Mathematical Biology

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The evolution of resource use

Abstract. The evolution of a consumer exploiting two resources is investigated. The strategy x under selection represents the fraction of time or energy an individual invests into extracting the first resource. In the model, a dimensionless parameter α quantifies how simultaneous consumption of both resources influences consumer growth; $\alpha < 0$ corresponds to hemi-essential resources, $0 < \alpha < 1$ corresponds to complementary resources, $\alpha = 1$ corresponds to perfectly substitutable resources, and $\alpha > 1$ corresponds to antagonistic resources. An analysis of the ecological and evolutionary dynamics leads to five conclusions. First, when $\alpha \leq 1$, there is a unique singular strategy x^* for the adaptive dynamics and it is evolutionarily stable and globally convergent stable. Second, when $\alpha = 1$, the singular strategy x^* corresponds to the populations exhibiting an ideal free distribution and a population playing this strategy can invade and displace populations playing any other strategy. Third, when $\alpha > 1$, the strategies $x = 0$ and $x = 1$ are evolutionarily stable and convergent stable. Hence, if the populations initially specialize on one resource, evolution amplifies this specialization. Fourth, when α is slightly larger than one (i.e. the resources are slightly antagonistic), there is a convergent stable singular strategy whose basin of attraction is almost the entire strategy space $(0, 1)$. This singular strategy is evolutionarily unstable and serves as an evolutionary branching point. Following evolutionary branching, our analysis and numerical simulations suggest that evolutionary dynamics are driven toward an end state consisting of two populations specializing on different resources. Fifth, when $\alpha \gg 1$, there is only one singular strategy and it is convergent unstable and evolutionarily unstable. Hence, if resources are overly antagonistic, evolutionary branching does not occur and ultimately only one resource is exploited.

1. Introduction

When considering situations in which a population utilizes multiple resources, questions about resource relationships arise. Inspired by microeconomic theory, ecologists classify resource relations as either essential, complementary, perfectly substitutable, or antagonistic [1, 20, 25–27]. For essential resources, population growth is only possible when all resources are consumed. For example, essential resources may include nitrogen and potassium for a plant or two obligate hosts for a parasite. Alternatively, for the remaining resource relations, population growth

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can occur with the consumption of a single resource. Complementary resources are more beneficial when consumed together than when consumed separately. For instance, humans eating certain kinds of beans together with rice can increase the useable protein content of their food by 40% [13]. In contrast, antagonistic resources are more beneficial when consumed separately than when consumed together. This can arise, for instance, if the resources contain different toxins which act synergistically on the consumer [12]. With perfect substitutes, the value derived from the consumption of one resource is a fixed fraction of the value derived from the second resource. This may be true for different grains in the diet of a chicken or antelope and gazelles in the diet of a lion.

The question with which we concern ourselves in this paper is, when presented with multiple resources, how does the evolution of consumer resource use depend on the interplay between the resources? In particular, we consider a population with access to two resources and try to understand how, for various resource relations, the amount of time or energy devoted to the exploitation of these resources evolves. Our modeling efforts begin in section 2 with the development of a basic model describing the dynamics of a population exploiting two resources and in which all the aforementioned resource interactions are represented by a single parameter. In section 3, we present in five parts our analysis of the ecological and evolutionary dynamics. First, we extend the basic model to an arbitrary number of competing strategies and state fundamental results about coexistence and competitive displacement for two and three competing strategies. Second, following the theory of adaptive dynamics (see, e.g., Hofbauer and Sigmund [10, 11], Metz et al. [17], Geritz et al. [6], Diekmann [4]), we discuss notions of evolutionarily stable and convergent stable strategies for a single strategy and coexisting strategies. The remainder of our analysis naturally divides itself into three parts corresponding to three types of resource interaction (perfectly substitutable, antagonistic, and complementary/hemiessential), and our model lends itself neatly to this simple and instructive division of resource types. In section 4, we discuss the implications of our results in the context of the existing ecological literature and state some open problems. This concluding section is followed by appendices devoted to rigorous support of the claims made in the paper.

2. The basic model

We consider a population of consumers that utilizes two resources. Let $R_i(N)$ with $i = 1, 2$ represent the availability of resource i if the density of consumers exploiting resource i is N. As increasing consumer density reduces resource availability, we assume that $R_i(N)$ is a decreasing function (i.e. $R_i'(N) < 0$ for all N) that approaches zero at high consumer density (i.e. $\lim_{N \to \infty} R_i(N) = 0$). For instance, the Schoener [21] resource functions $R_i(N) = \frac{a_i}{1 + b_i N}$ (where a_i is proportional to the rate at which resource i enters the system and b_i is proportional to the searching efficiency of the consumer with respect to resource i) satisfy these assumptions. While Schoener derived these functions as an approximation to a less tractable model, we show in Appendix C how to derive this model directly. If $f(R_1, R_2)$

represents the per capita reproductive rate of the consumers as a function of resource consumption, each consumer spends a fixed portion x of searching time on resource 1 and the remaining portion $1 - x$ on resource 2, and the per-capita mortality rate is μ, then a model of the consumer dynamics is given by

$$\frac{dN}{dt} = Nf(xR_1(xN), (1-x)R_2((1-x)N)) - \mu N. \tag{1}$$

To capture the effects of different resource relations [25, 26], we introduce the following one-parameter family of conversion functions:

$$f(R_1, R_2) = \left(R_1^\alpha + R_2^\alpha\right)^{\frac{1}{\alpha}}$$

When $\alpha = 1$, the resources are perfectly subtitutable: the level curves of f are lines with constant negative slope in the R_1–R_2 plane. When $\alpha > 1$, the level curves of f in the R_1–R_2 plane bow away from the origin and the resources are antagonistic. When $0 < \alpha < 1$, the level curves of f in the R_1–R_2 plane bow toward the origin and the resources are complementary. When $\alpha < 0$, the resources are hemi-essential. As $\alpha \downarrow -\infty$, $f(R_1, R_2) \to \min\{R_1, R_2\}$, the consumption of both resources is essential for the persistence of the consumer. These relationships are summarized in Table 1.

3. The analysis

To study the evolution of resource use, our analysis separates into two parts, an ecological analysis concerning the population dynamics of competing strategies and an evolutionary analysis. Throughout this analysis, we assume that

$$f(xR_1(0), (1-x)R_2(0)) > \mu$$

for all $x \in [0, 1]$. This assumption coupled with our assumptions that the $R_i(N)$ are decreasing functions which approach zero for high densities imply that for each $0 \le x \le 1$ there exists a unique non-zero equilibrium density N_x to (1) (i.e. $f(xR_1(xN_x), (1-x)R_2((1-x)N_x)) = \mu$).

Table 1. Classification of Resources

Parameter Range	Resource Type
$\alpha > 1$	Antagonistic
$\alpha = 1$	Perfectly substitutable
$0 < \alpha < 1$	Complementary
$-\infty < \alpha < 0$	Hemi-essential
$\alpha = -\infty$	Essential

3.1. Dynamics of competing strategies

To talk about the evolution of the strategy x, it is necessary to extend (1) to a model of competing strategies. If there are n populations playing strategies, $x_1, \ldots, x_n$, with densities $N_1, \ldots, N_n$, then the population dynamics of these competing strategies are given by

$$\frac{dN_i}{dt} = N_i f(x_i r_i, (1 - x_i) r_i) - \mu N_i \quad i = 1, \ldots, n \tag{2}$$

where

$$r_1 = R_1 \left(\sum_i x_i N_i \right)$$

$$r_2 = R_2 \left(\sum_i (1 - x_i) N_i \right)$$

We are able to characterize the dynamics of two or three competing strategies. For notational convenience, we define $x = x_1$, $y = x_2$, and $z = x_3$, and $N = N_1$, $M = N_2$, and $Q = N_3$. To understand the dynamics of (2) with two competing strategies (i.e. $n = 2$), it is useful to introduce the invasion rate $s(x, y)$ of strategy y at the equilibrium $(N_x, 0)$ determined by strategy x,

$$s(x, y) = f(y R_1(x N_x), (1 - y) R_2((1 - x) N_x)) - \mu.$$

Regarding the global behavior of (2) with $n = 2$, we prove two results in Appendix A (see Thm. 1). First, in the case of mutual invasibility (i.e. $s(x, y) > 0$ and $s(y, x) > 0$), there is a unique globally stable equilibrium $(N_{x,y}, M_{x,y})$ in the interior of the positive quadrant (i.e. $N_{x,y} > 0$, $M_{x,y} > 0$, and $\lim_{t \to \infty} (N(t), M(t)) = (N_{x,y}, M_{x,y})$ whenever $N(0) > 0$ and $M(0) > 0$). Second, when $s(x, y) > 0$ and $s(y, x) < 0$, the population playing strategy y competitively displace the population playing strategy x (i.e. $\lim_{t \to \infty} (N(t), M(t)) = (0, N_y)$ whenever $M(0) > 0$). Thus, these results imply that knowing the signs of $s(x, y)$ and $s(x, y)$ determines the global behavior of the population dynamics.

Regarding the dynamics of three competing strategies, Theorem 2 in Appendix A proves that if all the equilibria supporting one or two strategies are hyperbolic (i.e. the eigenvalues of the Jacobian at these equilibria have non-zero real parts), then all solutions to (2) with $n = 3$ approach an equilibrium on the boundary of the positive orthant. Hence, generically, populations with three strategies reduce to populations with one or two strategies. Interestingly, when $\alpha = 1$, the assumption of hyperbolic equilibria on the boundary is often violated as there can exist a line of equilibria that passes through the positive orthant.

3.2. Evolutionary analysis

To understand how the strategy x evolves, we follow the adaptive dynamics framework reported in Geritz et al. [6] and Hofbauer and Sigmund [10, 11]. In this framework, one imagines a population, "the residents," plays the strategy x and is

at equilibrium. If a small population playing the strategy y, "the mutants", enters the population, then our results about competing strategies imply that either the mutants are unable to invade (i.e. $s(x, y) < 0$), the mutants invade and displace the residents (i.e. $s(x, y) > 0$ and $s(y, x) < 0$), or the mutants invade and ultimately coexist at equilibrium with residents (i.e. $s(x, y) > 0$ and $s(y, x) > 0$).

A strategy x is called an *evolutionarily stable strategy* (ESS) if residents playing this strategy can not be displaced by mutants playing a different strategy (i.e. the equilibrium $(N_x, 0)$ is asymptotically stable for (2) with $n = 2$, $x_1 = x$, and for all $x_2 \neq x$). A sufficient condition for x to be an ESS is $s(x, y) < 0$ for all $y \neq x$. However, as illustrated in our analysis of perfectly subsitutable resources, this sufficient condition is not necessary.

While evolutionarily stable strategies identify potential evolutionary end states, they do not indicate how the strategy x actually evolves. To this end, we define the local fitness gradient by

$$D(x) = \frac{\partial s}{\partial y}(x, x).$$

$D(x)$ indicates in what direction the strategy x should evolve if mutations are small. If $D(x) > 0$, then mutants with strategy y slightly larger than x can invade and displace the resident strategy x (i.e. $s(x, y) > 0$ and $s(y, x) < 0$ for y slightly larger than x). Alternatively, if $D(x) < 0$, then mutants with strategy y slightly smaller than x can invade and displace the resident strategy x. Thus, if mutations are small and sufficiently infrequent, then in evolutionary time we expect x to follow the fitness gradient $D(x)$ (i.e. increase when $D(x) > 0$ and decrease when $D(x) < 0$).

A strategy $x = x^*$ is a *singular strategy* if the local fitness gradient is zero (i.e. $D(x^*) = 0$). A singular strategy is *convergent stable* if populations playing strategies near x^* can be invaded by mutants playing a strategy closer to x^* (i.e. $D(y) > 0$ for $y < x^*$ near x^* and $D(y) < 0$ for $y > x^*$ near x^*). A sufficient condition for convergent stability is that $D'(x^*) < 0$. In addition to the singular strategies, the strategies $x = 0$ and $x = 1$ can play import roles as evolution may force x to these extremal values. Consequently, we say $x = 0$ (resp. $x = 1$) is *convergent stable* if $D(x) < 0$ for $x \in (0, 1]$ sufficiently close to 0 (resp. $D(x) > 0$ for $x \in [0, 1)$ sufficiently close to 1).

A graphical means to visualize the evolutionary dynamics is with a pairwise invasibility plot (PIP) in $[0, 1] \times [0, 1]$. In these plots (see, e.g., Figs. 2a, 3a, 4a and 6a), the horizontal axis corresponds to the resident strategy x and the vertical axis corresponds to the mutant strategy y. The white and grey regions in the PIP correspond to points (x, y) where $s(x, y) > 0$ and $s(x, y) < 0$, respectively. In these plots singular strategies correspond to x values where there are singularities in the figure. Evolutionary stability is ensured for a strategy x^* if the line $y = x^*$ lies in the grey region of the PIP. Convergent stability of x^* corresponds to there being white above the diagonal of the PIP to the left of $y = x^*$ and there being white below the diagonal of the PIP to the right of $y = x^*$.

A strategy x which is convergent stable and evolutionarily stable is a possible end state for evolution. On the other hand, when a convergent stable strategy x is evolutionarily unstable, strategies to either side of the convergent strategy can

coexist (i.e. mutual invasibility occurs) and evolutionary branching may occur. To continue the evolutionary analysis, it becomes necessary to consider a resident population consisting of two coexisting strategies, say x and y, with densities N and M. If a mutant population arrives at low density Q playing the strategy z, then the invasion rate of this mutant population at the resident equilibrium, $(N_{x,y}, M_{x,y})$, is

$$\tilde{s}(x, y, z) = f(z R_1 (x N_{x,y} + y M_{x,y}), (1-z) R_2 ((1-x) N_{x,y} + (1-y) M_{x,y})) - \mu.$$

When $\tilde{s}(x, y, z) > 0$, mutants playing the strategy z can invade. When $\tilde{s}(x, y, z) < 0$, mutants playing the strategy z are repelled by the resident community.

A pair of coexisting strategies (x, y) are *coevolutionarily stable* if the equilibrium determined by these two strategies is locally asymptotically stable for (2) for all $z \neq y$ and $z \neq x$. Associated with $\tilde{s}$ is the local fitness gradient,

$$\tilde{D}(x, y) = \left(\frac{\partial \tilde{s}}{\partial z}(x, y, x), \frac{\partial \tilde{s}}{\partial z}(x, y, y) \right).$$

The signs of the fitness gradient indicate in what direction the strategies x and y coevolve. For example, if the first component of the gradient is positive and x is not a singular strategy (i.e. $D(x) \neq 0$), our results about the dynamics of competing strategies imply that mutant strategies z slightly larger than x can invade and displace the population of x strategists. To see why this assertion is true, we begin with several observations. First, since $s(x, y) > 0$, $s(y, x) > 0$, and z is sufficiently close to x, the strategies y and z are able to coexist (i.e. $s(z, y) > 0$ and $s(y, z) > 0$). Second, since $\frac{\partial \tilde{s}}{\partial z}(x, y, x) > 0$, $\tilde{s}(x, y, x) = 0$, and z is slightly larger than x, we get that $\tilde{s}(x, y, z) > 0$ and $\tilde{s}(z, y, x) < 0$. Third, since x is not a singular strategy (i.e. $D(x) \neq 0$) and z is sufficiently close to x, we have either strategy z can displace strategy x (i.e. $s(x, z) > 0$ and $s(z, x) < 0$) or vice versa. These three observation imply the dynamics of the $N-M-Q$ phase space are similar to those shown in Fig. 1. Since we have shown convergence to a boundary equilibrium for this system, the invasion of strategy z drives the dynamics to the equilibrium at which only strategies y and z coexist. Alternatively, if the second component of the fitness gradient is negative, then a similar argument implies that mutants playing a strategy z slightly smaller than y can invade and displace the residents playing strategy y. A pair of strategies $(x^*, y^*) \in (0, 1) \times (0, 1)$ is *singular* if $D(x^*, y^*) = (0, 0)$. We say $(0, 1)$ (resp. $(1, 0)$) is *convergent stable* if the first and second components of $\tilde{D}(0, 1)$ (resp $\tilde{D}(1, 0)$) are negative and positive (resp. positive and negative).

In the next three sections, we study the singular strategies and their stability properties when $\alpha = 1$, $\alpha > 1$, and $\alpha < 1$, respectively.

3.3. Perfectly substitutable resources

We begin our analysis with the case of perfectly substitutable resources (i.e. $\alpha = 1$). Lemma 2 in Appendix B shows that there is a unique singular strategy given by
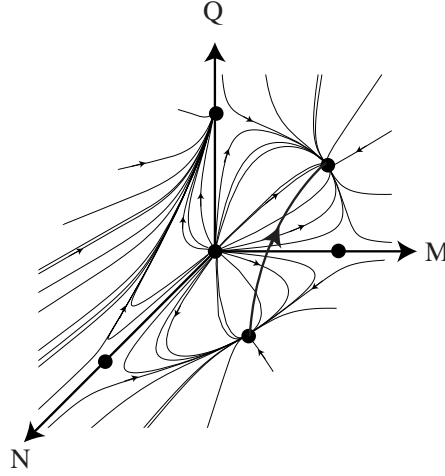
$$x^* = \frac{R_1^{-1}(\mu)}{N_{x^*}}$$

Fig. 1. Dynamics for three competing strategies consisting of the resident strategies x and y with densities N and M and the mutant strategy z with density Q. The figure assumes that $\frac{\partial \bar{s}}{\partial z}(x, y, x) > 0$, z is slightly larger than x and x is not a singular strategy.

where

$$N_{x^*} = R_1^{-1}(\mu) + R_2^{-1}(\mu).$$

This singular strategy is characterized by the fact that when it is played at equilibrium, the per-capita growth rate with respect to each resource is zero. Lemma 2 furthermore shows that $D(x) > 0$ for $x < x^*$ and $D(x) < 0$ for $x > x^*$ which implies the singular strategy is globally convergent stable. Lemma 3 in Appendix B implies that the PIP is always of the form shown in Fig. 2a. (i.e. $s(x, y) < 0$ if and only if $y < x < x^*$ or $y > x > x^*$, and $s(x, y) > 0$ if and only if either $x < y$ and
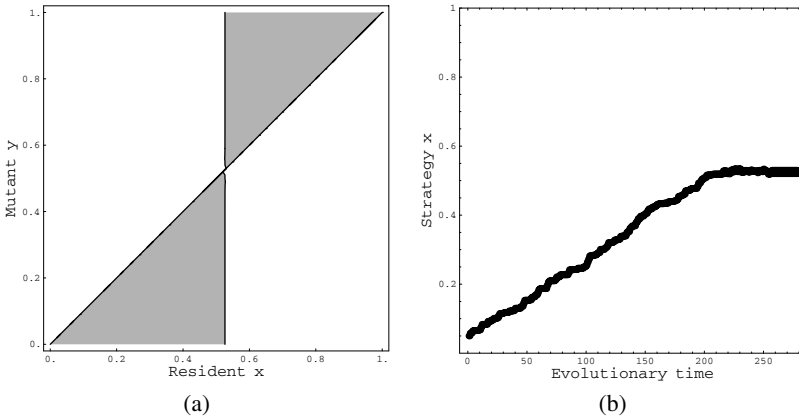

| (a) | (b) |

Fig. 2. *Perfectly substitutable Resources.* (a) a pairwise invasibility plot and (b) simulated evolutionary tree. In both figures $R_1(N) = \frac{1.5}{1+N}, R_2(N) = \frac{1}{1+N}, \mu = 0.1$, and $\alpha = 1.0$.

$x < x^*$ or $x > x^*$ and $y < x$). This leads to two interesting conclusions. First, the singular strategy can invade any other resident strategy (i.e. $s(x, x^*) > 0$ whenever $x \neq x^*$). Second, the invasion rate of every mutant strategy y is zero when x^* is the resident strategy (i.e. $s(x^*, y) = 0$ for all y). Because of these zero invasion rates, we can not determine from the PIP whether x^* is an ESS. A more careful analysis (Thm. 3 in Appendix B) of the dynamics of (2) when $x = x^*$, $y \neq x^*$, and $\alpha = 1$ reveals that the equilibrium $(N_{x^*}, 0)$ for (2) is globally attracting. Consequently, not only is x^* an ESS, but a population playing x^* can invade and competitively displace populations playing any other strategy.

Based on these results, we expect the strategy x to initially evolve toward the ESS x^* (see Fig. 2b). However, what happens after this initial phase of evolution is delicate. This delicacy stems from the fact (as the PIP shows) that any pair of strategies $x < x^* < y$ can coexist. Furthermore, whenever two (or more) strategies coexist at equilibrium the per-capita growth rate with respect to either resource is zero (i.e. $R_1(x N_{x,y} + y M_{x,y}) = R_2((1 - x)N_{x,y} + (1 - y)M_{x,y}) = \mu$). Hence, when these strategies x and y are coexisting, $\tilde{s}(x, y, z) = 0$ for all z. In fact, (see Thm. 2 in Appendix A), the inclusion of any third strategy z results in a line of equilibria that passes through the three strategy phase space. Numerical simulations suggest that whenever the strategy z enters in small numbers, the three strategies approach an equilibrium at which z's density is slightly smaller than its invasion density and at which x and y's densities are close to $N_{x,y}$ and $M_{x,y}$, respectively. Assuming demographic stochasticity would wipe out these low z strategists, then the evolutionary end state would consist of coexisting strategies near x^* (see Fig. 2b). However to show this more rigorously would require a more careful analysis of three competing strategies when $\alpha = 1$ and there is a line of equilibria passing through the positive orthant.

3.4. Antagonistic Resources

When $\alpha > 1$, the resources are antagonistic. Since $D(0) < 0$ and $D(1) > 0$ when $\alpha > 1$, the strategies $x = 0$ and $x = 1$ are convergent stable and evolutionarily stable. It follows that there always exists at least one singular strategy $0 < x^* < 1$. Lemma 4 in Appendix C shows that all singular strategies are evolutionarily unstable. While we are unable to determine in general how the number of singular strategies depend on α, we can say two things. First, when α is slightly larger than one, there exist at least three singular strategies in the interval $(0, 1)$ (see Fig. 3a). One of these singular strategies is convergent stable and its domain of stability approaches the entire interval as α decreases to 1 (see Fig. 5). Second, when the resource functions are given by the Schoener equations $R_i(N) = \frac{a_i}{1+b_i N}$ and α is sufficiently large (more precisely we show $\alpha \geq a_i/\mu$ for $i = 1, 2$ suffices), Thm. 4 in Appendix C implies that there exists a unique singular strategy which is evolutionarily unstable and convergent unstable (see Fig 4a.) Hence, when α is sufficiently large, the adaptive dynamics for almost every initial condition converges either to the ESS $x = 0$ or the ESS $x = 1$ (see Figs. 4b and 4c). Fig. 5 shows how the singular strategies depend on α (i.e. the extent of antagonism).
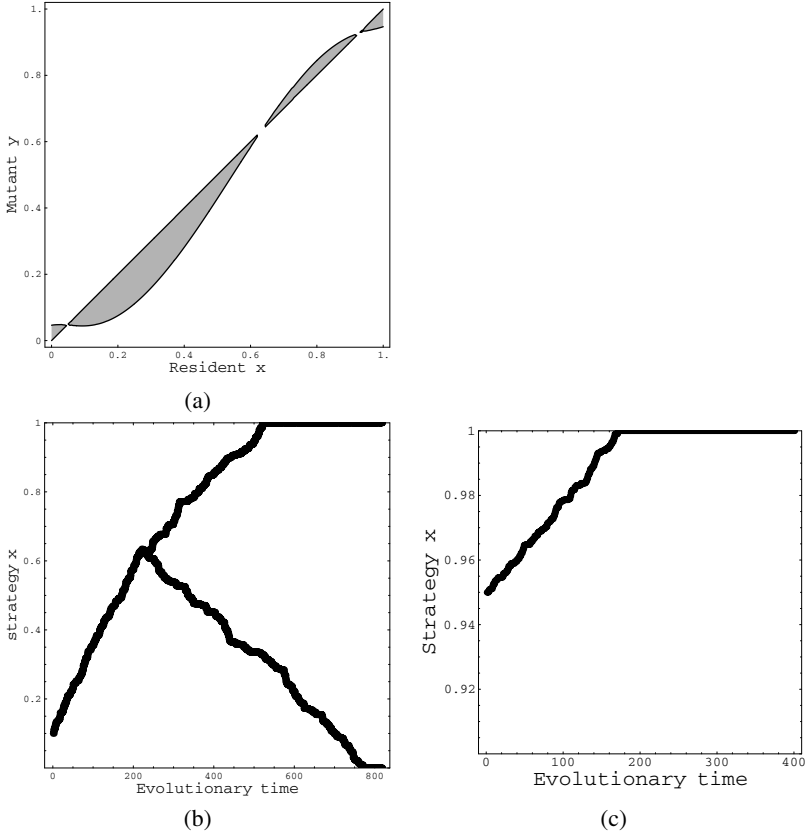
(a)

(b)

(c)

Fig. 3. *Antagonistic Resources.* (a) a pairwise invasibility plot and (b), (c) simulated evolutionary tree with differential initial values of x. In both figures $R_1(N) = \frac{1.1}{1+N}, R_2(N) = \frac{1}{1+N}$, $\mu = 0.1$, and $\alpha = 3.0$.

Evolutionary branching can occur when there exists a convergent stable yet evolutionarily unstable singular strategy. For instance, if the resources are slightly antagonistic, then x initially evolves toward the convergent stable singular strategy (see Fig. 3b). However, as the strategy approaches this evolutionarily unstable strategy, mutants to either side of the singular strategy can coexist and it becomes necessary to consider the dynamics of three competing strategies and the associated adaptive dynamics. Lemma 5 in Appendix C shows that the coexisting strategies $(x, y) = (1, 0)$ and $(x, y) = (0, 1)$ are coevolutionarily stable and convergent stable. The simulations (whose computations are significantly simplified by Thm. 1 and Thm. 2) suggest that following the evolutionary branching, the coexisting strategies converge to one of these stable states (see Fig. 3b).

3.5. Complementary and Hemiessential Resources

When the resource functions are given by $R_i(N) = \frac{a_i}{1+b_i N}$ and $\alpha < 1, \alpha \neq 0$, Thm. 4 in Appendix C implies that there is a unique singular strategy x^* in $(0, 1)$
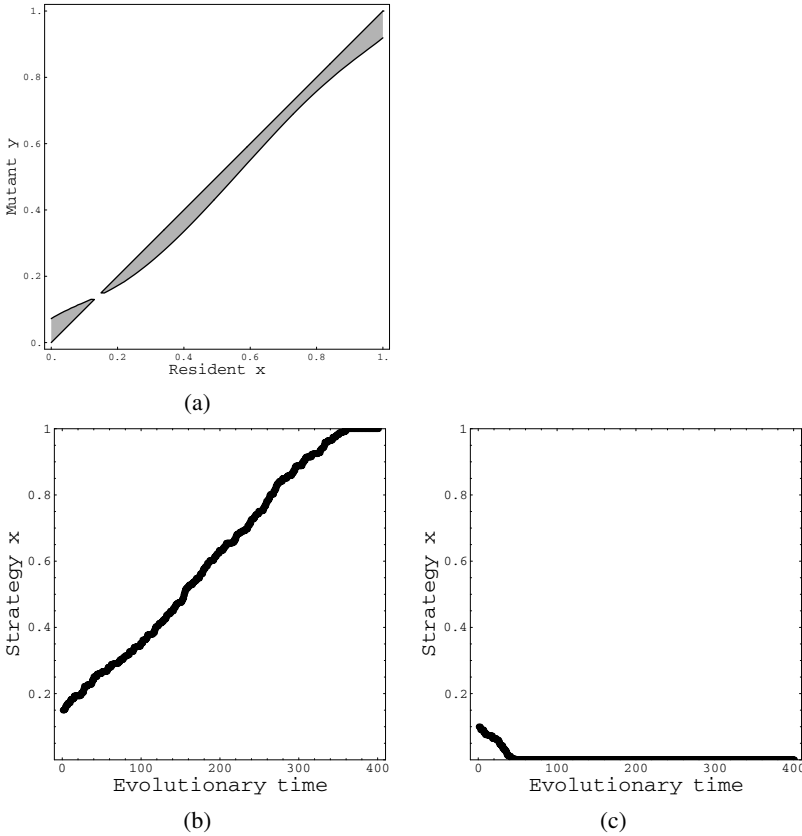
(a)

(b)

(c)

Fig. 4. *Antagonistic Resources.* (a) a pairwise invasibility plot and (b), (c) simulated evolutionary tree with differential initial values of x. In both figures $R_1(N) = \frac{1.1}{1+N}$, $R_2(N) = \frac{1}{1+N}$, $\mu = 0.1$, and $\alpha = 5.0$.

and this strategy is evolutionarily stable and convergent stable. Hence, for complementary and essential resources evolution leads to an evolutionary end state in which the consumers consume both resources (see Fig. 6). We conjecture that this assertion holds for all resource functions $R_i(N)$.

4. Discussion

We studied the evolution of resource use for consumers with access to two resources. After developing basic results about coexistence and competitive displacement of two or three competing strategies, we used the framework of adaptive dynamics [4, 6, 10, 11, 17] to determine how resource interactions influence the evolution of consumer choice.

In the cases of hemi-essential and complementary resources, our results imply that evolution will result in populations that consume both resources. For hemi-essential resources, this stems from the fact that the population can not survive
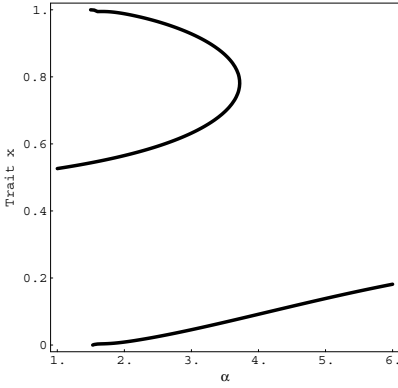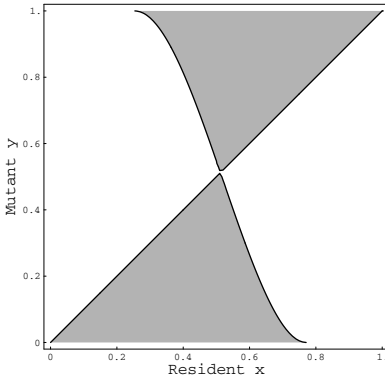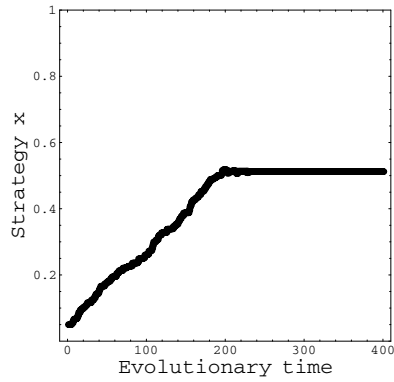
Fig. 5. *Antagonistic Resources.* Singular strategies as a function α.

(a)   (b)

Fig. 6. *Complementary and Hemiessential Resources.* (a) a pairwise invasibility plot and (b) simulated evolutionary tree. In both figures $R_1(N) = \frac{1.1}{1+N}, R_2(N) = \frac{1}{1+N}$, $\mu = 0.1$, and $\alpha = 1/2$.

exclusively on a single resource. On the other hand, for complementary resources, it is natural to guess that natural selection favors populations that consume both resources rather than one. Evidence supporting this conclusion can be seen in many ecological studies. We mention two studies corresponding to two ways that resource complementarity can arise; individuals can improve the nutritional quality of their diets by mixing food items that complement one another, or when food items that are protected by toxic compounds are consumed in mixtures the toxicity of one food item can be diluted by the consumption of another food item. Whelan et al. [27] conducted field experiments in 1994 and 1995 to determine whether fleshy fruits consumed by North American, migrant passerines are antagonistic, complementary, or perfectly substitutable resources. Of ten pairs of fruit species tested, eight exhibited resource complementarity (sign test, $P < 0.05$) and two exhibited

resource antagonism which we discuss further below. Based on these results, Whelan et al. suggest that resource complementarity is generally common among fruits, which may help explain why so few frugivores are found to specialize on only a single or even a small number of fruit species. On the other hand, Schmidt et al. [20] tested for complementarity due to plant defenses with fox and gray squirrels consuming sunflower seeds treated with tannic or oxalic acids. Their results showed that squirrels treat foods containing the different acids as complementary resources.

In contrast to resource evolution on hemi-essential and complementary resources, our results confirm Tilman's assertion that "if two resources are antagonistic, a diet based toward mainly one or the other i.e., specialization, would seem beneficial." [25, pg. 370]. Our analysis also reveals a subtle yet important aspect about antagonistic evolution. If antagonism is sufficiently weak, then there are two types of evolutionary outcomes. If the initial strategy is sufficiently specialized on one of the resources, then evolution will amplify this specialization. Alternatively, if the initial strategy is sufficiently generalized, evolution will initially amplify this tendency to consume both resources. Following this initial phase, evolutionary branching occurs resulting in diverging strategies that eventually specialize on different resources. However, if antagonism is sufficiently strong, evolutionary branching does not occur and the evolutionary end state will consist of a single strategy specializing on a single resource. Ecological studies suggest that resource anatagonism can occur either by synergestic effects of toxic compounds contained in the resources [25] or by physiological constraints in which the ability of a consumer to digest one resource limits the ability of it to digest another resource. For instance, Janzen et al. [12] demonstrated that certain nonprotein amino acids found in seeds had no significant effect on the growth rate of bruchnid beetles if consumed separately but had a significant negative effect when consumed together. Whelan et al. [27] found that in two of their ten studies on consumption of fleshy fruits by migratory birds, the fruits exhibited antagonistic relations. In both of these studies, one species of fruit was high in lipids and low in sugar, while the other fruit was high in sugar and low in lipids. Migratory passerines are known to discriminate among fruit resources based upon their respective digestive physiologies. For example, cedar waxwings preferentially consume fruits high in sugars and low in lipids [28], in contrast starlings tend to avoid fruits high in sugar [15], and American robins consume both sugar-rich and lipid-rich fruits [28]. In a study of Whetlan et al. that exhibited antagonistic resources, one of the dominant species was a species of starling. This suggests that for some migratory birds (e.g. cedar waxwings and starlings) their digestive physiology is such that the two types of fruit are antagonistic (i.e. the ability to digest one inhibits ability to digest the other) and natural selection favors specialization on one of the fruits.

Perfectly substitutable resources lie at the boundary of antagonistic and complementary resources. Our analysis of this structurally unstable resource relationship reveals that there are evolutionarily and convergent stable strategies in which consumers exhibit an ideal free distribution (IFD) [5]. Namely, at equilibrium, the per-capita growth rate of the consumer with respect to either resource is equal to zero. This special case arises due to the linearity of the mutant's invasion rates. The

implications of linearity of mutant invasion rates, as pointed out to us recently, has been considered in greater detail in a paper by Mézena and colleagues [16]. The IFD has been observed in a variety of field and experimental studies [7, 14, 19]. For example, a study of Lemel [14] compared reproductive success and dominance for Great Tit populations in deciduous and coniferous forests in an attempt to establish whether the birds are distributed between habitats containing different resources in a despotic or ideal free manner. Since no critical differences could be found in reproductive output, Lemel concluded that Great Tits populations conform to an IFD. In our analysis, the structural instability of perfectly substitutable resources made verifying the evolutionary stability of the IFD delicate. Since the slightest degree of resource antagonism leads to specialization, our results suggest that populations exhibiting the IFD distribution are most likely consuming slightly complementary resources, not slightly antagonistic.

In conclusion, our analysis reveals the need for more mathematical results concerning the ecological and evolutionary dynamics of coexisting strategies. We believe work in this direction especially with multiple species interactions [22, 23] is likely to lead to exciting mathematics and important insights for evolutionary ecology.

Appendices

In these appendices, we provide the details of many of the results alluded to in the main text. Unless stated otherwise, our standing assumptions are that $R_i(N)$ are positive, decreasing, and continuously differentiable functions such that $\lim_{N \to \infty} R_i(N) = 0$ and $R_i(0) > \mu$.

Appendix A: Coexistence and competitive displacement

We begin by proving some basic results about (2).

Theorem 1. *Consider (2) with $n = 2$, $x = x_1$, $y = x_2$, $N = N_1$, and $M = N_2$.*

1. *If $s(x, y) > 0$ and $s(y, x) > 0$, then (2) has a unique equilibrium $(\hat{N}, \hat{M})$ in the interior of the positive quadrant and every solution $(N(t), M(t))$ to (2) with $N(0) > 0$ and $M(0) > 0$ satisfies*

$$\lim_{t \to \infty} (N(t), M(t)) = (\hat{N}, \hat{M}).$$

2. *If $s(x, y) > 0$ and $s(y, x) < 0$, then every solution $(N(t), M(t))$ to (2) with $M(0) > 0$ satisfies*

$$\lim_{t \to \infty} (N(t), M(t)) = (0, N_y).$$

Proof. Consider (2) with $x = x_1$, $y = x_2$, $N = N_1$, and $M = N_2$. The proof of this theorem relies upon the following lemma.

Lemma 1. *If $x, y \in [0, 1]$ and $x \neq y$, then (2) has at most one equilibrium in the positive quadrant.*

Proof. Assume $x, y \in [0, 1]$ and $x \neq y$. Any equilibrium $(\hat{N}, \hat{M})$ to (2) with $\hat{N} > 0$ and $\hat{M} > 0$ must satisfy

$$\begin{bmatrix} x^\alpha \ (1-x)^\alpha \\ y^\alpha \ (1-y)^\alpha \end{bmatrix} \begin{bmatrix} R_1(x\hat{N} + y\hat{M})^\alpha \\ R_2((1-x)\hat{N} + (1-y)\hat{M})^\alpha \end{bmatrix} = \begin{bmatrix} \mu^\alpha \\ \mu^\alpha \end{bmatrix}. \tag{3}$$

Since $x \neq y$, the matrix $\begin{bmatrix} x^\alpha \ (1-x)^\alpha \\ y^\alpha \ (1-y)^\alpha \end{bmatrix}$ is invertible. Hence, there exist a unique solution $\begin{bmatrix} X_1 \\ X_2 \end{bmatrix}$ to $\begin{bmatrix} x^\alpha \ (1-x)^\alpha \\ y^\alpha \ (1-y)^\alpha \end{bmatrix} \begin{bmatrix} X_1 \\ X_2 \end{bmatrix} = \begin{bmatrix} \mu^\alpha \\ \mu^\alpha \end{bmatrix}$. If $X_1 \leq 0$ or $X_2 \leq 0$, then there exists no solution to (3) as $R_i(N) > 0$ for all N. Thus, we are done in this case. Suppose that $X_i > 0$ for $i = 1, 2$. Since we have assumed that $\lim_{N\to\infty} R_i(N) = 0$ and $R_i(N)$ is decreasing, $R_i^{-1}(X_i^{1/\alpha})$ is uniquely defined for $i = 1, 2$. Therefore, solving (3) is equivalent to solving

$$\begin{bmatrix} x & y \\ 1-x & 1-y \end{bmatrix} \begin{bmatrix} \hat{N} \\ \hat{M} \end{bmatrix} = \begin{bmatrix} R_1^{-1}(X_1^{1/\alpha}) \\ R_2^{-1}(X_2^{1/\alpha}) \end{bmatrix}$$

which has exactly one solution as $\begin{bmatrix} x & y \\ 1-x & 1-y \end{bmatrix}$ is invertible. Note that this unique solution may or may not satisfy $\hat{N} > 0$ and $\hat{M} > 0$. ★

To prove the first assertion, assume that $s(x, y) > 0$ and $s(y, x) > 0$. In this case, (2) is permanent (i.e. the flow is dissipative and the boundary is repelling). The permanence index Thm. [11, Thm. 13.3.1] implies that (2) supports at least one equilibrium in the interior of the positive quadrant. Since $s(x, x) = 0$ and $s(x, y) > 0$, $y \neq x$. Lemma 1 implies that there is exactly one such equilibrium, call it $(\hat{N}, \hat{M})$. Since (2) is a competitive system (i.e. the off diagonal entries of the derivative matrix of the right hand side of (2) are negative), a result of Hirsch and Smale [9, Thm in 12.3] and the Poincaré-Bendixson Theorem imply that

$$\lim_{t\to\infty} (N(t), M(t)) = (\hat{N}, \hat{M})$$

whenever $(N(t), M(t))$ is a solution to (2) satisfying $N(0) > 0$ and $M(0) > 0$.

To prove the second assertion, assume that $s(x, y) > 0$ and $s(y, x) < 0$. In addition, we shall assume that $\alpha > 0$ as the proof for the case $\alpha < 0$ follows in a similar manner. We begin by showing that there is no equilibrium in the positive quadrant. More precisely we show that the N and M nullclines do not intersect in the positive quadrant. In the nonnegative quadrant, the N and M nullclines are determined by the equations $(x R_1(xN + yM))^\alpha + ((1-x)R_2((1-x)N + (1-y)M))^\alpha = \mu^\alpha$ and $(y R_1(xN + yM))^\alpha + ((1-y)R_2((1-x)N + (1-y)M))^\alpha = \mu^\alpha$, respectively. Our assumptions that $R_i'(N) < 0$ and $\lim_{N\to\infty} R_i(N) = 0$ for $i = 1, 2$ imply that the N and M nullclines are the graphs of decreasing functions, say

$M = n(N) : [0, a] \to [0, \infty)$ and $M = m(N) : [0, b] \to [0, \infty)$, respectively. Since $(N_x, 0)$ and $(0, N_y)$ are equilibria, we get that $m(0) = N_y$, $n(a) = 0$, and $a = N_x$. Our assumption that $s(x, y) > 0$ implies that $b > N_x = a$. Our assumption that $s(y, x) < 0$ implies that $m(0) = N_y > n(0)$. Lemma 1 implies the nullclines can intersect in the positive quadrant in at most one point. Hence, either the nullclines do not intersect or if they intersect, the nullclines are tangent at the point of intersection. We will show the latter case is impossible via a proof by contradiction. Suppose to the contrary that the nullclines do intersect, say at $(\hat{N}, \hat{M})$ with $\hat{N} > 0$ and $\hat{M} > 0$, and are tangent at this intersection point. Let

$$G(N, M) = (g_1(N, M), g_2(N, M))$$

where

$$g_1(N, M) = (x R_1(xN + yM))^\alpha + ((1 - x)R_2((1 - x)N + (1 - y)M))^\alpha$$

and

$$g_2(N, M) = (y R_1(xN + yM))^\alpha + ((1 - y)R_2((1 - x)N + (1 - y)M))^\alpha.$$

We will arrive at a contradiction by showing that $DG(\hat{N}, \hat{M})$ is singular and invertible. To show that $DG(\hat{N}, \hat{M})$ is singular notice that $g_1(N, n(N)) = \mu^\alpha$ and $g_2(N, m(N)) = \mu^\alpha$. Therefore, taking the derivative of these expressions evaluated at $N = \hat{N}$, $M = n(\hat{N}) = \hat{M}$ and using the fact that the nullclines are tangent, we either get

$$n'(\hat{N}) = -\frac{\frac{\partial g_1}{\partial N}(\hat{N}, \hat{M})}{\frac{\partial g_1}{\partial M}(\hat{N}, \hat{M})} = -\frac{\frac{\partial g_2}{\partial N}(\hat{N}, \hat{M})}{\frac{\partial g_2}{\partial M}(\hat{N}, \hat{M})} = m'(\hat{N})$$

or

$$\frac{\partial g_1}{\partial M}(\hat{N}, \hat{M}) = \frac{\partial g_2}{\partial M}(\hat{N}, \hat{M}) = 0.$$

In either case, we get that the determinant of $DG(\hat{N}, \hat{M})$ equals zero. Next, we will show that the determinant of $DG(\hat{N}, \hat{M})$ can not be zero. We can rewrite G as

$$G(N, M)^T = \begin{bmatrix} x^\alpha & (1 - x)^\alpha \\ y^\alpha & (1 - y)^\alpha \end{bmatrix} \begin{bmatrix} r_1(xN + yM) \\ r_2((1 - x)N + (1 - y)M) \end{bmatrix}$$

where $r_1(N) = R_1(N)^\alpha$, $r_2(N) = R_2(N)^\alpha$, and G^T denotes the transpose of G. Differentiating G^T we get

$$\begin{bmatrix} x^\alpha & (1-x)^\alpha \\ y^\alpha & (1-y)^\alpha \end{bmatrix}$$
$$\times \begin{bmatrix} xr_1'(xN+yM) & yr_1'(xN+yM) \\ (1-x)r_2'((1-x)N+(1-y)M) & (1-y)r_2'((1-x)N+(1-y)M) \end{bmatrix} \quad (4)$$

The determinant of the matrix on the left hand side of (4) is non-zero. The determinant of the matrix on the right hand side of (4) equals

$$r_1'(xN+yM)r_2'((1-x)N+(1-y)M))(x-y)$$

Since $r_1'r_2' > 0$ and $x \neq y$, we get that the determinant of $DG(\hat{N}, \hat{M})$ is not zero completing our contradictory quest. Hence, the nullclines can not intersect in the positive quadrant. Since there exist no equilibria in the positive quadrant and the only linearly stable equilibrium on the boundary of the positive quadrant is $(0, N_y)$, the Poincaré-Bendixson theorem implies that every solution $(N(t), M(t))$ to (2) with $M(0) > 0$ satisfies $\lim_{t\to\infty}(N(t), M(t)) = (0, N_y)$. ★

Theorem 2. *Consider (2) with $n = 3$, $x = x_1$, $y = x_2$, $z = x_3$, $N = N_1$, $M = N_2$, and $Q = N_3$. If all the equilibria supporting one or two strategies are hyperbolic, then every solution $(N(t), M(t), Q(t))$ converges to an equilibrium on the boundary of the positive orthant (i.e. an equilibrium supporting one or two strategies).*

Proof. The proof of this theorem requires results from theory of competitive systems. We refer the reader to the monograph of Smith [24] for details. Since (2) is totally competitive, dissipative, and the origin is a repellor, work of Hirsch [8, Thm. 1.7] implies there exists a Lipshitz surface Γ in the non-negative orthant such that Γ is homeomorphic to a two simplex and such that the ω-limit sets of all non-zero solutions to (2) are contained in Γ.

We begin by showing that the positive orthant contains no equilibrium. Any equilibrium $(\hat{N}, \hat{M}, \hat{Q})$ in the positive orthant must satisfy

$$\begin{aligned} x^\alpha r_1 + (1-x)^\alpha r_2 &= \mu^\alpha \\ y^\alpha r_1 + (1-y)^\alpha r_2 &= \mu^\alpha \\ z^\alpha r_1 + (1-z)^\alpha r_2 &= \mu^\alpha \end{aligned} \quad (5)$$

where $r_1 = R_1(x\hat{N}+y\hat{M}+z\hat{Q})^\alpha$ and $r_2 = R_2((1-x)\hat{N}+(1-y)\hat{M}+(1-z)\hat{Q})^\alpha$. If there exist values of r_1 and r_2 such that (5) hold, then the points $(x^\alpha, (1-x)^\alpha)$, $(y^\alpha, (1-y)^\alpha)$ and $(z^\alpha, (1-z)^\alpha)$ are colinear as their inner products with (r_1, r_2) all equal μ^α. However, as x, y, and z are distinct (this follows from the assumption that the equilibria on the boundary are hyperbolic), colinearity is only possible if $\alpha = 1$. Consequently, when $\alpha \neq 1$ there is no interior equilibrium. Alternatively when $\alpha = 1$, (5) implies $r_1 = r_2 = \mu$. Therefore, the equilibria must satisfy $x\hat{N}+y\hat{M}+z\hat{Q} = R_1^{-1}(\mu)$ and $(1-x)\hat{N}+(1-y)\hat{M}+(1-z)\hat{Q} = R_2^{-1}(\mu)$. Hence, there is a line of equilibria determined by (5). Our assumption that the equilibria supporting one or two strategies are hyperbolic implies that this line equilibria can not pass through the positive orthant. Hence, when $\alpha = 1$, there is no equilibrium in the positive orthant.

To complete the proof, we argue why all solutions converge to an equilibrium on the boundary. Without any equilibria in the positive orthant, the Poincaré Index Theorem implies there is no periodic orbit in Γ. Hyperbolicity of the equilibria and the Poincaré-Bendixson Theorem implies that Γ contains no cycles of equilibria (i.e. a union $\bigcup_{j=1}^{k}(\{e_j\} \cup \gamma_j)$ with $k \geq 1$ consisting of equilibria e_j and connecting orbits γ_j such that the α-limit set of $\gamma_j = e_{j-1}$ and the ω-limit set of $\gamma_j = e_j$ for all $j = 1, \ldots, k$ with the convention that $e_0 = e_n$). Since there are no cycles of equilibria in Γ, no periodic orbits in Γ, and all equilibria are hyperbolic, Poincaré-Bendixson theory implies that all solutions $(N(t), M(t), Q(t))$ in Γ must converge to an equilibrium. Even though we have shown that solutions in Γ converge to an equilibrium and all solutions in the non-negative orthant converge to Γ, the last step to conclude that all solutions in the non-negative orthant converge to an equilibrium is surprisingly subtle and requires the notions of internal chain recurrence and asymptotic pseudo-orbits (alternatively asymptotically autonomous differential equations). The definitions of these terms can be found in the papers by Benaïm and Hirsch [3] and Mischaikow, Smith, and Thieme [18]. The main result of these papers in our context implies that the set of limit points for a solution $(N(t), M(t), Q(t))$ as $t \to \infty$ must be an internally chain recurrent set for Γ. Benaïim and Hirsch [2] have shown that internally chain recurrent sets for a flow on a two simplex with isolated equilibria are either an equilibrium, a cycle of equilibria, or a periodic orbit. As Γ has no periodic orbits or cycles of equilibria, the only internally chain recurrent sets for Γ are sets consisting of a single equilibrium. Thus, we may conclude that all solutions in the non-negative orthant converge to an equilibrium supporting one or two strategies.
⋆

Appendix B: Perfectly substitutable resources

In this section, we assume that $\alpha = 1$. In which case,

$$s(x, y) = yR_1(xN_x) + (1 - y)R_2((1 - x)N_x)) - \mu$$

is a linear function in y and

$$D(x) = R_1(xN_x) - R_2((1 - x)N_x).$$

Lemma 2.
$$D(x) \begin{cases} > 0 \text{ if } x < x^* \\ = 0 \text{ if } x = x^* \\ < 0 \text{ if } x > x^* \end{cases}$$

where

$$x^* = \frac{R_1^{-1}(\mu)}{R_1^{-1}(\mu) + R_2^{-1}(\mu)}.$$

Proof. We begin by showing the unique solution of $D(x) = 0$ is $x = x^*$. Suppose $D(x) = 0$. Then $R_1(xN_x) = R_2((1 - x)N_x))$. Since N_x is an equilibrium of (1), we get

$$\mu = x R_1(x N_x) + (1 - x) R_2((1 - x) N_x)$$
$$= x R_1(x N_x) + (1 - x) R_1(x N_x) = R_1(x N_x)$$

Since $R_1(x N_x) = R_2((1-x)N_x) = \mu$, $x N_x = R_1^{-1}(\mu)$ and $(1-x)N_x = R_2^{-1}(\mu)$. Thus $N_x = R_1^{-1}(\mu) + R_2^{-1}(\mu)$ and $x = R_1^{-1}(\mu)/N_x$. Thus x^* is unique.

Notice that $D(0) = R_1(0) - R_2(N_0) = R_1(0) - \mu > 0$ where the second equality follows from the definition of N_0 and the last inequality follows from our assumption that both resources sustain a population. Similarly, $D(1) < 0$. Continuity of $D(x)$ completes the proof of the lemma. ★

Lemma 3. $s(x, y) < 0$ if and only if $y < x < x^*$ or $y > x > x^*$. $s(x, y) > 0$ if and only if either $x < y$ and $x < x^*$ or $y < x$ and $x > x^*$.

Proof. Consider $x < x^*$. Lemma 2 implies that $\frac{\partial s}{\partial y}(x, x) = D(x) > 0$. Since $s(x, y)$ is a linear function in y and $s(x, x) = 0$, the claim follows for $x < x^*$. The case $x > x^*$ is proved similarly. ★

Theorem 3. *Consider (2) with $n = 2$, $x_1 = x^*$, $y = x_2 \neq x^*$, $N = N_1$, and $M = N_2$. Then*
$$\lim_{t \to \infty} (N(t), M(t)) = (N_{x^*}, 0).$$
for every solution $(N(t), M(t))$ to (2) with $N(0) > 0$.

Proof. We begin by showing that if $x = x^*$ and there exists an equilibrium $(\hat{N}, \hat{M})$ of (2) satisfying $\hat{N} > 0$ and $\hat{M} > 0$ then $y = x^*$. Suppose there exists an equilibrium $(\hat{N}, \hat{M})$ of (2) satisfying $\hat{N} > 0$ and $\hat{M} > 0$. Then

$$0 = x R_1(x \hat{N} + y \hat{M}) + (1 - x) R_2((1 - x)\hat{N} + (1 - y)\hat{M}) - \mu$$
$$0 = y R_1(x \hat{N} + y \hat{M}) + (1 - y) R_2((1 - x)\hat{N} + (1 - y)\hat{M}) - \mu$$

Setting $A = R_1(x\hat{N} + y\hat{M}) - R_2((1-x)\hat{N} + (1-y)\hat{M})$ and $B = R_2((1-x)\hat{N} + (1-y)\hat{M}) - \mu$, these equations are equivalent to $xA + B = 0$ and $yA + B = 0$. Thus either $x = y$ or $A = B = 0$. If $x = y$, we are done. Suppose $A = B = 0$. Then $R_1(x\hat{N} + y\hat{M}) = R_2((1-x)\hat{N} + (1-y)\hat{M}) = \mu$ and

$$x\hat{N} + y\hat{M} = R_1^{-1}(\mu) \tag{6}$$
$$(1 - x)\hat{N} + (1 - y)\hat{M} = R_2^{-1}(\mu). \tag{7}$$

Adding (6) and (7) together, we get $\hat{N} + \hat{M} = R_1^{-1}(\mu) + R_2^{-1}(\mu)$. In particular, $\hat{N} = R_1^{-1}(\mu) + R_2^{-1}(\mu) - \hat{M}$. Since $x = x^* = \frac{R_1^{-1}(\mu)}{R_1^{-1}(\mu) + R_2^{-1}(\mu)}$, equation (6) implies that

$$R_1^{-1}(\mu) = \frac{R_1^{-1}(\mu)}{R_1^{-1}(\mu) + R_2^{-1}(\mu)} \left(R_1^{-1}(\mu) + R_2^{-1}(\mu) - \hat{M} \right) + y\hat{M}$$

$$= R_1^{-1}(\mu) + \hat{M} \left(\frac{R_1^{-1}(\mu)}{R_1^{-1}(\mu) + R_2^{-1}(\mu)} - y \right)$$

Since we have assumed that $\hat{M} > 0$, we get $y = x^*$.

Now suppose that $x = x^*$ and $y \neq x^*$. The contrapositive of the statement we just proved implies that there is no equilibrium $(\hat{N}, \hat{M})$ for (2) satisfying $\hat{N} > 0$ and $\hat{M} > 0$. Thus the only equilibria for (2) in the non-negative quadrant are $(0, 0)$, $(N_x, 0)$ and $(0, M_y)$. Since $x R_1(0) + (1 - x) R_2(0) - \mu > 0$ and $y R_1(0) + (1 - y) R_2(0) - \mu > 0$, $(0, 0)$ is a source. Lemma 3 implies that $s(y, x) > 0$. This in addition to our assumption that $R_1'(\cdot) < 0$ and $R_2'(\cdot) < 0$, imply that the linearization about $(0, M_y)$ is a saddle. The Poincaré-Bendixson Theorem and Stable Manifold Theorem imply that $\lim_{t \to \infty} (N(t), M(t)) = (N_x, 0)$ whenever $N(0) > 0$. ★

Appendix C: Cases $\alpha \neq 0, 1$

To deal with the cases $\alpha \neq 0, 1$, we introduce the quantities

$$\sigma(x, y) = (s(x, y) + \mu)^\alpha = (y R_1(x N_x))^\alpha + ((1 - y) R_2((1 - x) N_x))^\alpha$$

and

$$D_\sigma(x) = \frac{\partial \sigma}{\partial y}(x, x) = \alpha x^{\alpha-1} R_1(x N_x)^\alpha - \alpha(1 - x)^{\alpha-1} R_2((1 - x) N_x)^\alpha.$$

The utility of σ and D_σ comes from the following three observations. First, since $s(x, x) = 0$, the definition of $D_\sigma(x)$ implies that

$$D_\sigma(x) = \alpha(s(x, x) + \mu)^{\alpha-1} \frac{\partial s}{\partial y}(x, x)$$

$$= \alpha \mu^{\alpha-1} D(x).$$

Hence $D(x) = 0$ if and only if $D_\sigma(x) = 0$. Second, $D_\sigma'(x) = \alpha \mu^{\alpha-1} D'(x)$. Hence, a singular strategy x^* is convergent stable (resp. convergent unstable) if $\alpha D_\sigma'(x) < 0$ (resp. $\alpha D_\sigma'(x) > 0$). Finally, if x^* is a singular strategy, then

$$\frac{\partial^2 \sigma}{\partial y^2}(x^*, x^*) = \alpha(\alpha - 1) \mu^{\alpha-2} \left(\frac{\partial s}{\partial y}(x^*, x^*) \right)^2 + \alpha \mu^{\alpha-1} \frac{\partial^2 s}{\partial y^2}(x^*, x^*)$$

$$= \alpha \mu^{\alpha-1} \frac{\partial^2 s}{\partial y^2}(x^*, x^*)$$

Hence, x^* is an ESS (resp. not an ESS) if $\alpha \frac{\partial^2 \sigma}{\partial y^2}(x^*, x^*) < 0$ (resp. > 0). Using these observations, we prove the following lemma.

Lemma 4. *Assume $\alpha \neq 0$ and x^* is a singular strategy. Then*

1. x^* *must satisfy*

$$(x^*)^{1-1/\alpha} R_1(x^* N_{x^*}) = (1 - x^*)^{1-1/\alpha} R_2((1 - x^*) N_{x^*}) = \mu \qquad (8)$$

2. *If $\alpha > 1$, then x^* is evolutionarily unstable, otherwise x^* is evolutionarily stable.*

3. *If $\alpha > 1$, then $x = 0$ and $x = 1$ are convergent stable and evolutionarily stable.*

Proof. Recall x^* is a singular strategy if and only if $0 = D_\sigma(x^*)$. Hence, $(x^*)^{\alpha-1} R_1(x^* N_{x*})^\alpha = (1-x^*)^{\alpha-1} R_2((1-x^*)N_{x*})^\alpha$. Since N_x^* is an equilibrium, we also get that $(x^*)^\alpha R_1(x^* N_{x*})^\alpha + (1-x^*)^\alpha R_2((1-x^*)N_{x*})^\alpha = \mu^\alpha$. The first assertion follows by combining these two expressions. The second assertion follows from

$$\frac{\partial^2 \sigma}{\partial y^2}(x^*, x^*) = \alpha(\alpha-1)\left(y^{\alpha-2}R_1(x^* N_{x*})^\alpha + (1-y)^{\alpha-2}R_2((1-x^*)N_{x*})^\alpha\right)$$

To prove the third assertion, suppose $\alpha > 1$. Since $D(0) = \alpha^{-1}\mu^{1-\alpha}D_\sigma(0) = -\mu^{1-\alpha}R_2(N_0)^\alpha = -\mu < 0$ and $s(0,0) = 0$, 0 is convergent stable and evolutionarily stable. Similarly, since $D(1) = \alpha^{-1}\mu^{1-\alpha}D_\sigma(1) = \mu^{1-\alpha}R_1(N_1)^\alpha = \mu > 0$ and $s(1,1) = 0$, 1 is convergent stable and evolutionarily stable. ★

Using this lemma, we can prove the following theorem.

Theorem 4. *Assume* $R_i(N) = \frac{a_i}{1+b_i N}$, $b_i > 0$, *and* $R_i(0) = a_i > \mu$ *for* $i = 1, 2$.

1. *If* $\alpha < 1$ *and* $\alpha \neq 0$, *then there exists a unique singular strategy and this strategy is (globally) convergent stable and evolutionarily stable.*
2. *If* $\alpha > \max\{a_1, a_2\}/\mu$, *then there exists a unique singular strategy and this strategy is convergent unstable and evolutionarily unstable.*

Proof. By Lemma 4, the singular strategy $x = x^*$ and the population density $N = N_{x*}$ must satisfy (8). Setting $x_1 = x$ and $x_2 = 1 - x$ and solving for N in both equations give

$$N_i(x_i) = \frac{x_i^{-1-\frac{1}{\alpha}}\left(a_i x_i - x_i^{\frac{1}{\alpha}}\mu\right)}{b_i \mu}.$$

Differentiating with respect to x_i gives

$$N_i'(x_i) = \frac{1 - \frac{a_i x_i^{\frac{-1+\alpha}{\alpha}}}{\alpha \mu}}{b_i x_i^2}$$

Suppose $0 < \alpha < 1$. Then $\frac{-1+\alpha}{\alpha} < 0$ and $x_i^{\frac{-1+\alpha}{\alpha}} > 1$ for $x_i \in (0, 1)$. This observation plus the fact that $a_i > \mu$ implies that $N_i'(x_i) < 0$ for $x_i \in (0, 1)$. Consequently, N_1 as a function of $x = x_1$ is decreasing and N_2 as a function of $x = 1 - x_2$ is increasing. Since at a singular strategy $N_1 = N_2$, it follows that there exists at most one singular strategy. Furthermore as $\lim_{x\to 0^+} D_\sigma(x) = +\infty$, $\lim_{x\to 1^-} D_\sigma(x) = -\infty$ and $D_\sigma(x)$ is continuous on $(0, 1)$, there exists exactly one singular strategy and it is globally convergent stable. The proof when $\alpha < 0$ follows similarly. Evolutionary stability of this singular strategy follows from Lemma 4.

Suppose $\alpha > \max\{a_1, a_2\}/\mu$. Since $\frac{-1+\alpha}{\alpha} > 0$, $0 \leq x_i^{\frac{-1+\alpha}{\alpha}} \leq 1$ for $x_i \in (0, 1)$. Since $a_i/(\alpha\mu) < 1$, it follows that $N_i'(x_i) > 0$ for $x_i \in (0, 1)$. Thus N_1 is increasing as a function of x, N_2 is decreasing as a function of x, and there exists at most one singular strategy. Since $D_\sigma(0) = -\alpha R_2(N_0)^\alpha = -\alpha\mu^\alpha < 0$,

$D_\sigma(1) = \alpha R_1(N_1)^\alpha = \alpha \mu^\alpha > 0$, and $D_\sigma(x)$ is continuous on $[0, 1]$, there exists a unique singular strategy in $(0, 1)$ and it is globally unstable. Evolutionary instability of this singular strategy follows from Lemma 4.   ★

Lemma 5. *Assume $\alpha > 1$. Then $(x, y) = (0, 1)$ is coevolutionarily stable for (2) and convergent stable.*

Proof. Suppose $(x, y) = (0, 1)$ and z lies in the open interval $(0, 1)$. Notice that

$$
\frac{d}{d\alpha} \left(R_1^\alpha + R_2^\alpha \right)^{1/\alpha}
$$
$$
= \frac{1}{\alpha^2} \left(R_1^\alpha + R_2^\alpha \right)^{1/\alpha - 1} \left(R_1^\alpha \ln \frac{R_1^\alpha}{R_1^\alpha + R_2^\alpha} + R_2^\alpha \ln \frac{R_2^\alpha}{R_1^\alpha + R_2^\alpha} \right) < 0
$$

Therefore, $\left(R_1^\alpha + R_2^\alpha \right)^{1/\alpha}$ is a decreasing function of α. Let $(N_{0,1}, M_{0,1})$ be the positive equilibrium of (2) with $x_1 = 0$, $x_2 = 1$, and $n = 2$. Since $N_{0,1} = R_1^{-1}(\mu)$, $M_{0,1} = R_2^{-1}(\mu)$, and $\left(R_1^\alpha + R_2^\alpha \right)^{1/\alpha}$ is a decreasing function of α, we get that

$$
\left((z R_1(N_{0,1}))^\alpha + ((1 - z) R_2(M_{0,1}))^\alpha \right)^{1/\alpha} < z R_1(N_{0,1}) + (1 - z) R_2(M_{0,1}) = \mu.
$$

Hence, $\tilde{s}(0, 1, z) = \left((z R_1(N_{0,1}))^\alpha + ((1 - z) R_2(M_{0,1}))^\alpha \right)^{1/\alpha} - \mu < 0$ and $(0, 1)$ is evolutionarily stable.

To see convergent stability of $(x, y) = (0, 1)$, notice that

$$
\frac{\partial \tilde{s}}{\partial z}(0, 1, z) = \frac{1}{\alpha} A \alpha \left(z^{\alpha-1} R_1(N_{0,1})^\alpha - (1 - z)^{\alpha-1} R_2(N_{1,0})^\alpha \right)
$$
$$
= \frac{1}{\alpha} A \alpha \mu^\alpha \left(z^{\alpha-1} - (1 - z)^{\alpha-1} \right)
$$

where $A = \left((z R_1(N_{0,1}))^\alpha + ((1 - z) R_2(M_{0,1}))^\alpha \right)^{\frac{1}{\alpha} - 1}$. Hence $\frac{\partial \tilde{s}}{\partial z}(0, 1, z) < 0$ for $z \in [0, 1]$ close to 0 and $\frac{\partial \tilde{s}}{\partial z}(0, 1, z) > 0$ for $z \in [0, 1]$ close to 1. Thus, $(0, 1)$ is convergent stable.   ★

Appendix D: A Derivation of the Schoener Equations

To derive the resource function $R(N) = \frac{a}{1+bN}$, we begin by explicitly modeling the resource dynamics. If the resource density is given by R, the resource that enters the system at a constant rate I (e.g. prey leaving a refuge at a constant rate, constant production of fruit or seeds by a tree), that in the absence of consumption is removed from the system (e.g., decay, leaching) at a rate proportional to the resource density, and that is consumed by each consumer at a rate proportional to its density, then the resource dynamics are given

$$
\frac{dR}{dt} = I - L R - \beta R N
$$

where $L > 0$ is the per-capita leaching rate, N is the consumer density, and $\beta > 0$ is the searching efficiency of the consumer. If we assume that resource dynamics

operate at a faster time scale than the consumer population dynamics, then one can assume that resource is an quasi-steady state which is given by

$$R = \frac{I}{L + \beta N} = \frac{I/L}{1 + \beta N/L}.$$

Setting $a = I/L$ and $b = \beta/L$ gives the desired resource function.

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