_1, r_2) admitting coexistence with $l=0$ and with $r_1 < r_1^*$. Those points correspond to situations where the effective growth rate r_1 is only slightly higher than what is needed for the first population to persist in the absence of the second. In estimating how far upward and to the right the shaded region should extend, we need the additional hypotheses of part (ii) of Theorem 4.3. These may be artifacts of the analysis; it is possible they could be removed by improving the mathematics. They will be satisfied if Ω_1 is completely surrounded by $\Omega - \Omega_1$ and the competition is relatively weak. In that case, the shaded region extends at least until the line given in (4.1) intersects that given by (4.4) at $r_1 = r_1^{**}$. For $r_1^* < r_1 < r_1^{**}$ the Janzen effect is predicted for those values of (r_1, r_2) lying between the line given in (4.1) and the top of the region of coexistence for $l=0$. Thus, even if r_1 is further away from the value $r_1 = \lambda_1(x_{\Omega_1})$ required for the first species to persist by itself, the Janzen effect is predicted if r_2 is relatively large so that a moderate increase in the effective growth rate r_2 of the second competitor on Ω_1 would result in exclusion of the first competitor. That result is not surprising, since either increasing the growth rate r_2 of the second competitor on Ω_1 or expanding the habitat favorable to the second competitor to all of Ω by letting $l=1$ but leaving r_2 fixed would have the effect of allowing the second competitor to increase in numbers more rapidly, in the first case by reproducing faster in a small area and in the second by reproducing at the same rate but throughout a larger area. In either case, the result would be to shift the balance of competition in favor of the second competitor, sometimes to the point of excluding the first.

conclusions of Theorem 4.2 parts (i) and (ii) hold when

$$r_2 \geq \lambda_1(\Omega) + \left(\frac{K_3 + ceK_4}{cK_3K_4} \right) (r_1 - \lambda_1(x_{\Omega_1})).$$

Remarks. Theorem 4.3 implies that the effects described in [14], [15] are predicted by our models wherever the parameter r_1 , measuring the effective population growth rate of the first competitor is close to the critical value $\lambda_1(x_{\Omega_1})$ required to sustain a population of the first competitor in the absence of the second. In this case, "close"

means $\lambda_1(\chi_{\Omega_1}) < r_1 < r_1^*$ with r_1^* given by (4.3). If $\lambda_1(\chi_{\Omega_1}) < r_1 < r_1^*$, then the effects described by Janzen are predicted by our models whenever the remaining coefficients of the model admit coexistence when $l=0$, i.e., when neither population is allowed to increase in numbers in the "buffer zone" $\Omega - \Omega_1$. It is easy to see that $\partial r_1^*/\partial e < 0$ and $\partial r_1^*/\partial c > 0$. Hence, if the coefficient c measuring the impact of the second competitor on the first is increased, then so is the range of values of r_1 for which the Janzen effect is predicted. Conversely, if the coefficient e measuring the competitive impact of the first species on the second is increased, then the condition $r_1 < r_1^*$ becomes more restrictive and that range of values shrinks. If $\bar{\Omega} \subset \Omega$ and the strength of competition is not too great, then part (ii) of Theorem 4.3 holds. If $r_1^* < r_1 < r_1^{**}$, then the Janzen effect may still occur for some values of r_2 , specifically those near the upper boundary of the region in the (r_1, r_2) plane in which coexistence is predicted in the case where $l=0$ corresponding to close cultivation or other management of the "buffer zone" $\Omega - \Omega_1$. Thus, even for larger values of r_1 , the effect may still occur if a small increase in the effective growth rate r_2 of the second population would result in the exclusion of the first even in the case where $l=0$. The dependence of r_1^* and r_1^{**} on Ω_1 is much more subtle and complicated. It could, in principle, be examined by an analysis of K_3 and K_4 , but that would require a separate article. We can, however, use the results of § 3 to make some observations about the effects of varying Ω_1 when all other coefficients in the system (including l) remain fixed.

Thus far, we have demonstrated that, for appropriate and quantifiable ranges of the parameters r_1 , r_2 , c , and e , the population dynamics inside a preserve Ω_1 of two species modeled by (1.1) exhibit the sensitivity to the surroundings of the preserve suggested by Janzen in [14], [15]. The qualitative aspects of our conclusions regarding (1.1) as the "environmental" or "interference" parameter changes from zero to one are relatively insensitive to the choice of preserve $\bar{\Omega}_1$, as long as $\bar{\Omega}_1$ is a domain properly contained within the larger habitat Ω ; i.e., $\bar{\Omega}_1 \subset \Omega$. However, the quantitative aspects of our conclusions are heavily dependent on the choice of Ω_1 . It is therefore of interest to compare and contrast the prescriptions of this section and the preceding one as Ω_1 itself is considered as a parameter. In general, this is a delicate and difficult issue which we will not pursue at length at this point. In [6] we considered the effects on a single population of changing the location of a region of favorable habitat within a larger unfavorable region. The following analysis addresses the corresponding question in the context of competition. It does not treat the effects described in [14], [15] but is motivated by related questions about refuge design such as those discussed in [4]–[6] in the case of a single species. Specifically, the results of § 3 make possible some immediate observations regarding the predictions about (1.1) if Ω_1 is replaced by a substantially smaller refuge Ω_2 within Ω (Ω_2 not necessarily contained within Ω_1), and we conclude this article with these observations.

We know from Theorem 3.4 that the wedge determined by

$$(4.6) \quad r_2 \geq er_1 + \lambda_1(\Omega_1)$$

and

$$(4.7) \quad r_2 \leq \frac{1}{c}r_1 - \frac{1}{c}\lambda_1(\Omega_1)$$

is contained within the region of the (r_1, r_2) plane where coexistence is predicted as described by (2.22)–(2.23) for $l=0$ and Ω_1 . Now, Theorem 3.1 states that, for $l=0$ and Ω_2 , the region described by (2.22)–(2.23) is contained within the wedge determined

by

$$(4.8) \quad r_2 \cong er_1 + (1-e)\lambda_1(\chi_{\Omega_2})$$

and

$$(4.9) \quad r_2 \cong \frac{1}{c}r_1 - \frac{(1-c)}{c}\lambda_1(\chi_{\Omega_2}),$$

so that the region where coexistence is predicted for $l=0$ and Ω_2 is contained in this new wedge. The wedge given by (4.8) and (4.9) will be contained within the wedge given by (4.6) and (4.7), provided that

$$(4.10) \quad \lambda_1(\chi_{\Omega_2}) > \left(\max \left\{ \frac{1}{1-c}, \frac{1}{1-e} \right\} \right) \lambda_1(\Omega_1).$$

The biological meaning of the wedge in (4.8) and (4.9) being contained in that given by (4.6) and (4.7) is that the growth rates r_1 and r_2 must be larger and more closely balanced for the competitors to coexist if they can increase their numbers only on Ω_2 than if they can increase their numbers only on Ω_1 . The implication is that Ω_1 is a better refuge, since the conditions for persistence are less restrictive for Ω_1 than for Ω_2 . Condition (4.10) holds if the size $|\Omega_2|$ of Ω_2 is sufficiently small, since $\lambda_1(\chi_{\Omega_2})$ goes to infinity as $|\Omega_2|$ shrinks toward zero; see [4, Thm. 3.1]. Thus, a refuge Ω_2 that is sufficiently small is less likely to sustain competing populations than a larger refuge Ω_1 independent of their relative location in Ω , provided that neither population may increase its numbers in the "buffer zones" $\Omega - \Omega_i$.

In the case where one species can reproduce itself and thus increase its numbers in $\Omega - \Omega_i$ and the other cannot, i.e., the case where $l=1$, the effects of the geometry of Ω_i on coexistence are much more complex. Suppose that $l=1$. If the hypothesis $ce < 1/\lambda_1(\Omega_1)|\Omega|K_1K_2$ of Theorem 3.5 is satisfied and remains true when Ω_1 is replaced by Ω_2 (recall that K_1, K_2 depend on Ω_i and change along with $\lambda_1(\Omega_i)$), then, for both Ω_1 and Ω_2 , there is a wedge-like region in the (r_1, r_2) plane determined by (2.22) and (2.23) for which our models predict coexistence. The region in (r_1, r_2) parameter space described by (2.22) and (2.23) for $l=1$ and Ω_1 emanates from $(r_1, r_2) = (\lambda_1(\chi_{\Omega_1}), \lambda_1(\Omega))$, while the region described by (2.22) and (2.23) for $l=1$ and Ω_2 emanates from $(r_1, r_2) = (\lambda_1(\chi_{\Omega_2}), \lambda_1(\Omega))$. If $\lambda_1(\chi_{\Omega_1}) \neq \lambda_1(\chi_{\Omega_2})$, then the regions may intersect but neither contains the other. If (4.10) holds, then $\lambda_1(\chi_{\Omega_2}) > \lambda_1(\Omega_1) > \lambda_1(\chi_{\Omega_1})$, and hence neither of the regions can be contained within the other. Assume now, in addition to (4.10), that

$$(4.11) \quad ce < \alpha(\Omega_1, \Omega_2),$$

where

$$\alpha(\Omega_1, \Omega_2) = \min \left\{ \frac{1}{\lambda_1(\chi_{\Omega_1})|\Omega|K_1(\Omega_1)K_2(\Omega_1)}, \frac{1}{\lambda_1(\chi_{\Omega_2})|\Omega|K_1(\Omega_2)K_2(\Omega_2)}, \frac{1}{\lambda_1(\chi_{\Omega_2})|\Omega|K_1(\Omega_2)K_2(\Omega_1)} \right\},$$

and $K_i(\Omega_j)$ for $i, j = 1, 2$ are as given in Theorem 3.5. Then, if $\lambda_1(r_2 - e\theta(r_1\chi_{\Omega_1})) = 1$,

$$(4.12) \quad r_2 - \lambda_1(\Omega) \cong e|\Omega|^{1/2}K_2(\Omega_1)(r_1 - \lambda_1(\chi_{\Omega_1})),$$

while, if $\lambda_1(r_1\chi_{\Omega_2} - c\theta(r_2)) = 1$, then

$$(4.13) \quad r_2 - \lambda_1(\Omega) \cong \frac{1}{c\lambda_1(\chi_{\Omega_2})|\Omega|^{1/2}K_1(\Omega_2)}(r_1 - \lambda_1(\chi_{\Omega_2})).$$

We see that the regions described by (2.22)–(2.23) for $l=1$ for Ω_1 and for Ω_2 must intersect provided the lines (4.12) and (4.13) intersect at a point (r_1, r_2) with $r_1 > \lambda_1(\chi_{\Omega_2})$. It is an easy matter to determine that (4.12) and (4.13) meet at a point (\hat{r}_1, \hat{r}_2) , where

$$(4.14) \quad \hat{r}_1 = \frac{\frac{\lambda_1(\chi_{\Omega_2})}{c\lambda_1(\chi_{\Omega_2})|\Omega|^{1/2}K_1(\Omega_2)} - e|\Omega|^{1/2}K_2(\Omega_1)\lambda_1(\chi_{\Omega_1})}{\frac{1}{c\lambda_1(\chi_{\Omega_2})|\Omega|^{1/2}K_1(\Omega_2)} - e|\Omega|^{1/2}K_2(\Omega_1)}$$

By (4.11), the denominator of the right-hand side of (4.14) is positive, so that

$$\begin{aligned} \hat{r}_1 &> \frac{\frac{\lambda_1(\chi_{\Omega_2})}{c\lambda_1(\chi_{\Omega_2})|\Omega|^{1/2}K_1(\Omega_2)} - e|\Omega|^{1/2}K_2(\Omega_1)\lambda_1(\chi_{\Omega_2})}{\frac{1}{c\lambda_1(\chi_{\Omega_2})|\Omega|^{1/2}K_1(\Omega_2)} - e|\Omega|^{1/2}K_2(\Omega_1)} \\ &= \lambda_1(\chi_{\Omega_2}). \end{aligned}$$

Thus, if Ω_2 is relatively small compared to Ω_1 (as required by (4.10)) and if competition is fairly weak (as required by (4.11)), then the ranges of parameters (r_1, r_2) where coexistence is predicted for refuges Ω_1 and Ω_2 overlap to some extent in the case where the second competitor can reproduce itself in the “buffer zone.” As noted previously, neither of those regions in parameter space contains the other.

In terms of refuge design, the preceding observations imply that when neither species may increase its numbers in the “buffer zone” $\Omega - \Omega_i$, then a refuge Ω_2 that is enough smaller than Ω_1 imposes greater restrictions on both of the growth rate parameters (r_1, r_2) for coexistence than does Ω_1 ; so Ω_2 can be regarded as a less secure refuge for the competing populations. This agrees with the conventional wisdom on refuge design. In the case where one species can increase in numbers in the “buffer zone” but the other cannot, a smaller refuge generally imposes different, but not necessarily stronger, conditions for coexistence than a larger one, so that direct comparison of the quality and effectiveness of the two refuges is impossible.

Beyond the specific implications of our discussion of the effects of replacing Ω_1 with Ω_2 , we can make two observations. First, the methods we have developed to study the problem of assessing the impact of “buffer zones” can also shed light on other geometric questions in refuge design. Second, as is already noted in [4]–[6] in the context of a single species, those questions may have very delicate and subtle answers. We intend to explore some of them further in future work.

5. General conclusions. We have established that the effects described by Janzen [14], [15] can be modeled by using reaction-diffusion systems with spatial variation in their coefficients. The reaction-diffusion models are obtained by adding diffusion as a dispersal mechanism to the classical Lotka-Volterra competition model. The specific situation of a refuge surrounded by a “buffer zone” is described by considering the spatial environment as a refuge Ω_1 on which both competitors have positive population growth rates surrounded by a “buffer zone” $\Omega - \Omega_1$ where the intrinsic growth rate of one competitor is zero. The second competitor might have zero growth rate on $\Omega - \Omega_1$ ($l=0$) or the same positive growth rate as on Ω_1 ($l=1$). If we assume that the two competitors can coexist when $l=0$, i.e., when neither can increase its population by reproduction in $\Omega - \Omega_1$, our analysis shows that there are generally values for the growth rates r_1 and r_2 that predict coexistence when $l=0$ but predict exclusion of the first competitor by the second when $l=1$, that is, when the second

competitor is permitted to increase in numbers on $\Omega - \Omega_1$ as well as Ω_1 . This corresponds to the phenomenon described by Janzen in [14], [15]. The mechanism in our models is the same as that proposed by Janzen: If the second competitor can raise its population density sufficiently on $\Omega - \Omega_1$, it can then flood Ω_1 by dispersal from $\Omega - \Omega_1$ and hence exclude the first competitor on Ω_1 as well as $\Omega - \Omega_1$. The mathematical analysis suggests that such an effect is more likely in two situations: when the growth rate r_1 of the first competitor is only slightly larger than what is needed to sustain a population in the absence of the second competitor or when the growth rate r_2 of the second competitor is only slightly less than what is needed to exclude the first when neither species can increase in numbers on the "buffer zone" $\Omega - \Omega_1$. The quantitative details of the phenomenon are affected by the geometry of Ω and Ω_1 and by the other parameters in the models, specifically the competition coefficients c and e . The results are based on eigenvalue inequalities. Since the eigenvalues vary continuously with the growth rate functions, we could replace $r_1\chi_{\Omega_1}$ with $r_1(\chi_{\Omega_1} + \varepsilon\chi_{\Omega - \Omega_1})$ for $\varepsilon \ll 1$, and the results would still hold. That means the effect described in [14], [15] would still be predicted even if the first competitor could increase its numbers to some extent on $\Omega - \Omega_1$, provided that the second competitor had a sufficient advantage in growth rate on $\Omega - \Omega_1$.

Many open questions remain regarding the effects of spatial variation on the dynamics of interacting populations. We examine some of these in articles currently in preparation. In future work, we plan to explore the quantitative aspects of the results of this article in more detail. We hope specifically to be able to determine numerical values for the sizes of Ω and Ω_1 , r_1 , r_2 , and so on, where our analysis is valid and which can be compared to the values for those quantities encountered in the field.

REFERENCES

- [1] H. AMANN, *Global existence for semilinear parabolic systems*, J. Reine Angew. Math., 360 (1985), pp. 47-83.
- [2] J. BLAT AND K. J. BROWN, *Bifurcation of steady-state solutions in predator-prey and competition systems*, Proc. Roy. Soc. Edinburgh Sect. A, 97 (1984), pp. 21-34.
- [3] R. S. CANTRELL, *Parameter ranges for the existence of solutions whose state components have specified nodal structure in coupled multiparameter systems of nonlinear Sturm-Liouville boundary value problems*, Proc. Roy. Soc. Edinburgh Sect. A, 119 (1991), pp. 347-365.
- [4] R. S. CANTRELL AND C. COSNER, *Diffusive logistic equations with indefinite weights: Population models in disrupted environments*, Proc. Roy. Soc. Edinburgh Sect. A, 112 (1989), pp. 293-318.
- [5] ———, *Diffusive logistic equations with indefinite weights: Population models in disrupted environments II*, SIAM J. Math. Anal., 22 (1991), pp. 1043-1064.
- [6] ———, *The effects of spatial heterogeneity in population dynamics*, J. Math. Biol., 29 (1991), pp. 315-338.
- [7] ———, *On the steady-state problem for the Volterra-Lotka competition model with diffusion*, Houston J. Math., 13 (1987), pp. 337-352.
- [8] ———, *On the uniqueness and stability of positive solutions in the Lotka-Volterra competition model with diffusion*, Houston J. Math., 15 (1989), pp. 341-361.
- [9] C. COSNER, *Eigenvalue problems with indefinite weights and reaction-diffusion models in population dynamics*, in Reaction-Diffusion Equations, K. J. Brown and A. A. Lacey, eds., Oxford University Press, Oxford, 1990.
- [10] C. COSNER AND A. C. LAZER, *Stable coexistence states in the Volterra-Lotka competition model with diffusion*, SIAM J. Appl. Math., 44 (1984), pp. 1112-1132.
- [11] D. G. DE FIGUEIREDO, *Positive solutions of semilinear elliptic problems*, in Lecture Notes in Mathematics 957, Springer, Berlin, 1982, pp. 34-88.
- [12] D. GILBARG AND N. S. TRUDINGER, *Elliptic Partial Differential Equations of Second Order*, Springer, Berlin, 1977.
- [13] D. HENRY, *Geometric Theory of Semilinear Parabolic Equations*, Lecture Notes in Mathematics 840, Springer, Berlin, 1981.

- [14] D. H. JANZEN, *No park is an island: Increase in interference from outside as park size decreases*, *Oikos*, 41 (1983), pp. 402-410.
- [15] ———, *The eternal external threat*, in *Conservation Biology (The Science of Scarcity and Diversity)*, M. E. Soulé, ed., Sinauer, Sunderland, MA, 1986.
- [16] S. LEVIN, *Population models and community structure in heterogeneous environments*, in *Mathematical Ecology*, T. G. Hallam and S. Levin, eds., *Biomathematics 17*, Springer-Verlag, Berlin, 1986.
- [17] J. LOPEZ-GOMEZ, *Positive periodic solutions of Lotka-Volterra reaction-diffusion systems*, *Differential Integrations Equations*, 5 (1992), pp. 55-72.
- [18] D. LUDWIG, D. G. ARONSON, AND H. F. WEINBERGER, *Spatial patterning of the spruce budworm*, *J. Math. Biol.*, 8 (1979), pp. 217-258.
- [19] A. MANES AND A. M. MICHELETTI, *Un' estensione della teoria variazionale classica degli autovalori per operatori ellittici del secondo ordine*, *Boll. Un. Mat. Ital.*, 7 (1973), pp. 285-301.
- [20] J. D. MURRAY AND R. P. SPERB, *Minimum domains for spatial patterns in a class of reaction-diffusion equations*, *J. Math. Biol.*, 18 (1983), pp. 169-184.
- [21] S. W. PACALA AND J. ROUGHGARDEN, *Spatial heterogeneity and interspecific competition*, *Theoret. Population Biol.*, 21 (1982), pp. 92-113.
- [22] J. SMOLLER, *Shock Waves and Reaction-Diffusion Equations*, Springer, Berlin, 1983.