EDGE-LINKED DYNAMICS AND THE SCALE-DEPENDENCE OF COMPETITIVE DOMINANCE

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ABSTRACT. Empirical data for several ecological systems suggest that how resource availability scales with patch geometry may influence the outcome of species interactions. To study this process, we assume a pseudoequilibrium to reduce the dimensionality of a two-consumer–two-resource model in which different resources are available in the interior of a patch versus at the edge. We analyze the resulting two species competition model to understand how the outcome of competition between consumers changes as the size of the patch changes, paying particular attention to the differential scaling of interior and edge-linked allochthonous resources as a function of patch size. We characterize conditions on patch size and parameters under which competitive exclusion, coexistence, and a reversal in competitive dominance occur. We find that the degree of exclusivity in the use of edge versus interior habitats influences the potential for transitions in competitive outcomes, but that differences in resource quality between interior and edge habitats can, depending on the scenario, have either qualitative or quantitative influences on the transitions. The work highlights the importance of patch size to understanding species interactions and demonstrates that competitive dominance can be a scale-dependent trait.

1. **Introduction.** Issues of scale are increasingly seen as critical to our understanding of ecological phenomena. Though much attention has been given to the problem of "scaling up" across levels of observation or complexity ([32, 39], [56]), the term scaling is also used in a geometric sense, referring to situations where the physical size of a patch or system changes (e.g., [20, 29, 30]). Well-known examples include the species-area relations of island biogeography (see [9]) and the "critical patch size" phenomenon, where populations can only persist on patches that are sufficiently large [10, 11, 28, 33, 52] . Typically the models used to study the effects of spatial scale on ecological processes are based on reaction-diffusion equations

[8, 10, 11, 28, 35, 52] . Those models are spatially explicit in that they track the spatial distribution of populations over time. They have the advantage that they can be derived by viewing the movements of individuals as random walks which can be scaled-up to diffusion equations at the population level [8, 35, 55], and thus they can incorporate mechanistic and empirical data about dispersal. They have the disadvantage that their analysis often requires relatively sophisticated mathematical methods. Our approach to scaling in this paper is conceptually simpler but can yield conclusions at the population level that are similar in their general nature and level of detail to those derived from reaction-diffusion models. Specifically, we describe the dynamics and interactions of populations in terms of a system of ordinary differential equations with coefficients that depend on the size of the patch inhabited by the populations.

Habitat geometry can influence ecological processes. For example, studies of the metapopulation capacity of landscapes [22, 38] and edge-density in forests [49] demonstrate the dynamic consequences of habitat geometry for cases involving multiple habitat patches, whose size and juxtaposition within a landscape matrix can determine species persistence or outbreak dynamics. Other researchers have studied the ecological consequences of habitat geometry in the context of single-patch problems, focusing on cases in which patterns or dynamics of a system depend upon the physical dimensions of the patch. For example, Post et al. [46] demonstrated that the size of lakes determines the complexity of foodwebs they can support. Likewise, Laurance et al. [31] found that biomass loss from tropical forest fragments was patch-size-dependent, driven in part by disturbance-mediated loss of canopy trees from patch edges. At a theoretical level, a classical example involves the "critical patch size" problem, in which persistence of a species is possible only in patches large enough that local recruitment exceeds loss of dispersers across the patch boundary [11, 28, 33, 52].

One reason the geometry of individual patches may influence ecological processes or patterns is that geometric traits of habitat patches (and hence components of heterogeneity associated with those traits) do not scale uniformly with patch size. Perhaps the most obvious such example involves the differential scaling of perimeter and area in two-dimensional patches. Holding patch shape constant, as the area of a patch increases, the length of the perimeter also increases, but does so more slowly, resulting in a net decrease in perimeter-to-area ratio. Likewise, the core area of a patch (i.e., the portion of a patch buffered from factors external to the patch; see [19], [21]) tends to scale more slowly than total area when patch size is increased. This basic relationship has been pointed out many times in ecological contexts, including discussions of ecosystem-level landscape flows [58] and species persistence in fragmented forests [48].

Because patch edges and interiors may constitute distinctly different habitats (see [7] and [19]), ecologists have explored a variety of issues relating to patch geometry, emphasizing perimeter-to-area ratio in particular. For example, in a comprehensive series of studies, Polis and colleagues examined how marine biomass washing up on the shores of desert islands influenced food web dynamics for islands of different sizes and perimeter-to-area ratios [43-45]. In agricultural systems, Bommarco [4] and Ostman et al. [37] demonstrated that the perimeter-to-area ratio of cultivated fields was an important determinant of fat reserves and body condition in carabid beetles, which are generalist predators that can make important contributions to

pest suppression. Under laboratory conditions, Pearman [40, 41] studied interspecific competition between two tadpole species in mesocosms where edge habitat corresponded to enclosure surface area near the air-water interface. He found that high edge-to-interior ratios favored the growth and survivorship of the tadpole species that more effectively fed on periphyton growing on enclosure surfaces. The preceding examples suggest that features of habitat geometry, such as the differential scaling of perimeter and area with patch size, may influence species interactions in diverse ecological systems. However, just how important habitat geometry per se is to species interactions remains unclear. Is it the case that habitat geometry plays a minor role that can always be ignored? Or might the effects of geometry be so substantial as to alter the outcomes of species interactions? Additional questions arise when one considers that differences in amount of habitat (e.g., edge vs. core) may also coincide with changes in habitat quality. For example, how does the interplay between habitat quality and size influence species interactions when edge and interior resources are of different values to consumers?

We seek a broader understanding of the consequences of geometric scaling for species interactions. Toward this goal, we examine here a case involving two competing consumer species, one of which predominantly uses patch interiors while the other prefers habitat at the patch edge. Although we do not attempt to model a specific natural system, the scenario we investigate captures important ecological and geometric features of studies of habitat size-dependence in interspecific competition between tadpoles [40, 41] and those investigating allochthonous input into desert ecosystems [43-45]. We ask how the competitive interaction between these hypothetical species changes when patch interior habitat scales quadratically, but edge habitat scales only linearly with patch size. We also explore how the degree of exclusivity in the use of edge versus interior habitats and differences in the quality of resources from those habitats may influence how the competitive dynamics depend upon patch size.

Our approach to modeling is to start with a system of equations describing two consumers and two resources, then to use a pseudoequilibrium hypothesis to reduce it to a pair of equations describing the competition between the consumers. This is the approach to modeling resource competition that was used by MacArthur [34] to develop niche theory; see also [60]. A potential difficulty with this approach is that in the original consumer-resource model one of the resources may be driven to zero, which typically invalidates the pseudoequilibrium hypothesis. This point is discussed in detail by Abrams [1]. To address it, we analyze the original consumer-resource system to determine when one of the resources is driven to zero versus when that does not occur so that the pseudoequilibrium hypothesis is valid. To capture scale effects we assume that, when no consumers are present, the equilibrium level of one of the resources in the original consumer-resource model scales linearly with patch size, while the other resource equilibrium scales quadratically. It turns out that this simple scaling can induce complex effects of patch size on population interactions, including multiple reversals in competitive dominance. This is somewhat surprising, because the models are quite elementary in the sense that they involve only some ordinary differential equations rather than reaction-diffusion equations, integral equations, interacting particle systems, or other more sophisticated spatial models. Although the analysis uses only undergraduate- level mathematics, it is fairly complicated and delicate, reflecting the complexity the models are capable of capturing. A similar type of modeling approach has been used by Chase et al.

[15] to study the effects of habitat patchiness on the coexistence of competing consumers, but the focus of that work is on the degree of fragmentation of the habitat rather than on spatial scale per se.

2. Model Formulation. A Consumer-Resource Model. We start with the two-consumer–two-resource model

$$\dot{u} = (A_1 R_1 + A_2 q R_2 - d_1)u$$

$$\dot{v} = (A_3 R_1 + A_4 q R_2 - d_2)v$$

$$\dot{R_1} = \rho\ell - d_3 R_1 - B_1 u R_1 - B_2 v R_1$$

$$\dot{R_2} = r\left(1 - \frac{R_2}{K\ell^2}\right)R_2 - C_1 u R_2 - C_2 v R_2.$$

(2.1)

Here R_1 is the available amount of a resource found at the patch edge, R_2 is the available amount of a resource found on the patch interior, and u and v are the populations of two generalist consumer species. The parameters in (2.1) are all positive. The parameter ℓ represents a linear dimension of the habitat such as length or perimeter. We envision R_1 as representing a resource which arrives at the patch boundary from the outside at a fixed rate per unit length of boundary. We envision R_2 as a biotic resource that grows on the patch interior.

2.1 A Note on Scaling. We have formulated the model in terms of the amounts of resources available rather than their densities so that we could scale the system with ℓ. However, that formulation requires the implicit assumption that the size of the patch is small enough that an individual can search the entire patch. As long as the entire patch is within the foraging range of each individual, the amount of resource available to each individual will increase as the total amount of resources increases. Once the size of the patch exceeds the foraging range of an individual, that generally will no longer be the case, and a different modeling approach will be required. However, the model is motivated by consideration of systems where the patches are small, and the spatial effects it is supposed to capture are typically associated with small patches. As an example, we will use the model to deduce the presence of a minimal patch size that can support a population of each consumer.

The parameters d_i represent mortality rates (or the rate of degradation of R_1 if R_1 represents a nonliving resource such as detritus.) The coefficients B_i and C_i represent resource consumption rates, while the coefficients A_i represent the rates of resource consumption modified by the efficiency of the consumers in converting resources into new consumers. The coefficient ρ represents the rate at which the resource R_1 arrives per unit length of patch boundary. The parameter K represents the carrying capacity of the resource R_2 on a patch of unit area, and r represents the intrinsic growth rate of R_2. Finally, the parameter q describes the relative quality of the resource R_2 compared to R_1. In the systems studied by Polis et al. [44] and Polis and Hurd [45], which motivated the present work, q is typically fairly small. Some other systems where that is the case are discussed in [18] and [57].

Equation (2.1) specifies that resource 1 has chemostat-type growth dynamics, whereas resource 2 has density-dependent, logistic-type dynamics. This distinction is critical to our attempt to capture, via resource 1, the effects of an allochthonous resource arriving along a patch edge as in Polis and Hurd [45] and Polis et al.

[44]. Allochthonous resource inputs are important in a variety of ecological systems (reviewed in [43]), constituting a major resource subsidy that enhances consumer densities and generates donor-control of foodwebs [50, 51]. Mathematically, such allochthonous inputs should usually be treated differently from a resource originating within a model's domain (e.g., [26]). For simplicity, we assume that resource 1 arrives at a rate that is constant per unit edge distance and is independent of the density of that resource already present locally. For resource 2, we assume that the overall carrying capacity of the patch is the product of patch area and a constant carrying capacity per unit area. The mathematical analysis we describe below would proceed analogously if we instead used logistic-type growth dynamics for both resource species. However, in contrast to many researchers' first impressions of that alternative model, the use of logistic dynamics throughout would not result in a sizeable reduction in algebraic difficulty.

Without loss of generality in (2.1) we may identify u as the consumer which is more efficient at utilizing the resource R_1; that is,

$$A_1/d_1 > A_3/d_2. \tag{2.2}$$

We shall see that if (2.2) is imposed, then certain other relations between the coefficients of (2.1) must hold for u and v to coexist; specifically, v must in some sense be a more efficient consumer of resource R_2 than u.

2.2 Scaling, Apparent Competition, and a Pseudoequilibrium Model.
To obtain a competition model from (2.1) we will follow the approach used by MacArthur [34] and Yodzis [60] and assume that the resources quickly reach a pseudoequilibrium that tracks the populations of the consumers. However, Abrams [1] has pointed out that in models such as (2.1) or those used by MacArthur [34] and Yodzis [60] there is a possibility that one of the resources will be driven to zero by a mechanism analogous to apparent competition, which would invalidate the pseudoequilibrium hypothesis. It turns out that such an effect is possible in (2.1), but only for relatively large values of ℓ. To make this precise, we will derive some results about (2.1). In the course of doing so we will obtain some necessary conditions for the possible coexistence of u and v.

It is clear from the structure of (2.1) that the set $u \geq 0$, $v \geq 0$, $R_1 \geq 0$, $R_2 \geq 0$ is invariant. We will consider only nonnegative solutions.

Lemma 1. All (nonnegative) solutions of (2.1) are bounded above as $t \to \infty$, with bounds that do not depend on the initial data.

Proof (sketch). See appendix.

It turns out that R_2 may be driven to zero by apparent competition but R_1 cannot be:

Lemma 2. There is a constant $\underline{R_1} > 0$ such that if $R_1(0) > 0$, then for t sufficiently large $R_1(t) > \underline{R_1}$.

Proof. See appendix.

Lemma 3. If ℓ is sufficiently large, $R_1(0) > 0$, and either $u(0) > 0$ or $v(0) > 0$ then $R_2(t) \to 0$ as $t \to \infty$. In particular, if $v(0) = 0$ but $u(0) > 0$, then $R_2(t) \to 0$ as $t \to \infty$ if

$$\ell > \frac{d_1 d_3 C_1 + B_1 d_1 r}{A_1 C_1 \rho}. \tag{2.3}$$

and if $u(0) = 0$, $v(0) > 0$ then $R_2(t) \to 0$ as $t \to \infty$ if

$$\ell > \frac{d_2 d_3 C_2 + B_2 d_2 r}{A_3 C_2 \rho}. \tag{2.4}$$

Proof. See appendix.

For the main parts of this paper, which will be based on the model derived from (2.1) by using the pseudoequilibrium hypothesis, we will assume the reverse inequalities to (2.3) and (2.4). The presence of apparent competition in (2.1) has some counterintuitive implications. It might be expected that the consumer v, which we will assume to be a more efficient consumer of resource R_2, would dominate the competing consumer u when ℓ is large because the equilibrium $K\ell^2$ for R_2 in the absence of u and v scales as ℓ^2, while the corresponding equilibrium $\rho\ell/d_3$ for R_1 only scales as ℓ. However, as suggested by Lemma 3, increasing ℓ may actually decrease the level of R_2 through apparent competition, and it turns out that the result can be exclusion of v.

Lemma 4. If (2.2) holds, $u(0) > 0$, $R_1(0) > 0$, and $R_2(t) \to 0$ as $t \to \infty$ then $v(t) \to 0$ as $t \to \infty$.

Proof. See appendix.

The proof of Lemma 4 has an additional implication.

Lemma 5. If (2.2) holds, $u(0) > 0$, $R_1(0) > 0$, and

$$A_2/d_1 > A_4/d_2, \tag{2.5}$$

then $v(t) \to 0$ as $t \to \infty$.

2.2.1 *Biological Implications*. Lemmas 3 and 4 imply that in the model (2.1) under the hypothesis (2.2) the consumer which uses R_1 more efficiently (which by (2.2) will be u) will exclude the other consumer for large ℓ, even though the relative abundance of R_2 compared to R_1 in the absence of consumers increases with ℓ. The mechanism behind this phenomenon is apparent competition. However, the assumptions underlying (2.1) are valid only for relatively small values of ℓ, so what the model can reveal of biological interest is how the interaction between u and v is affected by ℓ when ℓ is small. The condition (2.5) implies that u is more efficient than v in utilizing the resource R_2, just as (2.2) implies that u is more efficient at using R_1. It is not surprising that if u is more efficient at using both resources, then u will exclude v for all values of ℓ which allow either consumer to persist. An examination of (2.1) when only u is present or only v is present reveals that if (2.2) and (2.5) hold, then the minimum value for ℓ which allows u to persist is smaller than the corresponding value for v. In particular, if v is not present, then u can increase from a small value (i.e., the consumer u can invade the patch) provided

$$A_1(\rho\ell)/d_3 + A_2 q(K\ell^2) - d_1 > 0. \tag{2.6}$$

The corresponding condition for invasibility by v is

$$A_3(\rho\ell)/d_3 + A_4q(K\ell^2) - d_2 > 0. \tag{2.7}$$

If (2.2) and (2.5) hold, then (2.7) implies (2.6); so, whenever v can invade the patch, so can u. If one prefers to think in terms of the existence of a positive equilibrium $(u^*, 0, R_1^*, R_2^*)$ rather than invasibility of the equilibrium $(0, 0, \rho\ell/d_3, K\ell^2)$ by u, this analysis is still valid, because (2.6) is a necessary and sufficient condition for such an equilibrium to exist, and (2.7) plays a similar role relative to v. In fact, (2.6) and (2.7) will play important roles in the formulation and analysis of the pseudoequilibrium model we will derive from (2.1).

If (2.2) and (2.5) hold, then $v \to 0$ in (2.1) if u and R_1 are present, so that u is always the dominant competitor if R_1 is present. If (2.2) holds the case which might admit interesting scaling effects is thus the one where (2.5) is reversed:

$$A_2/d_1 < A_4/d_2. \tag{2.8}$$

Condition (2.8) implies that v is the consumer that is more efficient at utilizing the resourse R_2. Note that (2.2) and (2.8) together imply $A_2/A_4 < d_1/d_2 < A_1/A_3$, so that

$$A_1A_4 - A_2A_3 > 0. \tag{2.9}$$

Throughout the rest of this paper we will assume that (2.2), (2.8), and hence (2.9) hold.

We still need to determine when it is reasonable to expect (2.1) to have solutions with $R_2 > 0$. If (2.1) has an equilibrium $(u^{**}, v^{**}, R_1^{**}, R_2^{**})$ with u^{**} and v^{**} both positive, then R_1^{**} and R_2^{**} must satisfy

$$A_1R_1^{**} + A_2qR_2^{**} = d_1$$

$$A_3R_1^{**} + A_4qR_2^{**} = d_2, \tag{2.10}$$

so

$$R_2^{**} = \frac{\begin{vmatrix} A_1 & d_1 \\ A_3 & d_2 \end{vmatrix}}{\begin{vmatrix} A_1 & A_2q \\ A_3 & A_4q \end{vmatrix}} > 0 \tag{2.11}$$

by (2.2) and (2.9). If (2.1) has an equilibrium with all components positive, then the pseudoequilibrium model we shall derive from it also has (u^{**}, v^{**}) as an equilibrium. We shall see that the pseudoequilibrium model may or may not admit such an equilibrium. In cases where $u \to 0$ and $v \to 0$ as $t \to \infty$, we have $R_2 \to K\ell^2$ as $t \to \infty$. If (2.1) has an equilibrium $(u^*, 0, R_1^*, R_2^*)$ (which requires that (2.6) holds) then the first equation in (2.10) holds with R_1^{**}, R_2^{**} replaced by R_1^*, R_2^*; also, we have

$$\rho\ell - d_3R_1^* - B_1u^*R_1^* = 0$$

$$r\left(1 - \frac{R_2^*}{K\ell^2}\right) - C_1u^* = 0. \tag{2.12}$$

Eliminating u^* from (2.12) leads to the relation

$$\frac{r}{C_1}\left(1 - \frac{R_2^*}{K\ell^2}\right) = \frac{\rho\ell - d_3R_1^*}{B_1R_1^*}. \tag{2.13}$$

Solving for R_1^* in (2.13), substituting into the first equation from (2.10) and moving the second and third terms in that equation yields the relation

$$\frac{A_1 \rho \ell}{\dfrac{B_1 r}{C_1}\left(1 - \dfrac{R_2^*}{K\ell^2}\right) + d_3} = d_1 - A_2 q R_2^*. \tag{2.14}$$

The left side of (2.14), viewed as a function of R_2^*, is positive and increasing for $0 \le R_2^* < K\ell^2 \left[1 + \dfrac{C_1 d_3}{B_1 r}\right]$ and is negative for $R_2^* > K\ell^2 \left[1 + \dfrac{C_1 d_3}{B_1 r}\right]$. The right side is positive and decreasing for $0 \le R_2^* < d_1/A_2 q$ and is nonpositive for larger values of R_2^*. Thus, (2.14) has a positive solution if and only if the left side is smaller than the right at $R_2^* = 0$; that is,

$$\frac{C_1 A_1 \rho \ell}{B_1 r + d_3 C_1} < d_1. \tag{2.15}$$

Solving (2.5) for ℓ yields the reverse inequality to (2.3). Similarly, (2.1) cannot have an equilibrium with $u = 0$, $v > 0$, $R_2 > 0$ unless the reverse inequality to (2.4) holds. For our pseudoequilibrium analysis we will always assume that the reverse inequalities to (2.3) and (2.4) hold. We will want to refer to the critical values of ℓ in (2.3) and (2.4), so we will label them as ℓ_u and ℓ_v respectively. To state this in terms of symbols, we will assume

$$\ell < \ell_u = \frac{d_1 d_3 C_1 + B_1 d_1 r}{A_1 C_1 \rho} \tag{2.16}$$

and

$$\ell < \ell_v = \frac{d_2 d_3 C_2 + B_2 d_2 r}{A_3 C_2 \rho}. \tag{2.17}$$

These restrictions on the size of ℓ are compatible with the hypothesis that ℓ must be small enough for the entire patch to be within the foraging range of an individual.

Under hypotheses (2.16) and (2.17) it is reasonable to consider a pseudoequilibrium model based on (2.1) subject to the additional hypothesis that the timescales for the dynamics of the resources are significantly faster than those for the consumers. To obtain the pseudoequilibrium model, we set the right sides of the equations for R_1 and R_2 in (2.1) equal to zero, solve for R_1 and R_2 in terms of u and v, then substitute into the equations for u and v. We obtain

$$R_1 = \frac{\rho \ell}{d_3 + B_1 u + B_2 v} \tag{2.18}$$

$$R_2 = K\ell^2 \left(1 - \frac{C_1}{r} u - \frac{C_2}{r} v\right) \tag{2.19}$$

so that u and v should satisfy

$$\begin{aligned}
\dot{u} &= \left[\left(\frac{A_1 \rho}{d_3 + B_1 u + B_2 v}\right)\ell + K\left(1 - \frac{C_1 u}{r} - \frac{C_2 v}{r}\right)A_2 q\ell^2 - d_1\right] u \\
\dot{v} &= \left[\left(\frac{A_3 \rho}{d_3 + B_1 u + B_2 v}\right)\ell + K\left(1 - \frac{C_1 u}{r} - \frac{C_2 v}{r}\right)A_4 q\ell^2 - d_2\right] v.
\end{aligned} \tag{2.20}$$

It is convenient to relabel some of the parameters in (2.20) as follows:

$$\begin{aligned}
a_1 &= A_1\rho/d_3 \\
a_2 &= A_2K \\
a_3 &= A_3\rho/d_3 \\
a_4 &= A_4K \\
b_1 &= B_1/d_3 \\
b_2 &= B_2/d_3 \\
c_1 &= C_1/r \\
c_2 &= C_2/r.
\end{aligned} \tag{2.21}$$

In terms of the new variables, (2.20) becomes

$$\dot{u} = \left[\left(\frac{a_1}{1+b_1u+b_2v}\right)\ell + (1-c_1u-c_2v)a_2q\ell^2 - d_1\right]u$$

$$\dot{v} = \left[\left(\frac{a_3}{1+b_1u+b_2v}\right)\ell + (1-c_1u-c_2v)a_4q\ell^2 - d_2\right]v. \tag{2.22}$$

The system (2.22) is the pseudoequilibrium model which will be the subject of the remainder of this paper. Note that the model incorporates both chemostat-type resource competition terms scaled by ℓ and Lotka-Volterra terms scaled by ℓ^2. This reflects the differences in the growth dynamics and spatial distribution of the resources.

3. **General Analysis of the Pseudoequilibrium Model.** . Our analysis of the model (2.22) will focus on how the dynamics depend on ℓ. For any fixed ℓ the dynamics of (2.22) are fairly simple, and are typical of those found in many models for two competitors, as discussed in [14], [35], and [53]. It turns out that there is at most one equilibrium with u and v both present and that the dynamics of (2.22) are essentially determined by the equilibria and their stability properties. We will first identify conditions on ℓ relative to the other parameters under which each consumer can persist in the absence of the other, and then study how changing ℓ affects the possible dynamics of the system when both species are present. In particular we will consider when the system admits an equilibrium with both species present, when it is possible for each species to invade the system if introduced at a low density while the other is at equilibrium, and when one species can exclude the other.

It will be convenient to formulate some of the hypotheses of the previous section in terms of the variables occurring in (2.22). Certain combinations of those parameters turn out to arise frequently in the analysis. Those are

$$\begin{aligned}
\alpha &= a_2a_3 - a_1a_4 \\
\beta &= a_2d_2 - a_4d_1 \\
\gamma &= a_1d_2 - a_3d_1.
\end{aligned} \tag{3.1}$$

In terms of these quantities, the hypotheses (2.2), (2.8), and (2.9) become (respectively)

$$\gamma > 0, \ \ \beta < 0, \ \ \alpha < 0. \tag{3.2}$$

Also, the maximum size for ℓ for which the model makes sense is the minimum of ℓ_u and ℓ_v. In terms of the parameters in (2.22), the definitions (2.16) and (2.17) of ℓ_u and ℓ_v become

$$\ell_u = \frac{d_1(b_1+c_1)}{a_1c_1}, \quad \ell_v = \frac{d_2(b_2+c_2)}{a_3c_2}. \tag{3.3}$$

In what follows we will always assume $0 \leq \ell \leq \min\{\ell_u, \ell_v\}$.

3.1 Single-species Equilibria (Minimal Patch Size).

In the absence of the other consumer species, each of the species described by u and v will satisfy an equation of the form $\dot{y} = h(y)y$ where $h(y)$ is decreasing and is negative for sufficiently large y. Such equations behave essentially like the logistic equation in that they will have a unique positive equilibrium provided $h(0) > 0$, and in that case the positive equilibrium will be globally stable among positive solutions; alternatively, the equation will not admit a positive equilibrium at all if $h(0) \leq 0$, and in that case all positive solutions will approach zero as $t \to \infty$. Thus, the equation for u will have the positive equilibrium u^* if and only if

$$a_2 q \ell^2 + a_1 \ell - d_1 > 0, \tag{3.4}$$

and in that case u^* is determined by the equation

$$\frac{a_1 \ell}{1 + b_1 u^*} + a_2 q \ell^2 (1 - c_1 u^*) - d_1 = 0. \tag{3.5}$$

The equation $a_2 q \ell^2 + a_1 \ell - d_1 = 0$ has one positive root, which we will denote as ℓ_1. For $\ell \geq 0$, (3.4) will hold precisely when $\ell > \ell_1$. Thus, a patch will sustain a population of the first consumer only if its size as measured by ℓ is larger than the critical patch size given by ℓ_1. Similarly, the second consumer can persist in the absence of the first at a positive equilibrium v^* if and only if

$$a_4 q \ell^2 + a_3 \ell - d_2 > 0, \tag{3.6}$$

and then v^* must satisfy

$$\frac{a_3 \ell}{1 + b_2 v^*} + a_4 q \ell^2 (1 - c_2 v^*) - d_2 = 0. \tag{3.7}$$

Note that the left side of (3.5) is decreasing in u^* but increasing in ℓ as long as $1 - c_1 u^* > 0$. Thus, if ℓ increases then u^* must also increase or the equation will be broken. Also, (3.5) implies that $1 - c_1 u^* = 0$ exactly when $\ell = d_1[1 + (b_1/c_1)]/a_1 = \ell_u$. It follows that the system will admit a unique single-species equilibrium of the form $(u^*, 0)$ with u^* positive when $\ell_1 < \ell < \ell_u$, and u^* will decrease toward zero as ℓ decreases toward ℓ_1.

Similarly, the system admits a single species equilibrium $(0, v^*)$ when $\ell_2 < \ell < \ell_v$, and $v^* \downarrow 0$ as $\ell \downarrow \ell_2$. We can solve explicitly for ℓ_1 and ℓ_2:

$$\ell_1 = \frac{2d_1}{a_1 + \sqrt{a_1^2 + 4a_2 q d_1}} = \frac{2}{\dfrac{a_1}{d_1} + \sqrt{\left(\dfrac{a_1}{d_1}\right)^2 + \left(\dfrac{4a_2 q}{d_1}\right)}}$$

while

$$\ell_2 = \frac{2d_2}{a_3 + \sqrt{a_3^2 + 4a_4 q d_1}} = \frac{2}{\dfrac{a_3}{d_2} + \sqrt{\left(\dfrac{a_3}{d_2}\right)^2 + \left(\dfrac{4a_4 q}{d_2}\right)}}.$$

By hypothesis (3.2) we have $a_1/d_1 > a_3/d_2$ so that $\ell_1 < \ell_2$ for q sufficiently small. This reflects the assumption that the first consumer is more efficient at using the first resource which is built into the hypothesis $\gamma > 0$ in (3.2), since having q small means that the quality of the second resource is low, so that it contributes less than the first to sustaining either consumer. As q increases we must eventually have $\ell_2 < \ell_1$, because the hypothesis $\beta < 0$ in (3.2) implies $a_2/d_1 < a_4/d_2$. (This

reflects the assumption that the second consumer uses the second resource more efficiently than the first consumer.) It turns out that the analysis of the system is facilitated by considering what happens near the value of q where $\ell_1 = \ell_2$.

Lemma 6. We have $\ell_1 = \ell_2$ if and only if

$$q = -\frac{\alpha\gamma}{\beta^2}, \tag{3.8}$$

and in that case

$$\ell_1 = \ell_2 = \beta/\alpha. \tag{3.9}$$

If $q < -\alpha\gamma/\beta^2$ then $\ell_2 > \ell_1 > \beta/\alpha$ while if $q > -\alpha\gamma/\beta^2$ then $\ell_2 < \ell_1 < \beta/\alpha$.

Proof. See appendix.

3.1.1 *Biological Implications.* The presence of the threshold values ℓ_1 and ℓ_2 such that the first consumer cannot persist by itself unless $\ell > \ell_1$ and the second cannot persist by itself unless $\ell > \ell_2$ is a version of the notion of a minimal patch size needed to sustain a population. The mechanism is simply that too small a patch will not support enough resources to sustain a population of consumers. This is a different mechanism than the one on which the traditional models for minimal patch size of Skellam [52] and Kierstead and Slobodkin [28] are based. In those models the population is modeled as growing inside the patch but diffusing out of the patch across the patch boundary. The minimal patch size that will sustain a population is then determined by the patch size needed for the growth rate on the inside to balance the loss rate across the boundary. More general versions of this diffusion-based mechanism can arise from spatial heterogeneity and often can be described in terms of the principal eigenvalues of elliptic operators; see [8, 9].

Which consumer can persist on a smaller patch depends on the relative quality of the resource growing on the patch and the resource entering the patch across the boundary. When the quality of the interior resource is low, the consumer which is more efficient at using the resource that enters through the boundary will be able to exist on smaller patches than the consumer which is more efficient at using the interior resource. If the quality of the interior resource is high that relationship is reversed.

3.2 **Coexistence Equilibria - General Considerations**. In general the system (2.22) may or may not admit equilibria with both consumers present. For any solution (u, v) of the full system with $v \geq 0$, u will be a subsolution of the single-species model obtained when $v = 0$. Thus, if the patch cannot sustain the first consumer by itself it cannot sustain an equilibrium with both consumers present. The situation relative to the second consumer is analogous. Thus, the model cannot have an equilibrium with both consumers present unless $\ell > \max\{\ell_1, \ell_2\}$. However, even if ℓ is larger than ℓ_1 and ℓ_2, there still may not be an equilibrium with both populations positive. The equations for a componentwise-positive equilibrium are

$$0 = \frac{a_1\ell}{1 + b_1u + b_2v} + a_2q\ell^2(1 - c_1u - c_2v) - d_1$$

$$\tag{3.10}$$

$$0 = \frac{a_3\ell}{1 + b_1u + b_2v} + a_4q\ell^2(1 - c_1u - c_2v) - d_2.$$

Multiplying the first by a_4, the second by a_2, subtracting, and simplifying yields

$$b_1 u + b_2 v = \frac{\alpha \ell}{\beta} - 1. \tag{3.11}$$

Similarly, multiplying the first equation of (3.10) by a_3, multiplying the second by a_1, subtracting, and simplifying yields

$$c_1 u + c_2 v = 1 + \frac{\gamma}{\alpha q \ell^2}. \tag{3.12}$$

In what follows we will assume the nondegeneracy hypothesis

$$\frac{b_1}{c_1} \neq \frac{b_2}{c_2}. \tag{3.13}$$

Under that hypothesis, (3.11) and (3.12) will always have a unique solution, but it need not be positive. Clearly the right sides of (3.11) and (3.12) must be positive if (3.11) and (3.12) are to admit positive solutions. From (3.11) we must have $\ell > \beta / \alpha$. From (3.12) we must have $\ell^2 > -\gamma / \alpha q$. We can solve (3.11) and (3.12) explicitly for an equilibrium (u^{**}, v^{**}):

$$u^{**} = \frac{\begin{vmatrix} \dfrac{\alpha \ell}{\beta} - 1 & b_2 \\[2ex] 1 + \dfrac{\gamma}{\alpha q \ell^2} & c_2 \end{vmatrix}}{b_1 c_2 - b_2 c_1}$$

$$= \frac{\left[c_2 \left(\dfrac{\alpha \ell}{\beta} - 1 \right) - b_2 \left(1 + \dfrac{\gamma}{\alpha q \ell^2} \right) \right]}{b_1 c_2 - b_2 c_1} \tag{3.14}$$

and

$$v^{**} = \frac{\begin{vmatrix} b_1 & \dfrac{\alpha \ell}{\beta} - 1 \\[2ex] c_1 & 1 + \dfrac{\gamma}{\alpha q \ell^2} \end{vmatrix}}{b_1 c_2 - b_2 c_1}$$

$$= \frac{b_1 \left(1 + \dfrac{\gamma}{\alpha q \ell^2} \right) - c_1 \left(\dfrac{\alpha \ell}{\beta} - 1 \right)}{b_1 c_2 - b_2 c_1}. \tag{3.15}$$

Combining the above observations, we obtain

Lemma 7. The model (2.22) can have a positive coexistence equilibrium (u^{**}, v^{**}) only if $\ell > \beta / \alpha$ and $1 + (\gamma / \alpha q \ell^2) > 0$. In that case:

i. If $b_1 / c_1 > b_2 / c_2$, then (2.22) has a positive equilibrium (u^{**}, v^{**}) if and only if

$$\alpha^2 \ell^3 - \alpha \beta \ell^2 \left[1 + \left(\frac{b_2}{c_2} \right) \right] - \left(\frac{\beta \gamma}{q} \right) \left(\frac{b_2}{c_2} \right) > 0 \tag{3.16}$$

and

$$\alpha^2 \ell^3 - \alpha\beta\ell^2 \left[1 + \left(\frac{b_1}{c_1} \right) \right] - \left(\frac{\beta\gamma}{q} \right) \left(\frac{b_1}{c_1} \right) < 0. \qquad (3.17)$$

ii. If $b_1/c_1 < b_2/c_2$, then (2.22) has a positive equilibrium (u^{**}, v^{**}) if and only if (3.16) and (3.17) are reversed.

Remark. Inequalities (3.16) and (3.17) are obtained by simplifying the sign conditions that must be imposed on the numerators in (3.14) and (3.15) for u^{**} and v^{**} to be positive. It turns out that the details of how (3.16) and (3.17) depend on ℓ are strongly influenced by the sizes of q, b_1/c_1, and b_2/c_2. We will analyze some particular cases in detail later in the paper.

3.3 **Linearized Stability**. The local stability or instability of equilibria is determined by the signs of the real parts of the eigenvalues of the Jacobian matrix for the system evaluated at those equilibria. The stability analysis is essentially a calculation. The following lemmas describe the results of the calculation; the details are given in the Appendix.

Lemma 8. Suppose the equilibrium (u^{**}, v^{**}) exists. If $b_1/c_1 > b_2/c_2$ then (u^{**}, v^{**}) is locally stable (as a stable node). If $b_2/c_2 > b_1/c_1$ then (u^{**}, v^{**}) is unstable (as a saddle point).

3.3.1 *Biological Interpretation.* The quotient b_i/c_i describes the relative rates of consumption of the two resources by the ith consumer, so that in effect it describes the consumer's preferences. The assumption $\alpha < 0$ implies that the first consumer is relatively more efficient at using the first resource than the second compared to the second consumer. Thus, if $b_1/c_1 > b_2/c_2$, each consumer prefers the resource which it is relatively more efficient at utilizing. Thus, each consumer has a stronger impact on the availability of the resource it can use best, so the effects of intraspecific competition (i.e. self-limitation) are stronger than those of interspecific competition. That has a tendency to promote coexistence. (See Cantrell et. al. [13] for a different but related discussion of how intraspecific competition can promote coexistence of competing consumers.) In the case $b_2/c_2 > b_1/c_1$, each consumer has a stronger impact on the resource which can be used more efficiently by the other consumer, so interspecific competition has a stronger effect than intraspecific competition. That has a tendency to destabilize the system and make coexistence less likely.

Lemma 9. Suppose the equilibrium $(u^*, 0)$ exists. If $1 + \dfrac{\gamma}{\alpha q\ell^2} \leq 0$, then it is locally stable (as a node). If $1 + \dfrac{\gamma}{\alpha q\ell^2} > 0$ and (3.17) holds, then $(u^*, 0)$ is locally unstable (as a saddle point.) If $1 + \dfrac{\gamma}{\alpha q\ell^2} > 0$ and (3.17) is reversed, then $(u^*, 0)$ is locally stable (as a node.) When $(u^*, 0)$ is unstable the linearization of (2.22) at $(u^*, 0)$ admits an eigenvector of the form $(p, 1)$ with $p < 0$ corresponding to the positive eigenvalue.

Lemma 10. Suppose $(0, v^*)$ exists. If $\dfrac{\alpha \ell}{\beta} - 1 \leq 0$, then $(0, v^*)$ is locally stable (as a node.) If $\dfrac{\alpha \ell}{\beta} - 1 > 0$ and (3.16) holds, then $(0, v^*)$ is locally unstable (as a saddle point.) If $\dfrac{\alpha \ell}{\beta} - 1 > 0$ and (3.16) is reversed, then $(0, v^*)$ is locally stable (as a node). When $(0, v^*)$ is locally unstable, the linearization of (2.22) at $(0, v^*)$ admits an eigenvector of the form $(1, q)$ with $q < 0$ corresponding to the positive eigenvalue.

Remarks. When $(u^*, 0)$ is unstable, the system is said to be invasible by v, which means that if a small population of the second consumer is introduced when the first consumer is present at equilibrium, the population of the second consumer will increase. Similarly, when $(0, v^*)$ is unstable, the system is said to be invasible by u. Note that in the case $b_1/c_1 > b_2/c_2$ the conditions for the existence of (u^{**}, v^{**}) given by (3.16) and (3.17) are the same as those for both $(u^*, 0)$ and $(0, v^*)$ to be invasible. That is no accident, but a consequence of the monotonicity properties of 2×2 competition systems. Those monotonicity properties have other consequences. Some of them are described in the next subsection.

3.4 **Two-species Competition, Monotonicity, and Invasibility**. The model (2.22) is a 2×2 competition system. Thus, it is order-preserving with respect to the ordering where $(u_1, v_1) < (u_2, v_2)$ means $u_1 > u_2$, $v_1 < v_2$. This is a feature of all 2×2 competitive systems, not just the Lotka-Volterra system; see ([53], Ch. 3, §5). It follows from the general properties of such autonomous order preserving systems that trajectories which start at a strict subsolution of the equilibrium problem must increase (with respect to the ordering specified for the system) and if bounded will approach an equilibrium as $t \to \infty$. This idea was used in the context of reaction-diffusion equations by Aronson and Weinberger [3]; see [8, 24, 53] for additional discussion and references. It can be used to show that a system is uniformly persistent via the notion of compressivity (see [24]) or to show that one competitor excludes the other (see [12]). The analogous results hold for supersolutions. A more abstract formulation of this idea is given by Smith ([53], Ch. 2, §5). In the present context we have

Lemma 11. Suppose that $(\bar{u}, \bar{v})$ is an equilibrium of (2.22) with $\bar{u} \geq 0$ and $\bar{v} > 0$, and that the Jacobian matrix J for the linearization of (2.22) about $(\bar{u}, \bar{v})$ has a positive eigenvalue with an eigenvector (ϕ, ψ) which is positive in the sense of the ordering preserved by (2.22); that is, $\phi > 0$ and $\psi < 0$. If (u, v) is a solution to (2.22) with $u(0) > \bar{u}$, $v(0) < \bar{v}$, and $|u(0) - \bar{u}|$, $|v(0) - \bar{v}|$ sufficiently small, then $u(t) \geq \tilde{u}_1(t)$ and $v(t) \leq \tilde{v}_1(t)$ where $\tilde{u}_1(t)$ will increase with t and $\tilde{v}_1(t)$ will decrease, and as $t \to \infty$, and $(\tilde{u}_1, \tilde{v}_1) \to (\hat{u}_1, \hat{v}_1)$ where $(\hat{u}_1, \hat{v}_1)$ is an equilibrium of (2.22) with $\hat{u}_1 > \bar{u}$ and $\hat{v}_1 < \bar{v}$. Similarly, if $\bar{u} > 0$, $\bar{v} \geq 0$, $\phi < 0$ and $\psi > 0$ then, for a solution with $u(0) < \bar{u}$, $v(0) > \bar{v}$, and $|u(0) - \bar{u}|$, $|v(0) - \bar{v}|$ small, there will be a solution $(\tilde{u}_2, \tilde{v}_2)$ with $\tilde{u}_2(t) > u(t)$, $\tilde{v}_2(t) < v(t)$ where $\tilde{u}(t)$ is decreasing in t, $\tilde{v}(t)$ is increasing in t, and $\tilde{u}_2(t) \to \hat{u}_2$, $\tilde{v}_2(t) \to \hat{v}_2$ as $t \to \infty$, where $(\hat{u}_2, \hat{v}_2)$ is an equilibrium of (2.22) with $\hat{u}_2 < \bar{u}$ and $\hat{v}_2 > \bar{v}$.

Lemma 11 has a number of important consequences. If $(\bar{u}, \bar{v}) = (0, v^*)$ and the linearized model at $(\bar{u}, \bar{v})$ has a positive eigenvalue λ with eigenvector (ϕ, ψ) such that $\phi > 0$, $\psi < 0$, then solutions to (2.22) starting near $(0, v^*)$ with $u > 0$, $v < v^*$

will have $u > \tilde{u}_1, \quad v < \tilde{v}_1$, where $(\tilde{u}_1, \tilde{v}_1)$ converges to an equilibrium of (2.22). In the case (u^{**}, v^{**}) exists we know it is unique, so in that case the convergence of $(\tilde{u}_1, \tilde{v}_1)$ to (u^{**}, v^{**}) implies a type of stability from one side for (u^{**}, v^{**}). If in addition $(u^*, 0)$ is unstable, with an eigenvector (ϕ, ψ) corresponding to a positive eigenvalue of the linearization at $(u^*, 0)$ such that $\phi < 0, \quad \psi > 0$, then (u^{**}, v^{**}) is stable from the other side, and since the rectangle $[0, u^*] \times [0, v^*]$ is attracting, that implies global stability for (u^{**}, v^{**}). In fact, having both $(u^*, 0)$ and $(0, v^*)$ unstable would imply that (u^{**}, v^{**}) exists, because in that case trajectories leaving $(0, v^*)$ could not approach $(u^*, 0)$ and hence would necessarily converge to an equilibrium with $u^{**} < u^*, \quad v^{**} < v^*$. On the other hand, if there is no coexistence equilibrium but $(0, v^*)$ is unstable in the sense described above, then we would necessarily have $(\tilde{u}_1, \tilde{v}_1) \to (u^*, 0)$ so that u would exclude v. In view of these observations and Lemmas 9 and 10 we have

Corollary 12. If $(u^*, 0)$ and $(0, v^*)$ are unstable, then (u^{**}, v^{**}) exists and is globally stable among positive solutions. If $(0, v^*)$ is unstable and (u^{**}, v^{**}) does not exist, then positive solutions of (2.22) approach $(u^*, 0)$ as $t \to \infty$; that is, u excludes v. If $(u^*, 0)$ is unstable and (u^{**}, v^{**}) does not exist, then positive solutions to (2.22) approach $(0, v^*)$ so that v excludes u.

Remarks. The case where $(u^*, 0)$ and $(0, v^*)$ are both unstable is an example of the principle that mutual invasibility implies coexistence.

The conditions for stability or instability of $(u^*, 0)$ and $(0, v^*)$ are related to each other and the conditions for existence of (u^{**}, v^{**}) in such a way that no contradictions can arise in Corollary 12. For example, if $(u^*, 0)$ is unstable and (u^{**}, v^{**}) fails to exist, then $(0, v^*)$ must be stable so the predictions of the model are consistent. (In such a case v would exclude u.)

3.5 **Summary of the General Analysis**. The general analysis of the model (2.22) provides conditions for the existence and stability or instability of the equilibria $(u^*, 0), \quad (0, v^*)$, and (u^{**}, v^{**}) in terms of the parameters of the system. Since (2.22) is a two-species competition model, it has order-preserving properties which imply that the equilibria and their stabilities essentially determine the dynamics. The details of how the dynamics of the model vary with ℓ depend on the remaining parameters and can be divided into a number of cases. In the next section we will analyze some of those cases in detail. That analysis will involve a careful examination of the conditions (3.4), (3.6), (3.16), and (3.17) which determine the existence and stability of equilibria.

4. **Detailed Scaling Analysis for the Pseudoequilibrium Model.** . In this section we will examine how the predictions of the pseudoequilibrium model (2.22) depend on ℓ. Recall that we always assume $0 \le \ell \le \min\{\ell_u, \ell_v\}$ where ℓ_u and ℓ_v are as in (3.3). Also, recall that (2.22) admits an equilibrium $(u^*, 0)$ with $u^* > 0$ if and only if $\ell > \ell_1$, where ℓ_1 is the positive root of

$$a_2 q \ell^2 + a_1 \ell - d_1 = 0. \tag{4.1}$$

Similarly, (2.22) admits the equilibrium $(0, v^*)$ if and only if $\ell > \ell_2$, where ℓ_2 is the positive root of

$$a_4 q \ell^2 + a_3 \ell - d_2 = 0. \tag{4.2}$$

Recall that by Lemma 7 we have $\ell_1 = \ell_2 = \beta/\alpha$ if $q = -\alpha\gamma/\beta^2$, with $\beta/\alpha < \ell_1 < \ell_2$ if $q < -\alpha\gamma/\beta^2$ and $\ell_2 < \ell_1 < \beta/\alpha$ if $q > -\alpha\gamma/\beta^2$. The existence of an equilibrium (u^{**}, v^{**}) and the stability of the equilibria $(u^*, 0)$ and $(0, v^*)$ depend on the inequalities (3.16) and (3.17). Note that the system (3.10) determining (u^{**}, v^{**}) can only have a positive solution if $\ell > \max(\ell_1, \ell_2)$. Much of the scaling analysis of (2.22) depends on how the roots of the cubics in (3.16) and (3.17) change with ℓ. That in turn depends on the parameters, specifically q, b_1/c_1, and b_2/c_2. To perform the analysis, we first consider what happens when $q = -\alpha\gamma/\beta^2$ and then determine the effects of increasing or decreasing q. The cubics in (3.16) and (3.17) play a central role in the analysis, so we will examine them in some detail first.

4.1 **Cubic Equations Related to Equilibria**. The expressions in (3.16) and (3.17) are cubics of the form $\alpha^2\ell^3 - \alpha\beta(1 + Q_i)\ell^2 - (\beta\gamma/q)Q_i$, where $Q_i = b_i/c_i$ for $i = 1, 2$. We assume the nondegeneracy condition $Q_1 \neq Q_2$.

Lemma 13. If $Q_1 \neq Q_2$, then the cubic equations

$$\alpha^2\ell^3 - \alpha\beta(1 + Q_i)\ell^2 - \left(\frac{\beta\gamma}{q}\right)Q_i = 0 \tag{4.3}$$

with $i = 1, 2$ have a common root if and only if $q = -\alpha\gamma/\beta^2$, and in that case the common root is β/α. The other positive root corresponding to Q_i is then $(\beta/2\alpha)[Q_i + \sqrt{Q_i^2 + 4Q_i}]$.

Proof. See appendix.

Recall that $\ell_1 = \ell_2$ if and only if $q = -\alpha\gamma/\beta^2$, and then $\ell_1 = \ell_2 = \beta/\alpha$. Thus, several significant changes in the predictions of the model occur at $\ell = \beta/\alpha$ when $q = -\alpha\gamma/\beta^2$.

The constant term in (4.3) is always positive. Calculating the first and second derivatives with respect to ℓ of the cubic in (4.3) shows that it has a local maximum at $\ell = 0$ and a local minimum when

$$\ell = (\beta/\alpha)(2/3)(1 + Q_i). \tag{4.4}$$

The cubic is increasing for $\ell < 0$. Thus, (4.3) has $0, 1,$ or 2 positive roots. (The value of the cubic at the local minimum is $(\beta^3/\alpha)[(-4/27)(1 + Q_i)^3 - (\alpha\gamma/\beta^2 q)Q_i]$, which is positive for q small but negative for q large for any fixed value of Q_i. In the interesting special case where $q = -\alpha\gamma/\beta^2$ the value of the cubic at the local minimum is $\beta^3/\alpha[-4/27)(1 + Q_i)^3 + Q_i]$, which is zero for $Q_i = 1/2$ but negative for all other $Q_i > 0$. (The expression is clearly negative for $Q_i = 0$ or $Q_i \to \infty$, increasing for $0 < Q_i < 1/2$ and decreasing for $1/2 < Q_i$.) The local minimum occurs when $\ell = \beta/\alpha$ when $q = -\alpha\gamma/\beta^2$ and $Q_i = 1/2$; for $Q_i < 1/2$ the local minimum occurs for $\ell < \beta/\alpha$; and for $Q_i > 1/2$, it occurs for $\ell > \beta/\alpha$.

Definition. If (4.3) has at least one positive root, denote the smallest positive root by ℓ_i^*. If (4.3) has two positive roots denote the second by ℓ_i^{**}. (Thus $\ell_i^{**} \geq \ell_i^*$ with equality only if the local minimum of the cubic in (4.3) also occurs at ℓ_i^*.)

As $q \to 0$, the constant term in the cubic in (4.3) increases and eventually the cubic becomes positive for all $\ell > 0$. As $q \to \infty$ the constant term goes to zero and the roots of the cubic approach 0 and $(\beta/\alpha)(1 + Q_i)$. Note that $a_1\beta - d_1\alpha = a_2\gamma > 0$ so $(\beta/\alpha) < d_1/a_1$ and hence $(\beta/\alpha)(1 + Q_1) < (d_1/a_1)(1 + Q_1) = \ell_u$. Similarly,

$a_3\beta - d_2\alpha = a_4\gamma > 0$, and so $(\beta/\alpha)(1 + Q_2) < (d_2/a_3)(1 + Q_2) = \ell_v$. Thus, the roots of the cubics in (4.3) occur within the intervals $(0, \ell_u)$ for $i = 1$ and $(0, \ell_v)$ for $i = 2$.

4.2 Perturbation Analysis:General Aspects.

If the roots of a polynomial occur at points where the derivative is nonzero then by the implicit function theorem they are differentiable functions of the coefficients. We will proceed by analyzing the behavior of the system when $q = -\alpha\gamma/\beta^2$ and then perturbing the system relative to q. Since the value $\ell = \beta/\alpha$ corresponds to a local minimum of the cubic in (4.3) when $Q_i = 1/2$, we will assume that $Q_i \neq 1/2$ for $i = 1, 2$ so that ℓ_i^* and ℓ_i^{**} will depend smoothly on the coefficients of (4.3), specifically q, if those roots exist. Suppose $\ell(q)$ is a root of (4.3) with $\ell(-\alpha\gamma/\beta^2) = \beta/\alpha$. Differentiating (4.3) and solving for $d\ell/dq$ yields

$$\frac{d\ell}{dq}(-\alpha\gamma/\beta^2) = \left(\frac{-\beta^3}{\alpha^2\gamma}\right)\left(\frac{Q_i}{1 - 2Q_i}\right). \tag{4.5}$$

The coefficient $-\beta^3/\alpha^2\gamma$ is positive, so $d\ell/dq$ is increasing in Q_i with $d\ell/dq > 0$ if $Q_i < 1/2$ but $d\ell/dq < 0$ for $Q_i > 1/2$.

4.3 Perturbation Analysis: Case by Case.

In view of our previous discussion of how the roots of (4.3) and the stability of (u^{**}, v^{**}) depend on $Q_i = b_i/c_i$, it seems natural to classify the various possible cases by the relationships between $1/2$, b_1/c_1, and b_2/c_2. We will give the details of the analysis in two cases and describe the others more briefly. Certain features occur in all cases. Specifically, if q, the quality of the logistically scale resource, is larger than $-\alpha\gamma/\beta^2$ then by Lemma 6 we have $\ell_2 < \ell_1 < \beta/\alpha$, which means that the second consumer can persist on a smaller patch than the first. If $q = -\alpha\gamma/\beta^2$ the critical patch size is $\ell_1 = \ell_2 = \beta/\alpha$ for both consumers. If $q < -\alpha\gamma/\beta^2$, then $\beta/\alpha < \ell_1 < \ell_2$; so, the first consumer can persist on a smaller patch. Also, for q sufficiently small, (3.16) holds for all $\ell > 0$ while, (3.17) never holds for $\ell > 0$; so, $(u^*, 0)$ is always stable, $(0, v^*)$ is always unstable (when these equilibria exist) and (u^{**}, v^{**}) does not exist. Hence, in such situations, the first consumer always excludes the second if it can persist on its own. What is happening is that the first consumer is more efficient than the second at using the first resource, so as the relative quality of the second resource is reduced, the first consumer gains an advantage relative to the second consumer.

Another universal feature of the system is that if $\ell_1 < \ell_2$ and $\ell \approx \ell_2$, $\ell > \ell_2$, then $(0, v^*)$ is unstable; similarly, if $\ell_2 < \ell_1$ and $\ell \approx \ell_1$, $\ell > \ell_1$ then $(u^*, 0)$ is unstable. To understand this feature, suppose $\ell_1 < \ell_2$, recall that $v^* \downarrow 0$ as $\ell \downarrow \ell_2$, and consider (3.4) and (A.18). At $\ell = \ell_2$ the inequality in (3.4) is strict because $\ell_2 > \ell_1$. On the other hand, as $\ell \downarrow \ell_2$, we have $v^* \downarrow 0$, so (A.18) must hold for $\ell > \ell_2$, $\ell \approx \ell_2$ since the expression on the left in (A.18) approaches the one in (3.4) as $v^* \to 0$. Since (A.18) holds, $(0, v^*)$ is unstable and in fact (3.16) holds. Note also that at $\ell = \ell_2$ we have equality in (3.6) but $u^* > 0$ so, (A.8) is reversed. By continuity (A.8) will remain reversed for $\ell \approx \ell_2$, so for $\ell \approx \ell_2$ the equilibrium $(u^*, 0)$ is stable. The analysis for $\ell \approx \ell_1$ in the case $\ell_2 < \ell_1$ is similar but with the roles of u and v reversed. We now turn to the cases.

4.3.1 **Case 1 (detailed analysis).** $1/2 < b_2/c_2 < b_1/c_1$.

i. First consider the case $q = -\alpha\gamma/\beta^2$. In that case $\ell_1 = \ell_2 = \ell_1^* = \ell_2^* = \beta/\alpha$, with $\ell_1^{**} > \ell_2^{**} > \beta/\alpha$. (This follows from Lemmas 6 and 13.) Thus, for $\ell < \beta/\alpha$ neither consumer can persist. If $\ell > \beta/\alpha$ then both single-species equilibria $(u^*, 0)$ and $(0, v^*)$ exist. For $\beta/\alpha < \ell < \ell_2^{**}$ inequality (3.16) does not hold but (3.17) does, so there is no coexistence equilibrium by Lemma 7. If $\ell > \beta/\alpha$ then $1 + \gamma/(\alpha q \ell^2) > 0$ for $q = -\alpha\gamma/\beta^2$ so by Lemma 9 the equilibrium $(u^*, 0)$ is locally unstable for $\beta/\alpha < \ell < \ell_2^{**}$. By Lemma 10, $(0, v^*)$ is locally stable for $\beta/\alpha < \ell < \ell_2^{**}$. By Corollary 12 we may conclude that v excludes u if $v(0) > 0$ when $\beta/\alpha < \ell < \ell_2^{**}$. For $\ell_2^{**} < \ell < \ell_1^{**}$, (3.16) and (3.17) both hold, so (u^{**}, v^{**}) exists. By Lemma 8 it is stable. The equilibrium $(u^*, 0)$ remains unstable, but the equilibrium $(0, v^*)$ becomes unstable. Thus for $\ell_2^{**} < \ell < \ell_1^{**}$ the model predicts coexistence. Finally, if $\ell_1^{**} < \ell$ but $\ell < \min\{\ell_u, \ell_v\}$, then (3.16) holds but (3.17) fails; so, (u^{**}, v^{**}) no longer exists, $(u^*, 0)$ is stable, $(0, v^*)$ is unstable, and thus by Lemma 11 u excludes v.

4.3.1 (i) Biological Discussion. The fact that the system does not support either consumer when ℓ is small is not suprising. The fact that v is competitively dominant for ℓ just larger than β/α while u is dominant for still larger values of ℓ seems somewhat counter-intuitive, because one might expect the consumer (u) that does best on the linearly scaled resource to dominate for moderate values of ℓ and the consumer (v) which does best on the quadratically scaled resource to dominate for large values. What is happening in this case is that q, the quality of the quadratically scaled resource, is high enough to compensate for the slower rate of increase of ℓ^2 compared to ℓ when ℓ is small. For large ℓ, the dominance of u arises from the differing effects of apparent competition on the resources. (Recall that in the original consumer-resource model u is always predicted to exclude v for ℓ large via apparent competition.)

ii. Further insight can be gained by considering how the model behaves if q is perturbed from $-\alpha\gamma/\beta^2$. Suppose that we reduce q from $-\alpha\gamma/\beta^2$. By Lemma 6 we have $\ell_2 > \ell_1 > \beta/\alpha$. By (4.5) we have $d\ell_2^*/dq < d\ell_1^*/dq < 0$ at $q = -\alpha\gamma/\beta^2$. So, as q is decreased from $-\alpha\gamma/\beta^2$ we initially have $\beta/\alpha < \ell_1^* < \ell_2^*$, and this arrangement persists as long as ℓ_1^* and ℓ_2^* exist, because roots of (4.3) corresponding to distinct values of Q_i can coincide only if $q = -\alpha\gamma/\beta^2$. Reducing q has the effect of raising the graphs of the cubics occurring in (4.3), so it reduces ℓ_1^{**} and ℓ_2^{**} but does not change the relation $\beta/\alpha < \ell_2^{**} < \ell_1^{**}$. Thus, when q is reduced from $-\alpha\gamma/\beta^2$, but not reduced enough to eliminate any of the roots ℓ_i^*, ℓ_i^{**}, then we have $\beta/\alpha < \ell_1 < \ell_2$. Also, $(u^*, 0)$ is unstable relative to v (that is, it is invasible by v) only if $(0, 0)$ is invasible by v, so we must have $\ell_1^* > \ell_2$. Thus, for $q < -\alpha\gamma/\beta^2$ but not too small we have $\beta/\alpha < \ell_1 < \ell_2 < \ell_1^* < \ell_2^* < \ell_2^{**} < \ell_1^{**}$. For $\ell < \ell_1$ neither consumer persists. For $\ell_1 < \ell < \ell_2$ the equilibrium $(u^*, 0)$ exists but $(0, v^*)$ and (u^{**}, v^{**}) do not, so u can persist but not v. For $\ell_2 < \ell < \ell_1^*$, $(u^*, 0)$ and $(0, v^*)$ both exist, (3.16) holds, but (3.17) does not, so $(u^*, 0)$ is stable, $(0, v^*)$ is unstable, and (u^{**}, v^{**}) does not exist, so u excludes v. For $\ell_1^* < \ell < \ell_2^*$, (3.16) and (3.17) both hold, so $(u^*, 0), (0, v^*)$, and (u^{**}, v^{**}) all exist. Also, $(u^*, 0)$ and $(0, v^*)$ are both unstable and (u^{**}, v^{**}) is stable, so the model predicts coexistence. For $\ell_2^* < \ell < \ell_2^{**}$ (3.17) holds but (3.16) does not, so $(u^*, 0)$ is unstable, $(0, v^*)$ is

stable, and (u^{**}, v^{**}) does not exist, so v excludes u. If $\ell_2^{**} < \ell < \ell_1^{**}$, then (3.16) and (3.17) both hold, so (u^{**}, v^{**}) exists and is stable; and $(u^*, 0)$ and $(0, v^*)$ are unstable, so again the model predicts coexistence. Finally, if $\ell > \ell_1^{**}$, then (3.16) holds but (3.17) does not, so $(u^*, 0)$ is stable, $(0, v^*)$ is unstable, and (u^{**}, v^{**}) does not exist, so u excludes v.

4.3.1 (ii) Biological Discussion. In this situation the predictions of the model for $\ell < \ell_2^{**}$ are essentially what one would expect. The consumer u that does best on the linearly scaled resource can persist on a smaller patch ($\ell_1 < \ell_2$) and is competitively dominant for $\ell < \ell_1^*$. For $\ell_1^* < \ell < \ell_2^*$ the quadratically scaled resource becomes sufficiently abundant for the consumer v which does best on it to coexist with u, and then for $\ell_2^* < \ell < \ell_2^{**}$ to exclude u. For $\ell > \ell_2^{**}$ things again seem counterintuitive because the advantage shifts back toward u, giving coexistence for $\ell_2^{**} < \ell < \ell_1^{**}$ and finally a prediction that u excludes v when $\ell > \ell_1^{**}$. Again, the mechanism underlying this counterintuitive result is the asymmetry in the nature of the resource equations, which allows R_2 (the quadratically scaled resource) to be forced toward zero by apparent competition but does not allow that for R_1.

iii. The arrangement described above persists until q is small enough that one of the cubics in (3.16) and (3.17) becomes positive for all $\ell > 0$. By (4.4) the minimum value of the cubic in (4.3) for $\ell > 0$ occurs at $\ell = (\beta/\alpha)(2/3)(1 + Q_i)$. (Recall that $Q_i = b_i/c_i$). The minimum is positive if

$$q < \frac{27}{4}\left(-\frac{\alpha\gamma}{\beta^2}\right)\frac{Q_i}{(1 + Q_i)^3}. \tag{4.6}$$

For $Q_i > 1/2$ the expression on the right side of (4.6) is decreasing in Q_i. In this scenario we are assuming that $1/2 < b_2/c_2 < b_1/c_1$. Thus, for q satisfying

$$\frac{27}{4}\left(-\frac{\alpha\gamma}{\beta^2}\right)\frac{(b_1/c_1)}{[1 + (b_1/c_1)]^3} < q < \frac{27}{4}\left(-\frac{\alpha\gamma}{\beta^2}\right)\frac{(b_2/c_2)}{[1 + (b_2/c_2)^3]} \tag{4.7}$$

condition (3.16) holds for all $\ell > 0$, so ℓ_2^* and ℓ_2^{**} do not exist, but ℓ_1^* and ℓ_1^{**} still exist. In that case we have $\beta/\alpha < \ell_1 < \ell_2 < \ell_1^* < \ell_1^{**}$. As before, for $\ell < \ell_1$ neither consumer persists. For $\ell_1 < \ell < \ell_2$ the equilibrium $(u^*, 0)$ exists and is attracting for all solutions of (2.22) with $u(0) > 0$, but there is no positive equilibrium $(0, v^*)$. For $\ell_2 < \ell < \ell_1^*$ both $(u^*, 0)$ and $(0, v^*)$ exist but $(0, v^*)$ is unstable by Lemma 10 because (3.16) holds, $(u^*, 0)$ is stable by Lemma 9 because (3.17) is reversed, and (u^{**}, v^{**}) does not exist by Lemma 7; hence by Corollary 12, u excludes v if both are present. For $\ell_1^* < \ell < \ell_1^{**}$ (3.17) holds, so $(u^*, 0)$ and $(0, v^*)$ are both unstable and (u^{**}, v^{**}) exists, so there is coexistence. For $\ell > \ell_1^{**}$ (3.17) is again reversed, so u excludes v.

4.3.1 (iii) Biological Discussion. For q in the range shown in (4.7), the quality of the second resource, which is scaled quadratically, is low enough that the consumer v which is more efficient at using it never gains competitive dominance but high enough that the two consumers can coexist for some values of ℓ. In the interval (ℓ_1^*, ℓ_1^{**}), where coexistence is possible, ℓ is large enough for the quadratic scaling to increase the relative abundance of the second resource but not so large that the effects of apparent competition as mediated by u reduce the second resource to the point that v cannot persist. For $\ell > \ell_1^{**}$ the effect of apparent competition reduces the level of the second resource to the point that v cannot persist.

If q is reduced still further so that

$$q < \frac{27}{4}\left(-\frac{\alpha\gamma}{\beta^2}\right)\frac{(b_1/c_1)}{[1+(b_1/c_1)]^3}, \tag{4.8}$$

then (3.16) always holds and (3.17) never holds. We have $\ell < \ell_1 < \ell_2$ but $\ell_1^*, \ell_2^*, \ell_1^{**}$, and ℓ_2^{**} do not exist. In that case there is never coexistence and u excludes v if $\ell > \ell_1$ and both species are present. When (4.8) holds the quality of the second resource is so low that v cannot compete effectively with u for any value of ℓ.

iv. Suppose that instead of decreasing q we increase q, so $q > -\alpha\gamma/\beta^2$. By Lemma 6, $\ell_2 < \ell_1 < \beta/\alpha$. We still have $d\ell_2^*/dq < d\ell_1^*/dq < 0$ at $q = -\alpha\gamma/\beta^2$ by (4.5), so $\ell_2^* < \ell_1^* < \beta/\alpha$. As $\ell \downarrow \ell_1$, we have $u^* \downarrow 0$. Also, since $\ell_2 < \ell_1$, (3.6) will hold for $\ell \approx \ell_1$, and in fact we must have $a_4q\ell^2 + a_3\ell - d_2 \geq \delta$ for some $\delta > 0$ if $\ell \geq \ell_1$. Thus, for $\ell > \ell_1$ but $\ell \approx \ell_1$ the condition (A.8) in the appendix must hold, so by the proof of Lemma 9 it follows that we must have $1 + (\gamma/\alpha q\ell^2) > 0$ and (3.17) must hold. Hence, we must have $\ell_1^* < \ell_1$. By Lemma 10 $(0, v^*)$ is stable for $\ell \in (\ell_2, \beta/\alpha)$. Since $\ell_2^* < \ell_1^*$, (3.16) is reversed for $\ell_1 < \ell < \ell_2^{**}$. (Note that we must still have $\ell_1^{**} \neq \ell_2^{**}$, so the relation $\ell_2^{**} < \ell_1^{**}$ remains valid.) Thus, there is no coexistence equilibrium (u^{**}, v^{**}) for $\ell_1 < \ell < \ell_2^{**}$ by Lemma 7, and $(0, v^*)$ is stable for $\ell_1 < \ell < \ell_2^{**}$ by Lemma 10, while $(u^*, 0)$ is unstable by Lemma 9. It follows that for $\ell_1 < \ell < \ell_2^{**}$, v excludes u when both consumers are present. When $\ell_2^{**} < \ell < \ell_1^{**}$, (3.16) and (3.17) both hold, so (u^{**}, v^{**}) exists and $(u^*, 0)$ and $(0, v^*)$ are both unstable, so the model predicts coexistence. For $\ell > \ell_1^{**}$ but $\ell < \min\{\ell_u, \ell_v\}$, (3.16) is reversed but (3.17) still holds so (u^{**}, v^{**}) does not exist, $(u^*, 0)$ is stable, and $(0, v^*)$ is unstable, so u excludes v if both are present. This arrangement persists as q is increased further.

4.3.1 (iv) Biological Discussion. When q is larger than $-\dfrac{\alpha\gamma}{\beta^2}$, the quality of the second resource is high enough that v has an advantage over u until ℓ is so large that u reduces the second resource enough first to coexist with and then exclude v.

4.3.2 **Case 2 (brief description).** $1/2 < b_1/c_1 < b_2/c_2$. The quantities that depend on b_1/c_1 and b_2/c_2 are $\ell_1^*, \ell_1^{**}, \ell_2^*$, and ℓ_2^{**}. Reversing the relation between b_1/c_1 and b_2/c_2 from Case 1 has the effect of reversing the relative positions of ℓ_1^* and ℓ_2^* and of ℓ_1^{**} and ℓ_2^{**}, but does not affect ℓ_1 or ℓ_2. The only other effect of reversing the relation between b_1/c_1 and b_2/c_2 is that by Lemma 8, (u^{**}, v^{**}) is unstable when it exists if $b_2/c_2 > b_1/c_1$. The net effect is that the pattern of spatial dependence in this case is the same as in Case 1, except that when Case 1 predicts stable coexistence, Case 2 predicts bistability. (Bistability means $(u^*, 0)$ and $(0, v^*)$ are both stable, but (u^{**}, v^{**}) is not, so the outcome of competition depends on the initial conditions.) Since the patterns and analysis are similar to those of Case 1, we merely summarize them.

If $q = -\alpha\beta/\gamma^2$, then $\ell_1 = \ell_2 = \ell_1^* = \ell_2^* = \beta/\alpha$, and $\ell_1^{**} < \ell_2^{**}$. For $0 < \ell < \beta/\alpha$ neither u nor v can persist. For $\ell > \beta/\alpha$ both $(u^*, 0)$ and $(0, v^*)$ exist, so by itself each competitor can persist. For $\beta/\alpha < \ell < \ell_1^{**}$ (3.17) holds but (3.16) does not, so (u^{**}, v^{**}) does not exist, $(u^*, 0)$ is unstable, $(0, v^*)$ is stable, and hence v excludes u if both are present. For $\ell_1^{**} < \ell < \ell_2^{**}$ neither (3.16) nor (3.17) holds; so, since $b_2/c_2 > b_1/c_1$ the state (u^{**}, v^{**}) exists but is unstable. However, $(u^*, 0)$ and $(0, v^*)$ are both stable, so the system is bistable and the outcome of competition is contingent on the initial data. For $\ell > \ell_2^{**}$ (but $\ell < \min\{\ell_u, \ell_v\}$), (3.16) holds but (3.17)

does not, so (u^{**}, v^{**}) does not exist; $(u^*, 0)$ is stable; and $(0, v^*)$ is unstable. Thus, u excludes v. This is essentially the pattern in Case 1, except that for intermediate values of ℓ where neither species necessarily excludes the other the prediction is bistability (so that either species may win the competition, depending on initial data) rather than stable coexistence. (See the discussion following Lemma 8 for some additional biological interpretation.)

4.3.3 **Case 3 (detailed analysis)**. $b_2/c_2 < 1/2 < b_1/c_1$. i. Again, consider the case where $q = -\alpha\gamma/\beta^2$, so that $\ell_1 = \ell_2 = \beta/\alpha$. Since $b_2/c_2 < 1/2 < b_1/c_1$, it follows from (4.4) that the local minimum for the cubic in (3.17) occurs for $\ell > \beta/\alpha$ and the local minimum for the cubic in (3.16) occurs for $\ell < \beta/\alpha$. When $q = -\alpha\gamma/\beta^2$ both cubics have roots at $\ell = \beta/\alpha$; thus, we have $\beta/\alpha = \ell_1^* = \ell_2^{**}$ so that (3.16) always holds for $\ell > \beta/\alpha$ while (3.17) holds for $\beta/\alpha < \ell < \ell_1^{**}$ but not for $\ell_1^{**} < \ell < \min\{\ell_u, \ell_v\}$. It follows that neither competitor can persist for $\ell < \beta/\alpha$, but both $(u^*, 0)$ and $(0, v^*)$ exist for $\ell > \beta/\alpha$. Since (3.16) holds for $\ell > \beta/\alpha$, $(0, v^*)$ is always unstable by Lemma 10. Since (3.17) holds for $\beta/\alpha < \ell < \ell_1^{**}$, it follows from Lemma 9 that $(u^*, 0)$ is unstable and from Lemma 7 that (u^{**}, v^{**}) exists for $\beta/\alpha < \ell < \ell_1^{**}$. Also, by Lemma 8, (u^{**}, v^{**}) is stable when it exists, so for $\beta/\alpha < \ell < \ell_1^{**}$ the model predicts coexistence. For $\ell > \ell_1^{**}$ (but $\ell < \min\{\ell_u, \ell_v\}$), (3.17) is reversed so $(u^*, 0)$ is stable and (u^{**}, v^{**}) does not exist. Thus, for $\ell > \ell_1^{**}$, u excludes v.

4.3.3 (i) Biological Discussion. This case differs from Case 1 in that there is no longer an interval in ℓ where v can exclude u. The reason is that b_2/c_2, which measures the relative preference of consumer v for the resource which is used more effectively by consumer u, is so small that v never consumes enough of it to exclude u. In other words, the niche occupied by v does not overlap a large enough fraction of the niche occupied by u for v to exclude u when $q = -\alpha\gamma/\beta^2$.

ii. If we decrease q, then as always we have $\beta/\alpha < \ell_1 < \ell_2$. Calculating $d\ell_2^{**}/dq$ and $d\ell_1^*/dq$ via (4.5) (or noting that decreasing q raises the graphs of the cubics in (3.16) and (3.17) and observing how this affects their roots) yields $\ell_2^{**} < \beta/\alpha$ and $\ell_1^* > \beta/\alpha$. Also, when $\ell \approx \ell_2$, $\ell > \ell_2$, we have $v^* \approx 0$ but u^* will be somewhat larger than zero for $\ell \approx \ell_2$ since $\ell_1 < \ell_2$. Thus, for $\ell \approx \ell_2$, $\ell > \ell_2$, the inequality (A.18) will hold (because (3.4) holds and v^* is small), but (A.8) will fail because (3.6) just barely holds and u^* is fairly large. Thus, $(u^*, 0)$ will be stable while $(0, v^*)$ will be unstable, so we must have $\ell_1^* > \ell_2$. In this situation neither competitor persists for $\ell \leq \ell_1$; there is an equilibrium $(u^*, 0)$ but v does not persist for $\ell_1 < \ell \leq \ell_2$, and both $(u^*, 0)$ and $(0, v^*)$ exist for $\ell > \ell_2$. The equilibrium $(0, v^*)$ is always unstable because $\ell_2^{**} < \beta/\alpha < \ell_2$ so that (3.16) holds whenever $v^* > 0$ exists. For $\ell_2 < \ell < \ell_1^*$ the equilibrium $(u^*, 0)$ is stable and (u^{**}, v^{**}) does not exist because (3.17) is reversed, so u excludes v if both are present. For $\ell_1^* < \ell < \ell_1^{**}$ both (3.16) and (3.17) hold, so $(u^*, 0)$ and $(0, v^*)$ are both unstable; (u^{**}, v^{**}) exists, and thus the model predicts coexistence. For $\ell > \ell_1^{**}$ (3.17) is again reversed, so (u^{**}, v^{**}) does not exist and $(u^*, 0)$ is stable, so that the model predicts u will exclude v. If q is reduced further the situation described above persists until the graph of the cubic in (3.17) is raised enough that (3.17) always holds. Once that happens, then whenever $(u^*, 0)$ and $(0, v^*)$ exist we have $(u^*, 0)$ stable and $(0, v^*)$ unstable. Also,

(u^{**}, v^{**}) fails to exist, so u excludes v.

4.3.3 (ii) Biological Discussion. Again, the situation is similar to Case 1, except that for $q < -\alpha\gamma/\beta^2$ with $q \approx -\alpha\gamma/\beta^2$ there is no longer any range of ℓ where v can exclude u. (This situation again is due to the relatively small impact of v on the resource preferred and used most effectively by u.

iii. If q is increased from $-\alpha\gamma/\beta^2$ then (as always) we have $\ell_2 < \ell_1 < \beta/\alpha$. In this situation we have $\ell_2^{**} > \beta/\alpha$ and $\ell_1^* < \beta/\alpha$. Thus, for $\ell_2 < \ell < \ell_1$, $(0, v^*)$ exists but $(u^*, 0)$ does not. At $\ell = \ell_1$ we have $v^* > 0$ but u^* still does not exist; and $u^* \to 0$ as $\ell \downarrow \ell_1$. It follows that $(u^*, 0)$ is unstable for $\ell \approx \ell_1$, $\ell > \ell_1$ (since $\ell_2 < \ell_1$ and thus $(0, 0)$ is unstable with respect to v), so we must have $\ell_1^* < \ell_1$. Thus, in this situation, $(0, v^*)$ exists and is stable for $\ell_2 < \ell < \ell_2^{**}$. For $\ell_1 < \ell < \ell_2^{**}$, $(u^*, 0)$ exists but is unstable, $(0, v^*)$ exists and is stable, and (u^{**}, v^{**}) does not exist (because (3.16) fails but (3.17) holds) so v excludes u if both are present. For $\ell_2^{**} < \ell < \ell_1^{**}$ both $(u^*, 0)$ and $(0, v^*)$ are unstable and (u^{**}, v^{**}) exists, so the species coexist, because (3.16) and (3.17) both hold. For $\ell > \ell_1^{**}$ (3.17) fails so $(u^*, 0)$ is stable while $(0, v^*)$ is still unstable and (u^{**}, v^{**}) does not exist, so u excludes v.

4.3.3 (iii) Biological Discussion. The pattern of how the outcome of competition depends on ℓ in this case with $q > -\alpha\gamma/\beta^2$ is qualitatively the same as in Case 1, so that v excludes u on relatively small patches, they coexist on patches of intermediate size, and u excludes v on larger patches. As in Case 1, the mechanism is that when the quality q of the resource used most effectively by v is sufficiently high, v will have an advantage until the patch is large enough for u to reduce that resource enough to impact v via apparent competition.

4.3.4 **Case 4 (brief description).** $b_1/c_1 < 1/2 < b_2/c_2$.

i. If $q = -\alpha\gamma/\beta^2$ in this case then $\ell_1 = \ell_2 = \ell_1^{**} = \ell_2^* = \beta/\alpha$ with $\ell_1^* < \beta/\alpha < \ell_2^{**}$. For $\beta/\alpha < \ell < \ell_2^{**}$ both $(u^*, 0)$ and $(0, v^*)$ will exist, but neither (3.16) nor (3.17) will hold, so $(u^*, 0)$ and $(0, v^*)$ will both be stable and (u^{**}, v^{**}) will exist but will be unstable. Thus, the system will be bistable for that range of ℓ. For $\ell > \ell_2^{**}$, (3.16) will hold but (3.17) will not, and so $(0, v^*)$ will be unstable, $(u^*, 0)$ will be stable, and (u^{**}, v^{**}) will not exist. Thus, for $\ell_2^{**} < \ell < \min\{\ell_u, \ell_v\}$, u will exclude v if both are present.

4.3.4 (i) Biological Discussion. This pattern of dependence on ℓ is similar to that of Case 2, but without the interval with $\ell > \beta/\alpha$, $\ell \approx \beta/\alpha$ in Case 2 where v excludes u. The state $(u^*, 0)$ is always stable when it exists. The hypothesis $b_1/c_1 < 1/2$ means that u has a very strong preference for the second resource, which is the resource used more effectively by v. Thus, u has a strong impact on v through apparent competition over a wide range of ℓ.

ii. If q is decreased from $-\alpha\gamma/\beta^2$, in this case we get $\beta/\alpha < \ell_1 < \ell_2$ (as always), $\ell_1^{**} < \beta/\alpha$, and $\ell_2^* > \beta/\alpha$. Again, we have $v^* \approx 0$ for $\ell \approx \ell_2$, $\ell > \ell_2$, and since $\ell_2 > \ell_1$, we must have strict inequality in (3.4) for $\ell = \ell_2$; so, (A.18) holds for $\ell \approx \ell_2$, $\ell > \ell_2$ and thus $(0, v^*)$ is unstable (and (3.16) holds) for such values of ℓ. For (3.16) to hold we must have either $\ell < \ell_2^*$ or $\ell > \ell_2^{**}$. When $q = -\alpha\gamma/\beta^2$,

we have $\ell_2 = \beta/\alpha < \ell_2^{**}$, so if $q < -\alpha\gamma/\beta^2$, $q \approx -\alpha\gamma/\beta^2$ we still have $\ell_2 < \ell_2^{**}$ by continuity in q, so since (3.16) holds for $\ell = \ell_2$ we must have $\ell_2 < \ell_2^*$. Using continuity in q again, we observe that if $\ell_2^* < \ell_2^{**}$; then ℓ_2 cannot become larger than ℓ_2^* without (3.16) being violated for $\ell > \ell_2$, $\ell \approx \ell_2$. However, $\ell_2^* < \ell_2^{**}$ for $q = -\alpha\gamma/\beta^2$ and the only value of q for which it is ever possible to have $\ell_2^* = \ell_2^{**}$ is $q = -\alpha\gamma/\beta^2$; so, for $q < -\alpha\gamma/\beta^2$ we must have $\ell_2^* < \ell_2^{**}$ and hence the relation $\ell_2 < \ell_2^*$ must remain valid as q is decreased. For $\ell_1 < \ell < \ell_2$, $(u^*, 0)$ exists but $(0, v^*)$ does not, nor does (u^{**}, v^{**}). For $\ell_2 < \ell < \ell_2^*$ both $(u^*, 0)$ and $(0, v^*)$ exist, (3.16) holds, but (3.17) does not; so, $(u^*, 0)$ is stable, $(0, v^*)$ is unstable and (u^{**}, v^{**}) does not exist. Hence for $\ell_2 < \ell < \ell_2^*$, u excludes v. For $\ell_2^* < \ell < \ell_2^{**}$ neither (3.16) nor (3.17) holds; so, both $(u^*, 0)$ and $(0, v^*)$ are stable, and (u^{**}, v^{**}) exists. The system is thus bistable for this range of ℓ. For $\ell_2^{**} < \ell < \min\{\ell_u, \ell_v\}$ (3.16) again is satisfied, but (3.17) is not; so (u^{**}, v^{**}) does not exist, $(0, v^*)$ is unstable, and $(u^*, 0)$ is stable, so u excludes v.

If q is decreased further, eventually (3.16) will hold for all $\ell > 0$ so that u will always exclude v if both can persist by themselves.

4.3.4 (ii) Biological Discussion. This case is similar to Case 3 except that when (u^{**}, v^{**}) exists (for $q < -\alpha\gamma/\beta^2$, but q not too small, and for intermediate values of ℓ) it is unstable, so the prediction in that range of ℓ is bistablity rather than coexistence. This pattern is also similar to Case 2 when $q << -\alpha\gamma/\beta^2$, but does not admit any range of ℓ where v excludes u for values of $q < -\alpha\gamma/\beta^2$. The assumption $b_1/c_1 < 1/2$ apparently makes u too good at reducing the resource which is used most efficiently by v to allow exclusion of u by v when the quality of that resource is low.

iii. If q is increased from $-\alpha\gamma/\beta^2$ then we have $\ell_2 < \ell_1 < \beta/\alpha$, $\ell_1^{**} > \beta/\alpha$, and $\ell_2^* < \beta/\alpha$. For $\ell_2 < \ell \leq \beta/\alpha$, $(0, v^*)$ is stable by Lemma 10. Since $\ell_2^* < \beta/\alpha$, (3.16) does not hold for $\beta/\alpha < \ell < \ell_2^{**}$, so we have $(0, v^*)$ stable for $\ell_2 < \ell < \ell_2^{**}$. For $\ell > \ell_2^{**}$, (3.16) holds, so $(0, v^*)$ is unstable. For $\ell_1 < \ell < \ell_1^{**}$, (3.17) holds, so $(u^*, 0)$ is unstable. For $\ell > \ell_1^{**}$, (3.17) is reversed so $(u^*, 0)$ is stable. Thus, for $\ell_2 < \ell < \ell_1$, $(0, v^*)$ exists but $(u^*, 0)$ does not; for $\ell_1 < \ell < \ell_1^{**}$ both $(u^*, 0)$ and $(0, v^*)$ exist, $(u^*, 0)$ is unstable and $(0, v^*)$ is stable, and (u^{**}, v^{**}) does not exist, so v excludes u. For $\ell_1^{**} < \ell < \ell_2^{**}$ both $(u^*, 0)$ and $(0, v^*)$ are stable and (u^{**}, v^{**}) exists but is unstable, so the system is bistable. For $\ell_2^{**} < \ell < \min\{\ell_u, \ell_v\}$, $(u^*, 0)$ is stable, $(0, v^*)$ is unstable, and (u^{**}, v^{**}) does not exist; so, u excludes v.

4.3.4 (iii) Biological Discussion. The pattern of scale dependence is similar to that seen in Case 3 for large q, except that for intermediate values of ℓ the prediction of coexistence is replaced with bistability. As noted before, this occurs when $b_2/c_2 > b_1/c_1$, because that relationship among parameters means that each consumer prefers the resource which is used most effectively by the other consumer, which results in strong competition and thus in some cases leads to bistability instead of coexistence.

4.3.5 **Case 5 (brief description)**. $b_2/c_2 < b_1/c_1 < 1/2$. For $q = -\alpha\gamma/\beta^2$ in this case we have $\ell_2^* < \ell_1^* < \ell_1 = \ell_2 = \ell_1^{**} = \ell_2^{**} = \beta/\alpha$. For $\ell > \beta/\alpha$ (3.16) holds and (3.17) is reversed, so u excludes v. If q is reduced, we have

$\beta/\alpha < \ell_1 < \ell_2$ but $\ell_1^{**} < \ell_2^{**} < \beta/\alpha$ so that situation is maintained. If q is increased then $\ell_2 < \ell_1 < \beta/\alpha < \ell_2^{**} < \ell_1^{**}$ so for $\ell_1 < \ell < \ell_2^{**}$ (3.17) holds but (3.16) does not, so $(u^*, 0)$ is unstable, $(0, v^*)$ is stable, and (u^{**}, v^{**}) does not exist, so v excludes u. For $\ell_2^{**} < \ell < \ell_1^{**}$, both (3.16) and (3.17) hold, so both $(u^*, 0)$ and $(0, v^*)$ are unstable, (u^{**}, v^{**}) exists, and hence the model predicts coexistence. For $\ell > \ell_1^{**}$ (3.16) holds but (3.17) does not, so $(u^*, 0)$ is stable, $(0, v^*)$ is unstable, and (u^{**}, v^{**}) does not exist, so u excludes v.

4.3.5 Biological Discussion . When q is large, this case shows the same pattern of dependence on ℓ as does Case 1 with q large, for the same reasons as in Case 1. For $q \leq -\alpha\gamma/\beta^2$, this case always predicts exclusion of v by u, which is similar to other cases when q is sufficiently small. Since we have $b_2/c_2 < b_1/c_1 < 1/2$, the coefficients c_1 and c_2 are relatively large compared to b_1 and b_2, so the second resource and specifically its quality q have a strong effect on the competition. Thus, it is not too surprising that the behavior of this case when $q < -\alpha\gamma/\beta^2$ is similar to others when q is very small.

4.3.6 Case 6 (brief description). $b_1/c_1 < b_2/c_2 < 1/2$. If $q = -\alpha\gamma/\beta^2$ we have $\ell_1^* < \ell_2^* < \beta/\alpha = \ell_1 = \ell_2 = \ell_1^{**} = \ell_2^{**}$; so, the system has the same behavior as in Case 5, namely that u excludes v for $\beta/\alpha < \ell < \min\{\ell_u, \ell_v\}$. If q is decreased, then $\ell_2^{**} < \ell_1^{**} < \beta/\alpha < \ell_1 < \ell_2$ so that situation is maintained. If q is increased, then $\ell_2 < \ell_1 < \beta/\alpha < \ell_1^{**} < \ell_2^{**}$. For $\ell_1 < \ell < \ell_1^{**}$, (3.17) holds, but (3.16) does not, so $(u^*, 0)$ is unstable, $(0, v^*)$ is stable, and v excludes u. For $\ell_1^{**} < \ell < \ell_2^{**}$ neither (3.16) nor (3.17) holds, so $(u^*, 0)$ and $(0, v^*)$ are both stable, while (u^{**}, v^{**}) exists but is unstable, so the system is bistable. For $\ell > \ell_2^{**}$ (3.16) holds but (3.17) does not; so, $(u^*, 0)$ is stable, $(0, v^*)$ is unstable, and (u^{**}, v^{**}) does not exist, so u excludes v.

4.3.6 Biological Discussion . This situation is analogous to Case 5 with q large, but with bistability replacing coexistence for an intermediate range of values of ℓ. That occurs because $b_2/c_2 > b_1/c_1$, which means each consumer prefers the resource that the other can use most effectively, resulting in strong competition and hence a tendency toward bistability instead of coexistence.

5. **Summary of Mathematical Conclusions.** The predictions of the original consumer-resource model (2.1) and the corresponding competition model (2.22) obtained from (2.1) by the pseudoequilibrium hypothesis can depend on the scale factor ℓ in a number of complicated ways. In particular, changes in ℓ can cause changes in competitive dominance. There are a few patterns which emerge from the analysis. When ℓ is too small, neither consumer can survive, because there are not enough resources available to sustain populations of consumers. Recall that the models envision two resources, one (R_1) that is supplied across the patch boundary at a fixed rate per unit length to boundary, and another (R_2) that grows logistically on the patch interior. Also, one of the consumers (u) is assumed to be more efficient than the other (v) in using R_1. It turns out that because of the different processes that act to increase R_1 and R_2, it is possible for the consumers to drive R_2 to extinction if the level of R_1 is sufficiently high, but R_1 cannot be driven to extinction. (This phenomenon could be viewed as a type of asymmetric apparent competition between R_1 and R_2; see Abrams [1] for a discussion of this and related

topics.) The significance of this observation is that while the equilibrium value of R_1 in the absence of consumers scales as ℓ while the equilibrium value of R_2 in the absence of consumers scales as ℓ^2, it is the consumer (u) that can use R_1 most effectively that is dominant when ℓ is large. The mechanism is that as ℓ becomes large, u can sustain itself at a high enough level on R_1 that it reduces R_2 sufficiently as to exclude v. For intermediate values of ℓ, the full model (2.1) admits positive equilibria for both R_1 and R_2, so the pseudoequilibrium hypothesis is reasonable.

In the pseudoequilibrium competition model (2.22), the effects of changing ℓ can be complicated; for example, there may be multiple reversals of competitive dominance. There are a few patterns that emerge from that analysis as well. If the quality q of the logistic resource R_2 is sufficiently low, then u will exclude v whenever both could exist on their own. In cases where either $b_1/c_1 > 1/2$ or $b_2/c_2 > 1/2$, values of q that are less than the critical value $-\alpha\gamma/\beta^2$ but not too small typically lead to a pattern where u excludes v for ℓ relatively small (but large enough that each consumer can exist by itself), there is either coexistence or bistability for intermediate sizes of ℓ_1 and u again excludes v if ℓ is large. This pattern reflects the fact that increasing ℓ from a small value to a moderate one tends to benefit the competitor (v) which can use the quadratically scaled resource most effectively, as observed by Pearman [40, 41]. It also reflects the results of apparent competition on the resources, because that is the mechanism by which u excludes v for large values of ℓ. (See [1] for a general discussion of apparent competition and resource depletion, especially as it relates to pseudoequilibrium models.) On the other hand, if q is larger than the critical value $q = -\alpha\gamma/\beta^2$ for which the minimal patch sizes needed to support the two consumers by themselves are the same, the pattern of competitive dominance is that for relatively small values of ℓ, v excludes u; for intermediate values either u and v coexist or the system is bistable (i.e., the outcome of competition depends on the initial data); and for large ℓ, u excludes v. Whether the model displays coexistence or bistability depends on whether $b_1/c_1 > b_2/c_2$ or $b_1/c_1 < b_2/c_2$. In the case $b_1/c_1 > b_2/c_2$, any equilibrium with both u and v present is stable, but for $b_1/c_1 < b_2/c_2$ such equilibria are always unstable. The mechanism is that when $b_1/c_1 > b_2/c_2$, each consumer prefers the resource it can use most effectively, which causes separation of their niches, which favors coexistence; but if $b_2/c_2 > b_1/c_1$ then each consumer prefers the resource which can be used most effectively by the other consumer, which increases niche overlap and makes coexistence less likely. If the values of b_1/c_1 and b_2/c_2 are switched, the only change in the way the predictions of the model (2.22) depend on ℓ is that coexistence is switched with bistability. In other words, if for a given set of parameters the model predicts v excludes u for ℓ small, coexistence for ℓ moderate, and u excludes v for ℓ large, then switching b_1/c_1 and b_2/c_2 would change the pattern only by replacing coexistence with bistability for moderate sizes of ℓ.

6. **Discussion.** This work explores how the spatial scaling of habitats can change species interactions. It formalizes a mechanism through which a change in habitat size can fundamentally alter the outcome of a competitive interaction, making competitive dominance a scale-dependent trait. The keys to the reversals of competitive dominance we found were differential use of patch interior and edge habitats by competing species and differential scaling of the relative availability of those habitats as patch size increased. In some parameter cases we considered in depth,

differences in quality between patch interior and patch edge habitats determined
the range of patch sizes over which competitive dominance occurred. In other cases,
habitat quality can qualitatively affect the existence of those outcomes, and allow
for more complex patterns of scale-dependence in competitive dominance.

Though apparently unique from the perspective of mathematical ecology, the
modeling scenario we discussed is not without meaningful parallels in the real world.
We identified several such examples in the introduction. Additional cases include
studies of birds, fish, and insects. Forest-dwelling birds provide probably the best-
studied examples of core- versus edge- dependent species (e.g., [48]), with interior
species often being replaced by edge-tolerant species in small forest patches. How-
ever, that phenomenon has more to do with predator incursions and nest parasitism
in edge habitats (e.g., [5, 11, 59]) than interspecific competition as we modeled
here. In another example, the competitive ranking of two fish species (perch and
loach) switch as one moves from shallow, macrophyte-dominated habitats to open-
water habitats [42]. This reversal in competitive advantage, which is mediated by
foraging efficiencies that change differentially as a function of habitat structural
complexity, suggests that the relative success of these two fish species may be as-
sociated with the geometric scaling of structurally complex habitats within a lake.
Because one has to consider vagaries of lake depth variation in differentiating shal-
low and openwater habitats, such scaling may not depend on something as simple
as perimeter-to-area ratio, but nevertheless a similarity exists to the hypothetical
cases we modeled. As a final example, Hurd [25] discusses the niche relationships
of praying mantis species that lay their egg cases at different heights in vegetation,
one species (*Tenodera angustipennis*) preferring trees as oviposition substrates while
the other (*Tenodera sinensis*) uses forbs or stalks of pasture grass. Both species
feed on insects from the pasture habitats and engage in size-dependent intraguild
predation. In most pastures studied, the grass-dependent species dominates, but
this may simply reflect the differential availability of oviposition substrates in core
versus edge habitats. Small pastures may feature enhanced opportunities for the
otherwise disadvantaged *T. angustipennis*. Ordinarily the grass-dependent species
dominates, but the asymmetry of the interaction between these mantis species may
lessen as pasture size decreases, increasing the relative availability of trees along
the field margins.

Having reemphasized the biological realities underlying our choice of model, we
briefly return to the issue of model structure. If we had not been interested in
the specific effects of allochthonous resource inputs, we could have rewritten (2.1)
using logistic-type growth dynamics for both edge and interior resource species.
This alternative model would have been entirely appropriate if instead of consider-
ing sea-wrack that washed ashore and subsidized the food webs of desert islands,
Polis and colleagues had focused on populations of shore-living species that might
reasonably be expected to exhibit strong connections between local densities and
local recruitment. However, even this "simpler" model would lead to interesting
scale-dependence in competitive interactions. In particular, note that if one were
to apply the pseudoequilibrium assumption to the alternative, logistic-based four
species model, one would still obtain expressions for the consumer dynamics involv-
ing some terms scaled by ℓ and other terms scaled by ℓ^2. Consequently, analysis
of that alternative model would still require some tedious algebra and would still
generate interesting dependence of competitive success on aspects of habitat geom-
etry. In some ways, the dynamics of that alternative model are actually richer, and

hence more interesting from a purely theoretical perspective, than those issues we discussed here. However, we save elaboration on this issue for future work.

The interplay between patch size, resource quality, and species interactions we modeled here has ramifications for several topics in community ecology. We briefly discuss two of these contact areas here: (1) immigration dynamics and community assembly, and (2) metapopulation dynamics of competing species.

First, we elaborate on the issue of immigration dynamics because of our analytical emphasis on invasibility and patch colonization. We have characterized threshold patch sizes below which a particular species cannot successfully colonize in the absence of competitors as well as patch sizes below which a particular species cannot successfully colonize when the competitors are at their carrying capacity. In the real world of course, other factors, such as the availability of potential dispersers (or dispersal propagules) would interact with patch size to determine species' colonization abilities. For some parameter combinations and patch sizes, initial densities of the competing species determine competitive dominance. In nature, this would give the advantage to species with a higher likelihood of early colonization. Priority effects, stochasticity in arrival sequence, opportunities for multiple colonization events, and other aspects of community assembly dynamics (e.g., [6, 17, 47]) would be major factors influencing species success at the regional level. However, because competitive outcomes are scale-dependent in this model, the same assembly process played out in larger or smaller patch sizes could yield very different results. For example, in some cases, competitive success would switch from being dependent on initial conditions to being a deterministic result.

Second, and arguably of broader importance, our finding that competitive dominance can be a scale-dependent trait bears directly on the subject of multi-species metapopulation dynamics. Under our modeling framework, competing species should be able to succeed within a multi-patch landscape by virtue of differential success in patches of different sizes (see also [2]). No among-patch heterogeneity (other than size) and no competition-colonization tradeoff would seem necessary to promote regional coexistence. In competitive metapopulation dynamics like those of Nee and May [36] or Tilman et al. [54], the competitive hierarchies are fixed and independent of underlying patch characteristics. In contrast, in the current modeling framework, if competitors consistently exhibited different preferences for core and edge resources, then competitive hierarchies would be locally reshuffled merely as a function of patch size. Add in predator success that is also patch-size dependent (e.g., [27, 33, 46]) and the potential for complex relationships between local and regional diversity quickly expands, remaining very strongly determined by the size distribution of patches within a landscape.

The differential scaling of interior and edge-linked resources and consequent scale-dependent opportunities for competitive exclusion may effectively exclude whole suites of patches from meaningful membership in a species' metapopulation. In such cases, the true number of patches available for colonization by the species (and hence available to offset the effects of local extinctions of occupied patches) may be far lower than the amount of available habitat would indicate. Consequently, human activities or landscape processes (e.g., fire) that change the distribution of patch sizes in a landscape could shift the competitive advantage in such systems by altering the "metapopulation capacity" of a landscape [22, 38]. Interestingly, addressing the related issues of scaling and patch size in the "one

patch problem" has yielded some direct, and novel, implications for multipatch, landscape-level issues that deserve further investigation.

In conclusion, this paper highlights that species interactions understood at one spatial scale may exhibit very different outcomes at larger or smaller scales. Consequently, it adds to a growing group of papers that document the importance of domain size to the understanding of ecological phenomena, including population persistence [8, 10, 11, 16, 28, 52] and species interactions [23, 25, 46, 49]. Although we focused on two species competitive interactions, we suspect that models featuring apparent competition, intraguild predation or omnivory would exhibit similar opportunities for scale-dependent outcomes when edge-linked and patch-interior resources scale differentially.

REFERENCES

[1] Abrams, P.A. (1998) *High competition with low similarity and low competition with high similarity: Exploitative and apparent competition in consumer-resource systems.* American Naturalist. 152: 114-128.

[2] Ali, S.W. and C. Cosner. (1995) *Models for the effects of individual size and spatial scale on competition between species in heterogeneous environments.* Mathematical Biosciences. 127: 45-76.

[3] Aronson, D.G. and H.F. Weinberger (1975) *Nonlinear diffusion in population genetics, combustion, and nerve pulse propagation.* In "Partial differential equations and related topics," Lecture notes in mathematics 446, Springer-Verlag, New York.

[4] Bommarco, R. (1998) *Reproduction and energy reserves of a predatory carabid beetle relative to agroecosystem complexity.* Ecological Applications. 8: 846-853.

[5] Britingham, M.C. and S.A. Temple. (1983) *Have cowbirds caused forest songbirds to decline?* Bioscience. 33: 31-35.

[6] Benke, A.C. (1978) *Interactions among coexisting predators: A field experiment with dragonfly larvae.* Journal of Animal Ecology. 47: 335-350.

[7] Bider, J.R. (1968) *Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique.* Ecological Monographs. 38: 269-308.

[8] Cantrell, R.S. and C. Cosner. (2003) "Spatial ecology via reaction-diffusion equations," Wiley, Chichester, West Sussex, UK.

[9] Cantrell, R.S. and C. Cosner. (1994) *Insular biogeographic theory and diffusion models in population dynamics.* Theoretical Population Biology. 45: 177-202.

[10] Cantrell, R.S., C. Cosner, and W.F. Fagan. (2002) *Habitat edges and predator-prey interactions: Effects on critical patch size.* Mathematical Biosciences. 175: 31-55.

[11] Cantrell, R.S., C. Cosner, and W.F. Fagan. (2001) *How predator incursions affect critical patch size: The role of the functional response.* American Naturalist. 158: 368-375.

[12] Cantrell, R.S., C. Cosner, and V. Hutson. (1993) *Permanence in some diffusive Lotka-Volterra models for three interacting species.* Dynamic Systems and Applications. 2: 505-530.

[13] Cantrell, R.S., C. Cosner, and S. Ruan. (2004) *Intraspecific interference and consumer-resource dynamics.* Discrete and Continuous Dynamical Systems. 4B: 527-546.

[14] Case, T.J. (2000) "An illustrated guide to theoretical ecology," Oxford University Press, Oxford, UK.

[15] Chase, J.M., W.G. Wilson, and S.A. Richards. (2001) *Foraging trade-offs and resource patchiness: Theory and experiments with a freshwater snail community.* Ecology Letters. 4: 304-342.

[16] Donaldson, D.D. and R.M. Nisbet. (1999) *Population dynamics and spatial scale: Effects of system size on population persistence.* Ecology. 80: 2492-2507.

[17] Drake, J.A. (1990) *The mechanics of community assembly and succession.* Journal of Theoretical Biology. 147: 213-233.

[18] Fagan, W.F. and J.G. Bishop. (2000) *Trophic interactions during primary succession: Herbivores slow a plant invasion at Mount St. Helens.* American Naturalist. 155: 238-251.

[19] Fagan, W.F., R.S. Cantrell, and C. Cosner. (1999) *How habitat edges change species interactions.* American Naturalist. 153: 165-182.

[20] Fahrig L., and J. Paloheimo. (1988) *Determinants of local-population size in patchy habitats.* Theoretical Population Biology. 34: 194-213.

[21] Groom, M.J. and N. Schumaker. (1990) *Evaluating landscape change: Patterns of worldwide deforestation and local fragmentation.* In: P.M. Kareiva, J.G. Kingsolver, and R.B. Huey, eds. "Biotic interactions and global change." Sinauer Associates, Sunderland, MA.

[22] Hanski, I. and O. Ovaskainen. (2000) *The metapopulation capacity of a fragmented landscape.* Nature. 404: 755-758.

[23] Hassell, M.P., N.H. Comins, and R.M. May. (1991) *Species coexistence and self-organizing spatial dynamics.* Nature. 230: 290-292.

[24] Hess, P. (1991) "Periodic-parabolic boundary value problems and positivity." Pitman research notes in mathematics 247. Longman Scientific and Technical, Harlow, Essex, UK.

[25] Hurd, L.E. (1999) *Ecology of praying mantids.* F.R. Prete, H. Wells, P.H. Wells, and L.E. Hurd, eds. "The Praying Mantids." Johns Hopkins University Press, Baltimore, MD, pp. 43-60.

[26] Huxel, G.R. and K. McCann (1998) *Food web stability: The influence of trophic flows across habitats.* American Naturalist. 152: 460-469.

[27] Kareiva, P.M. (1987) *Habitat fragmentation and the stability of predator-prey interactions.* Nature. 326: 388-390.

[28] Kierstead, H. and L.B. Slobodkin. (1953) *The size of water masses containing plankton blooms.* Journal of Marine Research. 12: 141-147.

[29] Kindvall, O., and I. Ahlen. (1992) *Geometrical factors and metapopulation dynamics of the bush cricket, Metrioptera bicolor philippi* (Orthoptera, Tettigoniidae). Conservation Biology. 6: 520-529.

[30] Lancaster, J. (2000) *Geometric scaling of microhabitat patches and their efficacy as refugia during disturbance.* Journal of Animal Ecology. 69: 442-457.

[31] Laurance W.F., S.G. Laurance, L.V. Ferreira, J.M. Rankin-de Merona, C. Gascon, and T.E. Lovejoy. (1997) *Biomass collapse in Amazonian forest fragments.* Science. 278: 1117-1118.

[32] Levin, S. (1992) *The problem of pattern and scale in ecology.* Ecology. 73: 1943-1967.

[33] Ludwig, D., D.G. Aronson, and H.F. Weinberger. (1979) *Spatial patterning of the spruce budworm.* Journal of Mathematical Biology. 8: 217-258.

[34] MacArthur, R.M. (1972) *Geographic ecology.* Harper and Row, New York.

[35] Murray, J.D. (1993) "Mathematical Biology," Springer-Verlag, Berlin, Germany.

[36] Nee, S. and R.M. May. (1992) *Dynamics of metapopulations: Habitat destruction and competitive coexistence.* Journal of Animal Ecology. 64: 141-144.

[37] Ostman, O., B. Ekbom, J. Bengtsson, and A.C. Weilbull. (2001) *Landscape complexity and farming practice influence the condition of polyphagous carabid beetles.* Ecological Applications. 11: 480-488.

[38] Ovaskainen, O. and O. Hanski. (2001) *Spatially structured metapopulation models: Global and local assessment of metapopulation capacity.* Theoretical Population Biology. 60: 281-302.

[39] Pascual, M. and S. Levin. (1999) *From individuals to population densities: Searching for the intermediate scale of nontrivial determinism.* Ecology. 80: 2225-2236.

[40] Pearman, P.B. (1993) *Effects of habitat size on tadpole populations.* Ecology. 74: 1982-1991.

[41] Pearman, P.B. (1995) *Effects of pond size and consequent predator density on two species of tadpoles.* Oecologia. 102: 1-8.

[42] Persson, L. and P. Eklöv. (1995) *Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach.* Ecology. 76(1): 70-81.

[43] Polis, G.A., W.B. Anderson, and R.D. Holt. (1997) *Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs.* Annual Review of Ecology and Systematics. 28: 289-316.

[44] Polis, G.A., S.D. Hurd, C.T. Jackson, and F. Sanchez-Piñero. (1998) *Multifactor population limitation: Variable spatial and temporal control of spiders on Gulf of California islands.* Ecology. 79: 490-502.

[45] Polis, G.A. and S.D. Hurd. (1996) *Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities.* American Naturalist. 147: 396-423.

[46] Post, D.M., M.L. Pace, and N.G. Hairston. (2000) *Ecosystem size determines food-chain length in lakes.* Nature. 405: 1047-1049.

[47] Robinson, J.V. and J.E. Dickerson. (1987) *Does invasion sequence affect community structure.* Ecology. 68: 587-595.

[48] Robinson, S.K., F.R. Thompson, T.M. Donovan, D.R. Whitehead, and J. Faaborg. (1995) *Regional nesting success of migratory birds.* Science. 267: 1987-1990.

[49] Roland, J. and P.D. Taylor. *Insect parasitoid species respond to forest structure at different spatial scales.* Nature. 386: 710-713.

[50] Rose, M.D. and G.A. Polis. (1998) *The distribution and abundance of coyotes: The effects of allochthonous food subsidies from the sea.* Ecology 79: 998-1007.

[51] Sanches-Piñero, F. and G.A. Polis. (2000) *Bottom-up dynamics of allochthonous input: Direct and indirect effects of seabirds on islands.* Ecology. 81: 3117-3132.

[52] Skellam, J.G. (1951) *Random dispersal in theoretical populations.* Biometrika. 38: 196-218.

[53] Smith, H.L. (1995) "Monotone dynamical systems." Mathematical surveys and monographs 41, American Mathematical Society, Providence, RI.

[54] Tilman, D., R.M. May, C.L. Lehman, and M.A. Nowak. (1994) *Habitat destruction and the extinction debt.* Nature. 371: 65-66.

[55] Turchin, P. (1998) "Quantitative analysis of movement," Sinauer. Sunderland, Massachusetts.

[56] Turner, M.G. and R.V. O'Neill. (1992) Exploring aggregation in space and time. C.G. Jones and J.H. Lawton, eds. "Linking species and ecosystems." Chapman and Hall, New York.

[57] Weathers, K.C., M.L. Cadnasso, and S.T.A. Pickett. (2001) *Forest edges as nutrient and pollutant concentrators: Potential synergisms between fragmentations, forest canopies, and the atmosphere.* Conservation Biology. 15: 1506-1514.

[58] Weins, J.A., C.S. Crawford, and J.R. Gosz. (1985) *Boundary dynamics: A conceptual framework for studying landscape ecosystems.* Oikos 45: 412-427.

[59] Wilcove, D.S. (1985) *Nest predation in forest tracts and the decline of migratory songbirds.* Ecology 66: 1211-1214.

[60] Yodzis, P. (1989) "Introduction to theoretical ecology," Harper and Row, New York.

Appendix

Sketch of Proof of Lemma 1. The quantities R_1 and R_2 are subsolutions to the equations

$$\dot{R}_1 = \rho\ell - d_3 R_1$$

and

$$\dot{R}_2 = r\left(1 - \frac{R_2}{K\ell^2}\right) R_2$$

respectively, so they are asymptotically bounded by $(\rho\ell/d_3) + \epsilon$ and $K\ell^2 + \epsilon$, respectively, for any $\epsilon > 0$. For constants $P, Q > 0$ we have

$$
\begin{aligned}
(Pu + Qv + R_1 + R_2)^\bullet \ &= (PA_1 - B_1)R_1 u \\
&\quad + (PA_2 q - C_1)R_2 u + (QA_3 - B_2)R_1 v \\
&\quad + (QA_4 q - C_2)R_2 v - Pd_1 u - Qd_2 v \\
&\quad + M(R_1, R_2)
\end{aligned}
\tag{A.1}
$$

where M is independent of u and v. If P and Q are chosen small enough that the coefficients of the first four terms on the right side of (A.1) are negative, then the asymptotic bounds on R_1 and R_2 together with (A.1) imply that for large t,

$$(Pu + Qv + R_1 + R_2)^\bullet \leq M_1 - \delta(Pu + Qv + R_1 + R_2) \tag{A.2}$$

where $\delta = \min\{d_1, d_2\}$ and M_1 depends only on the asymptotic bounds on R_1 and R_2 and the coefficients of (2.1). The asymptotic boundedness of u and v then follows from (A.2).

Proof of Lemma 2. By Lemma 1, there is a constant M_2 (independent of the initial conditions on u, v, R_1, R_2) such that for t sufficiently large $B_1 u + B_2 v + d_3 \le M_2$, so that for large t, $\dot{R}_1 \ge \rho\ell - M_2 R_1$. Any solution of $\dot{R} = \rho\ell - M_2 R$ with $R(0) > 0$ must eventually become larger than $(\rho\ell/M_2) - \epsilon$ for any $\epsilon > 0$. Since R_1 is a supersolution, we have $R_1(t) > R(t)$ if $R(0) = R_1(0)$, so for large t we have $R_1(t) > (\rho\ell/M_2) - \epsilon$ as well. We may choose ϵ so that $(\rho\ell/M_2) - \epsilon > 0$.

Proof of Lemma 3. Consider first the case where $u(0), v(0), R_1(0)$, and $R_2(0)$ are all positive. Let $w = u^{-\mu} v^{-\nu} R_1^{-\tau} R_2$, where μ, ν, and τ are positive constants to be chosen later. By Lemma 1, $u^{-\mu} v^{-\nu} R_1^{-\tau}$ is bounded from below by some positive constant for t sufficiently large, so if $w \to 0$ as $t \to \infty$ then $R_2(t) \to 0$ as $t \to \infty$. Computing $\dot{w}$ yields

$$\dot{w} = [-\mu(A_1 R_1 + A_2 q R_2 - d_1) - \nu(A_3 R_1 + A_4 q R_2 - d_2)$$

$$-\tau\left(\frac{\rho\ell}{R_1} - d_3 - B_1 u - B_2 v\right)$$

$$+r\left(1 - \frac{R_2}{k\ell^2}\right) - C_1 u - C_2 v]w.$$

Thus, we have

$$\dot{w} \le [-\mu A_1 R_1 + \mu d_1 - \nu A_3 R_1 + \nu d_2 - \frac{\tau\rho\ell}{R_1}$$

$$+\tau d_3 + \tau B_1 u + \tau B_2 v + r - C_1 u - C_2 v]w$$

Choosing $\tau = \min\{C_1/B_1, C_2/B_1\}$ we have

$$\dot{w} \le [-(\mu A_1 + \nu A_3)R_1 - \frac{\tau\rho\ell}{R_1} + \mu d_1 + \nu d_2 + \tau d_3 + r]w. \qquad (A.3)$$

The minimum of the expression

$$(\mu A_1 + \nu A_3)R_1 + \frac{\tau\rho\ell}{R_1}$$

for $R_1 > 0$ is given by

$$2\sqrt{(\mu A_1 + \nu A_3)\tau\rho\ell}$$

so (A.3) implies

$$\dot{w} \le [-2\sqrt{(\mu A_1 + \nu A_3)\tau\rho\ell} + \mu d_1 + \nu d_2 + \tau d_3 + r]w. \qquad (A.4)$$

In general if we choose any fixed positive values for μ and ν, then the expression in square brackets on the right side of (A.4) is clearly negative if ℓ is sufficiently large; so, in that case $w(t) \to 0$ as $t \to \infty$ and thus $R_2(t) \to 0$ as $t \to \infty$.

If $v(0) = 0$, then $v(t) = 0$ for all t. If we take $\nu = 0$ and $\tau = C_1/B_1$, then in that case we may replace (A.3) with

$$\dot{w} \le \left[-\mu A_1 R_1 - \frac{C_1 \rho\ell}{B_1 R_1} + \mu d_1 + \frac{C_1 d_3}{B_1} + r\right]w \qquad (A.5)$$

and then we may replace (A.4) with

$$\dot{w} = \left[-2\sqrt{\mu A_1 C_1 \rho \ell / B_1} + \mu d_1 + \frac{C_1 d_3}{B_1} + r \right] w. \qquad (A.6)$$

Choosing $\mu > 0$ to minimize the first two terms inside the square brackets yields

$$\dot{w} \leq \left[-\frac{A_1 C_1 \rho \ell}{B_1 d_1} + \frac{C_1 d_3}{B_1} + r \right] w. \qquad (A.7)$$

The expression inside the square brackets in (A.7) is negative provided (2.3) holds, so in that case $w(t) \to 0$ and hence $R_2(t) \to 0$ as $t \to \infty$. The case with $u(0) = 0$, $v(0) > 0$ can be treated analogously and leads to the conclusion $R_2(t) \to 0$ as $t \to \infty$ if (2.4) holds.

Proof of Lemmas 4 and 5. We have

$$(u^{-d_2/d_1} v)^\bullet = u^{-d_2/d_1} v \left[-\frac{d_2}{d_1}(A_1 R_1 + A_2 R_2 q - d_1) + (A_3 R_1 + A_4 R_2 q - d_2) \right]$$

$$= u^{-d_2/d_1} v \left[-\left(\frac{A_1}{d_1} - \frac{A_3}{d_2} \right) d_2 R_1 + \left(\frac{A_4}{d_2} - \frac{A_2}{d_1} \right) d_2 q R_2 \right]$$

By (2.2) $(A_1/d_1) - (A_3/d_2) > 0$, and by Lemma 2, $R_1(t) > \underline{R}_1 > 0$ for large t; so, if $R_2(t) \to 0$ as $t \to \infty$ then for large t $(u^{-d_2/d_1} v)^\bullet \leq -c(u^{-d_2/d_1} v)$ for some $c > 0$. That would imply $u^{-d_2/d_1} v \to 0$ as $t \to \infty$ and hence $v \to 0$ as $t \to \infty$. If (2.5) holds then

$$(u^{-d_2/d_1} v)^\bullet \leq (u^{-d_2/d_1} v) \left[-\left(\frac{A_1}{d_1} - \frac{A_3}{d_2} \right) d_2 R_1 \right]$$

for all t so again $(u^{-d_2/d_1} v) \to 0$ and hence $v \to 0$ as $t \to \infty$.

Proof of Lemma 6. We already know that $\ell_1 < \ell_2$ for q small and $\ell_2 < \ell_1$ for q large. It remains to verify that the value of q for which $\ell_1 = \ell_2$ is uniquely determined as $q = -\alpha\gamma/\beta^2$. If $\ell_1 = \ell_2 = \ell$, then (3.4) and (3.6) imply

$$a_2 q \ell^2 + a_1 \ell - d_1 = 0$$

$$a_4 q \ell^2 + a_3 \ell - d_2 = 0.$$

Multiplying the first equation by a_4 and the second by a_2 and subtracting yields

$$(a_1 a_4 - a_2 a_3)\ell - a_4 d_1 + a_2 d_2 = 0,$$

so that in terms of the quantities in (3.1) we have $\ell = \beta/\alpha$. Solving for q in the first of the quadratics above when $\ell = \beta/\alpha$ gives

$$q = \frac{\alpha^2}{a_2 \beta^2} \left[d_1 - \frac{a_1 \beta}{\alpha} \right] = \frac{\alpha}{a_2 \beta^2}(\alpha d_1 - a_1 \beta) = -\frac{\alpha\gamma}{\beta^2}$$

since $\alpha d_1 - \beta a_1 = -a_2\gamma$. (The corresponding calculation using the second equation gives the same result.) Thus, we can have $\ell_1 = \ell_2$ only in the case described in Lemma 6. In that case it is straightforward to verify $\ell_1 = \ell_2 = \beta/\alpha$ by using the relation $\alpha d_1 - \beta a_1 = -a_2\gamma$. Since decreasing q increases ℓ_1 and ℓ_2, $\ell_1 < \ell_2$ for q small, and we can have $\ell_1 = \ell_2$ only if $q = -\alpha\gamma/\beta^2$, it follows that $\ell_2 > \ell_1 > \beta/\alpha$ for $q < -\alpha\gamma/\beta^2$. Similarly, since $\ell_1 > \ell_2$ for q large we must have $\beta/\alpha > \ell_1 > \ell_2$ for $q > -\alpha\gamma/\beta^2$.

Stability Analysis (Lemmas 8-10).

The system (2.22) has the form

$$\dot{u} = f(u, v)u$$

$$\dot{v} = g(u, v)v$$

so the Jacobian has the form

$$J = \begin{pmatrix} uf_u + f & uf_v \\ vg_u & vg_v + g \end{pmatrix}.$$

Proof of Lemma 8. At a coexistence equilibrium (u^{**}, v^{**}) we have $f = g = 0$. Computing f_u, f_v, g_u, g_v gives

$$f_u = \frac{-a_1 b_1 \ell}{(1 + b_1 u + b_2 v)^2} - c_1 a_2 q \ell^2$$

$$f_v = \frac{-a_1 b_2 \ell}{(1 + b_1 u + b_2 v)^2} - c_2 a_2 q \ell^2$$

$$g_u = \frac{-a_3 b_1 \ell}{(1 + b_1 u + b_2 v)^2} - c_1 a_4 q \ell^2$$

$$g_v = \frac{-a_3 b_2 \ell}{(1 + b_1 u + b_2 v)^2} - c_2 a_4 q \ell^2.$$

At (u^{**}, v^{**}) we have $1 + b_1 u^{**} + b_2 v^{**} = \alpha \ell / \beta$ by (3.11), so at the equilibrium,

$$J = \begin{pmatrix} \left[\dfrac{-a_1 b_1 \beta^2}{\alpha^2 \ell} - c_1 a_2 q \ell^2 \right] u^{**} & \left[\dfrac{-a_1 b_2 \beta^2}{\alpha^2 \ell} - c_2 a_2 q \ell^2 \right] u^{**} \\ \left[\dfrac{-a_3 b_1 \beta^2}{\alpha^2 \ell} - c_1 a_4 q \ell^2 \right] v^{**} & \left[\dfrac{-a_3 b_2 \beta^2}{\alpha^2 \ell} - c_2 a_4 q \ell^2 \right] v^{**} \end{pmatrix}.$$

Computing $|J - \lambda I|$ yields (after some algebra)

$$\lambda^2 + \left[u^{**} \left(\frac{a_1 b_1 \beta^2}{\alpha^2 \ell} + c_1 a_2 q \ell^2 \right) + v^{**} \left(\frac{a_3 b_2 \beta^2}{\alpha^2 \ell} + c_2 a_4 q \ell^2 \right) \right] \lambda$$

$$+ \frac{u^{**} v^{**} \beta^2 q \ell}{\alpha^2} [b_1 c_2 a_1 a_4 + b_2 c_1 a_2 a_3 - b_2 c_1 a_1 a_4 - b_1 c_2 a_2 a_3].$$

The term multiplying λ is positive. Since all the entries in J have the same sign, the eigenvalues of J must be real. (If $J = \begin{pmatrix} P & Q \\ R & S \end{pmatrix}$ then the equation $|J - \lambda I| = 0$ has the form

$$\lambda^2 - (P + S)\lambda + PS - RQ = 0$$

with discriminant $(P + S)^2 - 4(PS - RQ) = (P - S)^2 + 4RQ$ which will be positive if R and Q have the same sign.) The equation $|J - \lambda I| = 0$ admits a positive root if and only if

$$b_1 c_2 a_1 a_4 + b_2 c_1 a_2 a_3 - b_2 c_1 a_1 a_4 - b_1 c_2 a_2 a_3 < 0,$$

which is equivalent to

$$c_1 c_2 \left(\frac{b_1}{c_1} - \frac{b_2}{c_2} \right) (a_1 a_4 - a_2 a_3) = c_1 c_2 (-\alpha) \left(\frac{b_1}{c_1} - \frac{b_2}{c_2} \right) < 0.$$

Since $\alpha < 0$, the equation $|J - \lambda I| = 0$ admits a positive root, and hence (u^{**}, v^{**}) is unstable, if and only if $\dfrac{b_1}{c_1} < \dfrac{b_2}{c_2}$.

Proof of Lemma 9. At $(u^*, 0)$ the Jacobian takes the form

$$J = \begin{pmatrix} u^* f_u(u^*, 0) & u^* f_v(u^*, 0) \\ 0 & g(u^*, 0) \end{pmatrix},$$

so the eigenvalues of J are $u^* f_u(u^*, 0)$ and $g(u^*, 0)$. Since $f_u < 0$, we have $u^* f_u(u^*, 0) < 0$; the corresponding eigenvector is $(1, 0)$. The eigenvalue

$$g(u^*, 0) = \frac{a_3 \ell}{1 + b_1 u^*} + a_4 q \ell^2 (1 - c_1 u^*) - d_2$$

may be of either sign, depending on the specific parameters. If $g(u^*, 0) = u^* f_u(u^*, 0)$, then that eigenvalue has algebraic multiplicity 2 but geometric multiplicity 1; that is, the eigenvalue admits only the eigenvector $(1, 0)$ but has a generalized eigenvector as well. In all other cases the eigenvector for $g(u^*, 0)$ can be chosen as $(u^* f_v(u^*, 0)/[g(u^*, 0) - u^* f_u(u^*, 0)], 1)$. The equilibrium $(u^*, 0)$ is unstable when $g(u^*, 0) > 0$; that is, when

$$\frac{a_3 \ell}{1 + b_1 u^*} + a_4 q \ell^2 (1 - c_1 u^*) - d_2 > 0. \tag{A.8}$$

In that case the first component of the eigenvector corresponding to $g(u^*, 0)$ is negative. Recall that u^* satisfies

$$\frac{a_1 \ell}{1 + b_1 u^*} + a_2 q \ell^2 (1 - c_1 u^*) - d_1 = 0. \tag{A.9}$$

Multiplying (A.9) by a_3/a_1 yields (after some algebra)

$$\frac{a_3}{1 + b_1 u^*} + a_4 q \ell^2 (1 - c_1 u^*) - d_2 = \left(a_4 - \frac{a_2 a_3}{a_1} \right) q \ell^2 (1 - c_1 u^*) + \frac{a_3 d_1}{a_1} - d_2$$

$$= \frac{1}{a_1} \left[-\alpha q \ell^2 (1 - c_1 u^*) - \gamma \right]. \tag{A.10}$$

Similarly, multiplying by a_4/a_2 yields

$$\frac{a_3 \ell}{1 + b_1 u^*} + a_4 q \ell^2 (1 - c_1 u^*) - d_2 = \frac{1}{a_2} \left[\frac{\alpha \ell}{1 + b_1 u^*} - \beta \right]. \tag{A.11}$$

Thus, the expressions on the right sides of (A.10) and (A.11) are equal, and (A.8) holds if and only if they are positive. Thus, if u^* exists, (A.8) holds if and only if

$$\frac{\alpha \ell}{1 + b_1 u^*} - \beta > 0, \tag{A.12}$$

or equivalently if and only if

$$-\alpha q \ell^2 (1 - c_1 u^*) - \gamma > 0. \tag{A.13}$$

Solving (A.12) and (A.13) for u^* yields

$$\left(1 + \frac{\gamma}{\alpha q \ell^2}\right)/c_1 > u^* > \left(\frac{\alpha \ell}{\beta} - 1\right)/b_1, \qquad (A.14)$$

so that if u^* exists and (A.8) holds then it is necessary that

$$\left(1 + \frac{\gamma}{\alpha q \ell^2}\right) b_1 - \left(\frac{\alpha \ell}{\beta} - 1\right) c_1 > 0, \qquad (A.15)$$

which is equivalent to (3.17). We still need to verify that (3.17) is sufficient for (A.8). Suppose (3.17) and hence (A.15) holds. Equating the two expressions on the right sides of (A.10) and (A.11) and rewriting them yields

$$\frac{-\alpha q \ell^2 c_1}{a_1}\left[\left(1 + \frac{\gamma}{\alpha q \ell^2}\right)\frac{1}{c_1} - u^*\right] = \frac{-\beta b_1}{a_2(1 + b_1 u^*)}\left[u^* - \frac{1}{b_1}\left(\frac{\alpha \ell}{\beta} - 1\right)\right] \qquad (A.16)$$

The left side of (A.16) is clearly decreasing in u^*. The right side of (A.16) is still equal to the form shown on the right side of (A.11), so it is increasing in u^* on the interval $(-1/b_1, \infty)$. (Recall that $\alpha < 0$.) Since $u^* > 0$ is uniquely determined when it exists, if $w > 0$ is a solution of

$$\frac{-\alpha q \ell^2 c_1}{a_1}\left[\left(1 + \frac{\gamma}{\alpha q \ell^2}\right)\frac{1}{c_1} - w\right] = \frac{-\beta b_1}{a_2(1 + b_1 w)}\left[w - \left(\frac{\alpha \ell}{\beta} - 1\right)\right] \qquad (A.17)$$

then we must have $w = u^*$. (Since the left side of (A.17) decreases in w and the right side increases, w is uniquely determined by (A.17) if w exists. If we take $w = \frac{1}{b_1}\left(\frac{\alpha \ell}{\beta} - 1\right)$ then the right side of (A.17) is zero while the left side is positive because of our assumption that (3.17) and hence (A.15) holds. If w is increased to $w = \frac{1}{c_1}\left(1 + \frac{\gamma}{\alpha q \ell^2}\right)$, then the right side of (A.17) becomes positive while the left side becomes zero. Thus, since $u^* = w$ for $w > 0$ satisfying (A.17), it must be the case that (A.14) holds so that (A.8) holds whenever (3.17) is satisfied and $u^* > 0$ exists. Note that by (A.14) we cannot have $u^* > 0$ with $(u^*, 0)$ unstable if $1 + \frac{\gamma}{\alpha q \ell^2} < 0$.

Remark on Lemma 10. The stability analysis for $(0, v^*)$ is analogous to that for $(u^*, 0)$ but in place of (A.8) one obtains

$$\frac{a_1 \ell}{1 + b_2 v^*} + a_2 q \ell^2 (1 - c_2 v^*) - d_1 > 0 \qquad (A.18)$$

and in place of (A.14) one obtains

$$\left(\frac{\alpha \ell}{\beta} - 1\right)\frac{1}{b_2} > v^* > \left(1 + \frac{\gamma}{\alpha q \ell^2}\right)\frac{1}{c_2}$$

and hence (3.16) follows.

Sketch of proof of Lemma 11. Write (2.22) as

$$\dot{u} = F(u, v)$$

$$\dot{v} = G(u, v).$$

For $\epsilon > 0$ we have

$$
\begin{pmatrix} F(\bar{u} + \epsilon\phi, \bar{v} + \epsilon\psi) \\ G(\bar{u} + \epsilon\phi, \bar{v} + \epsilon\psi) \end{pmatrix} = \begin{pmatrix} F(\bar{u}, \bar{v}) \\ G(\bar{u}, \bar{v}) \end{pmatrix} + \epsilon J \begin{pmatrix} \phi \\ \psi \end{pmatrix} + h.o.t.
$$

$$
= \epsilon\lambda \begin{pmatrix} \phi \\ \psi \end{pmatrix} + h.o.t.
$$

so $F(\bar{u} + \epsilon\phi, \bar{v} + \epsilon\psi) > 0$ and $G(\bar{u} + \epsilon\phi, \bar{v} + \epsilon\psi) < 0$ for $\epsilon > 0$ small. We can choose $\epsilon > 0$ so that those inequalities hold and so that $u(0) > \bar{u} + \epsilon\phi$ and $v(0) < \bar{v} + \epsilon\psi$. Let $(\tilde{u}_1, \tilde{v}_1)$ be the solution of (2.22) with $\tilde{u}_1(0) = \bar{u} + \epsilon\phi$ and $\tilde{v}_1(0) = \bar{v} + \epsilon\psi$. We have $u > \tilde{u}_1$ and $v < \tilde{v}_1$ by the order-preserving property of the system. Also, $d\tilde{u}_1/dt > 0$ and $d\tilde{v}_1/dt < 0$ at $t = 0$, so for $\delta > 0$ sufficiently small we have $\tilde{u}_1(\delta) > \tilde{u}_1(0)$, $\tilde{v}_1(\delta) < \tilde{v}_1(0)$. By the order-preserving property of the system, $\tilde{u}_1(t + \delta) > \tilde{u}_1(t)$ and $\tilde{v}_1(t + \delta) < \tilde{v}_1(t)$, so $\tilde{u}_1$ must increase and $\tilde{v}_1$ must decrease. All nonnegative solutions to (2.22) are bounded and nonnegative, so $\tilde{u}_1(t)$ and $\tilde{v}_1(t)$ must converge as $t \to \infty$. By continuity of F and G they must converge to an equilibrium. The proof in the case $\phi < 0$, $\psi > 0$ is similar.

Proof of Lemma 13. Suppose ℓ satisfies (4.3) for $i = 1, 2$. Subtracting (4.3) with $i = 1$ from (4.3) with $i = 2$ yields $(Q_2 - Q_1)(\alpha\beta\ell^2 + \beta\gamma/q) = 0$ so $q = -\gamma/\alpha\ell^2$. Multiplying (4.3) with $i = 1$ by Q_2, multiplying (4.3) with $i = 2$ by Q_1, then subtracting yields $(Q_2 - Q_1)(\alpha^2\ell^3 - \alpha\beta\ell^2) = 0$ so $\ell = \beta/\alpha$. Using $q = -\alpha\gamma/\beta^2$, we see that $\ell - (\beta/\alpha)$ is a factor of the cubic for $i = 1, 2$. Dividing it out and applying the quadratic formula to the result yields $\ell = (\beta/2\alpha)[Q_i \pm \sqrt{Q_i^2 + 4Q_i}]$.