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## Coexistence of competitive species with a stage-structured life cycle

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**Abstract** Ecological theory provides explanations for exclusion or coexistence of competing species. Most theoretical works on competition dynamics that have shaped current perspectives on coexistence assume a simple life cycle. This simplification, however, may omit important realities. We present a simple two-stage structured competition model to investigate the effects of life-history characteristics on coexistence. The achievement and the stability of coexistence depend not only on competition coefficients but also on a set of life-history parameters that reflect the viability of an individual, namely, adult death rate, maturation rate, and birth rate. High individual viability is necessary for a species to persist, but it does not necessarily facilitate coexistence. Intense competition at the juvenile or adult stage may require higher or lower viability, respectively, for stable coexistence to be possible. The stability mechanism can be explained by the refuge effect of the less competitive stage, and the birth performance, which preserves the less competitive stage as a refuge. Coexistence might readily collapse if the life-history characteristics, which together constitute individual viability, change, even though two species have an inherent competitive relation conducive to stable coexistence.

**Keywords** Competition · Stage structure · Complex life cycle · Viability · Stable coexistence

### Introduction

Competitive interaction has been investigated to explain coexistence and exclusion of species (Lotka 1925; Gause 1934; MacArthur 1958, 1972; Park 1962; MacArthur

and Wilson 1967; Lack 1971; May 1972). Niche theory conceptualizes intraspecific and interspecific competition by integrating the various life histories of competitive species (MacArthur 1958; Hutchinson 1978) and links life-history characteristics to competition coefficients in dynamics models (MacArthur and Levins 1967; Vandermeer 1972; Pianka 1976). Since the publication of the classic theoretical studies (Lotka 1925), competitive interaction and its consequences have been evaluated by examining competition coefficients among species (but see Tilman 1982; Abrams 1983). Competition coefficients, which are synthetic variables, are used in dynamics models to integrate all of the underlying mechanisms, but they conceal important realities of competitive interaction and its consequences.

Various organisms experience abrupt ontogenetic niche shifts in morphology, physiology, or behavior, usually associated with a change in prey or habitat (Wilbur 1980; Werner and Gilliam 1984). Generally, an ontogenetic niche shift separates interactions among individuals across life stages (Werner and Gilliam 1984). Ontogenetic niche shifts in organisms that undergo metamorphosis, such as amphibians and multiparasitoid insects, may include shifts not only in prey but also in habitat (Wilbur 1980; Werner and Gilliam 1984). Among fishes, ontogenetic changes in habitat and resource use are common. In two Michigan lakes in the United States, for example, two congeneric sunfishes, the pumpkinseed sunfish and the bluegill, undergo ontogenetic dietary shifts (Osenberg et al. 1992).

Such a complex life cycle has important implications for competitive interaction as well as for various biological interactions (Grosberg and Levitan 1992; Nakashizuka 2001). Life-cycle structure is expected to have a critical role in interspecific competitive interaction. We thus deduce that ontogenetic niche shifts link the dynamics of communities by way of the processes of recruitment and reproduction, which therefore have significant effects on those dynamics (Polis et al. 1996). However, few theoretical studies address the dynamics of competing species with complex life cycles. Because

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previous analyses have been limited to narrow biological scenarios (e.g., Hassell and Comins 1976), little is known about how complex life cycles of competing species affect their dynamics. We expect that exclusion or coexistence of competing species is determined not only by competition per se but also by life-cycle characteristics. Coexistence may be sustained by an antagonistic balance between the within-stage competitions of each stage (Istock 1966; Zwolfer 1971; Schroder 1974; Briggs 1993; Holt and Polis 1997; Amarasekare 2000a, b, 2003). But such an antagonistic balance may not be the only way to stabilize coexistence of competing species with complex life cycles.

In this article, the conditions necessary for two competing species with juvenile–adult stage-structured life cycles to coexist were investigated by modifying the classical Lotka–Volterra two-species competition model. We demonstrate how the stage-structure characteristics influence whether coexistence is possible.

For analytical tractability, our model analyzes competitive interaction with reference to the essential processes of a stage-structured life cycle. These processes, maturation, reproduction, and mortality, are potentially influenced at each stage by competitive interaction. Of these, adult mortality is least likely to be affected by competition. Many studies, however, have shown that competition has a negative effect on reproduction (Moe et al. 2002; Finn and Gittings 2003), and competition is likely to influence individual survival during the vulnerable juvenile stage (Bardsley and Beebe 1998; Agnew et al. 2002; Finn and Gittings 2003). Therefore, among these three processes, we focus on the essential processes of reproduction and juvenile survivorship as targets of intraspecific and interspecific competitive interaction.

## Model

### Single-species stage-structured population

As a preliminary step, we start with single-species stage-structured population models.

### Unconstrained stage-structured population

Consider a population that consists of two stages, juvenile and adult. Two processes, maturation and reproduction, connect the two stages. The following is the simplest population dynamics model of this stage-structured population:

$$\dot{X} = \gamma x - cX, \quad (1a)$$

$$\dot{x} = bX - \gamma x - \phi x, \quad (1b)$$

where  $X$  and  $x$  denote adult density and juvenile density, respectively,  $\gamma$  is the juvenile maturation rate,  $b$  the birth

rate,  $c$  the adult mortality rate, and  $\phi$  the juvenile mortality rate.

The necessary and sufficient condition to maintain a positive population number is

$$\frac{\gamma}{\gamma + \phi} \cdot \frac{b}{c} \geq 1. \quad (2)$$

A newborn individual would survive and definitely mature with probability  $\gamma/(\gamma + \phi)$ , and the expected time that the individual spends in the adult stage is  $1/c$ , during which the instantaneous birth rate is  $b$ ; therefore, the left-hand side (l.h.s.) of Ineq. 2 indicates the lifetime reproduction rate per born individual. Thus, Ineq. 2 implies the persistence condition according to which the l.h.s. should equal or exceed unity for the population to persist and avoid extinction. If either birth rate,  $b$ , or maturation rate,  $\gamma$  is low, compensation by low mortality rates,  $c$  and  $\phi$ , would be required for persistence of the population. The compensation effect of the maturation rate,  $\gamma$ , is weak if the juvenile death rate,  $\phi$ , is high.

### Intraspecific competition in a stage-structured population

Next, we incorporate intraspecific competition effects into the above simplest model by assuming that intraspecific competition operates via the birth and death processes at the juvenile stage. We make an assumption concerning the density dependence of both processes and describe the dynamics as follows:

$$\dot{X} = \gamma x - cX, \quad (3a)$$

$$\dot{x} = b(X)x - \gamma x - \phi(x)x, \quad (3b)$$

where  $b(X)$  is the per capita birth rate and  $\phi(x)$  is the per capita death rate of juveniles. The former is a decreasing function of adult density, and the latter is an increasing function of juvenile density. We adopt the simple linear functions  $b(X) = b_0(1 - X)$  (we restrict the initial condition of  $X$  to be less than unity for a biologically feasible condition; same applies to two-species competition model) and  $\phi(x) = \phi_0 + x$  to describe each density effect. The parameters  $b_0$  and  $\phi_0$  indicate the intrinsic birth rate and the intrinsic juvenile mortality rate, respectively. This system results in a nontrivial equilibrium solution  $(X^*, x^*)$ , and the total number of individuals in the population in the equilibrium state is

$$X^* + x^* = \frac{(c + \gamma)[b_0\gamma - c(\gamma + \phi_0)]}{c^2 + b_0\gamma^2}. \quad (4)$$

With logic identical to that used to explain the l.h.s. of Ineq. 2, we can evaluate the lifetime reproduction rate  $r(X, x)$  for a given set of adult and juvenile densities as

$$r(X, x) = \frac{\gamma}{\gamma + \phi(x)} \cdot \frac{b(X)}{c}. \quad (5)$$

The lifetime reproduction rate is unity at equilibrium, that is,  $r(X^*, x^*) = 1$ . If  $r(0, 0) > 1$ , or, alternatively, the

persistence condition,  $b_0\gamma - c(\gamma + \phi_0) > 0$  (an analog of Ineq. 2), holds, then the equilibrium density is positive. Since Eq. 5 is a monotonically decreasing function of  $x$  and  $X$  and is less than unity in the case that either  $x$  or  $X$  is larger than the equilibrium value, the equilibrium is stable.

#### Two-species stage-structured population with intraspecific and interspecific competition

We extend the above single-species stage-structured population model to a two-species stage-structured population model. We assume that interspecific competition, as well as intraspecific competition, operates via the birth and death processes of juveniles. As with the previous single-species model, we make an assumption of linear density dependence in the competition processes. For mathematical simplicity, we assume that the parameters unrelated to interspecific competition are identical in the two species, and that the parameters related to interspecific competition are symmetrical between the two species. Based on these assumptions, the dynamics are given by the following differential equations:

$$\dot{X} = \gamma x - cX \quad (6a)$$

$$\dot{x} = b_X(X, Y)X - \gamma x - \phi_x(x, y)x \quad (6b)$$

$$\dot{Y} = \gamma y - cY \quad (6c)$$

$$\dot{y} = b_Y(X, Y)Y - \gamma y - \phi_y(x, y)y, \quad (6d)$$

where  $b_X(X, Y) = b_0(1 - X - \alpha Y)$ ,  $b_Y(X, Y) = b_0(1 - Y - \beta X)$ ,  $\phi_x(x, y) = \phi_0 + x + \alpha' y$  and  $\phi_y(x, y) = \phi_0 + y + \beta' x$ .  $X$  and  $Y$  are the adult densities of the two species;  $x$  and  $y$  are the juvenile densities;  $b_X(X, Y)$  and  $b_Y(X, Y)$  are per capita birth rates of species  $x/X$  and species  $y/Y$ , respectively;  $\phi_x(x, y)$  and  $\phi_y(x, y)$  are per capita juvenile mortality rates of species  $x/X$  and species  $y/Y$ , respectively;  $\alpha$  and  $\beta$  are the adult interspecific competition coefficients; and  $\alpha'$  and  $\beta'$  are the juvenile interspecific competition coefficients. Note that the other parameters are defined as in Eqs. 3a and 3b.

In the section “Stability of coexistence,” we demonstrate the conditions for achieving both the coexistence equilibrium and local stability of the coexistence equilibrium. Then, we give biological interpretations to the conditions required for coexistence and its stability.

#### Conditions for coexistence

We can get a nontrivial equilibrium solution ( $X^*$ ,  $x^*$ ,  $Y^*$ ,  $y^*$ ) for Eqs. 6a–d. The total numbers of the two species at the equilibrium are

$$X^* + x^* = A \frac{C_1}{B} \quad (7a)$$

$$Y^* + y^* = A \frac{C_2}{B}, \quad (7b)$$

where  $A = (1/c^2)(c + \gamma)[b_0\gamma - c(\gamma + \phi_0)]$ ,  $B = (-1 + \alpha\beta)v^2 + (-2 + \alpha\beta' + \alpha'\beta)v + (-1 + \alpha'\beta')$ ,  $C_1 = v(-1 + \alpha) - (1 - \alpha')$ ,  $C_2 = v(-1 + \beta) - (1 - \beta')$ , and  $v = b_0\gamma^2/c^2$  (Appendix 1). The conditions necessary for positive numbers of both species at equilibrium are analyzed in Appendix 2.

Logic identical to that used for interpreting Eq. 5 implies that the expected lifetime reproduction rate of each species for a given set of adult and juvenile densities of each species is, respectively

$$r_{X,x}(X, x, Y, y) = \frac{\gamma}{\gamma + \phi_x(x, y)} \cdot \frac{b_X(X, Y)}{c} \quad (8a)$$

$$r_{Y,y}(X, x, Y, y) = \frac{\gamma}{\gamma + \phi_y(x, y)} \cdot \frac{b_Y(X, Y)}{c} \quad (8b)$$

At equilibrium,  $r_{X,x}(X^*, x^*, Y^*, y^*) = 1$  and  $r_{Y,y}(X^*, x^*, Y^*, y^*) = 1$ . If  $r_{X,x}(0, 0, 0, 0) = r_{Y,y}(0, 0, 0, 0) > 1$ , or, alternatively, if  $b_0\gamma - c(\gamma + \phi_0) > 0$  (an analog of Ineq. 2) holds, then persistence is possible for each species.

The persistence condition of either species can be rearranged as

$$\frac{b_0\gamma^2}{c^2} > \frac{\gamma}{c}(\gamma + \phi_0). \quad (9)$$

The l.h.s. of Ineq. 9, which appears in  $B$ ,  $C_1$ , and  $C_2$  of Eqs. 7a and 7b can be regarded as the “individual viability parameter” (or “viability parameter”) denoted hereafter by  $v$ . The synthetic parameter  $v$  is informative for the following analyses.

To emphasize that both sides of Ineq. 9 are composites of one of the unique parameters  $b_0$  or  $\phi_0$  and of the common parameters  $\gamma$  and  $c$ , we denote the two sides as

$$v(b_0|\gamma, c) > v'_{\text{inf}}(\phi_0|\gamma, c), \quad (10)$$

where  $v'_{\text{inf}}$  is the inferior value of  $v$  for persistence of each species. This implies that the inferior threshold value,  $v'_{\text{inf}}$ , and the value of viability,  $v$ , allowing the persistence of the population, are not independent because they share the common parameters  $c$  and  $\gamma$ . Figure 1 shows the relation between  $\gamma$  and  $c$  that allows persistence for given values of  $b_0$  and  $\phi_0$ . Large  $\gamma$  and small  $c$  tend to result in a large value of individual viability,  $v$ , so that Ineq. 10 holds and the population persists.

If the persistence condition holds, then, provided all of the terms except for  $A$  on the r.h.s. of Eqs. 7a and b have the same sign (positive or negative), a biologically feasible nontrivial equilibrium, that is, coexistence, can be achieved.

#### Stability of coexistence

We used a standard local stability analysis of the linearized approximation of the dynamic system to analyze the stability of the coexistence equilibrium.

*Analysis of stable conditions* We linearized the dynamic system of Eqs. 6a–d for the nontrivial equilibrium state and examined the stability of the equilibrium. First, the Jacobian matrix of the linearized system of Eqs. 6a–d for the nontrivial equilibrium state was obtained, and then the stability was evaluated from the sign of the dominant eigenvalue. If the dominant eigenvalue of the Jacobian matrix is a negative real number or a complex number with a negative real part, the equilibrium is locally stable. On the other hand, if the dominant eigenvalue is a positive real number or a complex number with a positive real part, the equilibrium is locally unstable.

Unfortunately, this analytical approach is intractable for evaluating stability in the case of small perturbations in all directions from the equilibrium. We therefore investigated the stability of the equilibrium numerically (Appendix 3). This inductive approach led us to the finding of the following simple stable conditions:

$$\begin{cases} v(-1 + \alpha) < 1 - \alpha' \\ v(-1 + \beta) < 1 - \beta' \end{cases} \quad (11)$$

where  $v = b_0\gamma^2/c^2$  (Appendix 3).

A stability analysis for perturbation in a restricted direction can also be conducted analytically, and the analysis results in the identical conditions (see Appendix 4), and validates the conditions in Ineq. 11, obtained inductively.

The stability conditions in Ineq. 11 imply biologically rationalized and recognizable mechanisms. These stability mechanisms reflect interspecific competition at each stage,  $\alpha$ ,  $\beta$ ,  $\alpha'$ , and  $\beta'$ , and the population structure itself, indicated by the viability parameter,  $v$ .

Next, we explore the stability condition for simplifying situations to recognize biological mechanisms. In the case that  $1 < \alpha$  and  $1 < \beta$ , the equilibrium is stabilized by satisfying the following inequality:

$$0 < v < v_{\text{sup}}, \quad (12)$$

where  $v_{\text{sup}} = \text{Min}[(1 - \alpha')/(-1 + \alpha), (1 - \beta')/(-1 + \beta)]$  for  $0 < \alpha' < 1$  and  $0 < \beta' < 1$ .

In the case that  $1 < \alpha$  and  $0 < \beta < 1$ , or  $1 < \beta$  and  $0 < \alpha < 1$ , the equilibrium is stabilized within certain lower and upper bounds of the viability parameter

$$v_{\text{inf}} < v < v_{\text{sup}}, \quad (13)$$

where

$$\begin{cases} v_{\text{inf}} = \text{Max}[0, (1 - \beta')/(-1 + \beta)] \\ v_{\text{sup}} = (1 - \alpha')/(-1 + \alpha) \end{cases} \quad (14)$$

when  $1 < \alpha$  and  $0 < \beta < 1$ , which requires that  $(1 - \beta')/(-1 + \beta) < (1 - \alpha')/(-1 + \alpha)$ , or

$$\begin{cases} v_{\text{inf}} = \text{Max}[0, (1 - \alpha')/(-1 + \alpha)] \\ v_{\text{sup}} = (1 - \beta')/(-1 + \beta) \end{cases} \quad (15)$$

when  $1 < \beta$  and  $0 < \alpha < 1$ , which requires that  $(1 - \alpha')/(-1 + \alpha) < (1 - \beta')/(-1 + \beta)$ . This leads to the following interpretations. An asymmetric interspecific competition

at the adult stage (i.e.,  $1 < \alpha$  and  $0 < \beta < 1$ ) can be compensated for by antagonistically asymmetric interspecific competition at the juvenile stage (i.e.,  $0 < \alpha' < 1$  and  $1 < \beta'$ ) to stabilize the equilibrium.

In the case that  $0 < \alpha < 1$  and  $0 < \beta < 1$ , the viability parameter stabilizing the equilibrium is lower-bounded

$$v_{\text{inf}} < v, \quad (16)$$

where  $v_{\text{inf}} = \text{Max}[0, (1 - \alpha')/(-1 + \alpha), (1 - \beta')/(-1 + \beta)]$ , with no requirement of interspecific competition at the juvenile stage.

When one or both species suffer intense interspecific competition at the adult stage, the viability parameter must be upper-bounded, and when one or both species are released from interspecific competition at the adult stage, the viability parameter must be lower-bounded and has a positive value to stabilize the equilibrium. The weaker the interspecific competition is for either species at either life stage, the higher the upper-boundary value is and the lower the lower-boundary value is, of the viability parameter stabilizing the equilibrium.

We also investigated stability of the boundary equilibrium ( $X^* + x^* = 0$  and  $Y^* + y^* > 0$ , or  $X^* + x^* > 0$  and  $Y^* + y^* = 0$ ). We found that both are stable if the interior equilibrium is unstable, and unstable if the interior equilibrium is stable.

*Requirements for coexistence and stability of coexistence* The conditions we demonstrated above are the conditions for stability of the nontrivial equilibrium. We also need to consider the persistence condition, in Ineq. 10, which is the requirement that the equilibrium be biologically feasible.

The persistence condition, which places a lower bound on the value of the viability parameter in Ineq. 10 must be superimposed on the ranges of the viability parameter presented in Ineqs. 12, 13, and 16 to determine the conditions necessary for stable coexistence. The conditions for achieving coexistence and its stability are classified into three cases:

$$\text{Max}[v'_{\text{inf}}, v_{\text{inf}}] < v, \text{ for } 0 < \alpha < 1 \text{ and } 0 < \beta < 1, \quad (\text{case I})$$

$$v'_{\text{inf}} < v < v_{\text{sup}}, \text{ for } 1 < \alpha \text{ and } 1 < \beta, \quad (\text{case II})$$

and

$$\text{Max}[v'_{\text{inf}}, v_{\text{inf}}] < v < v_{\text{sup}}, \text{ for } 1 < \alpha \text{ and } 0 < \beta < 1, \text{ or } 1 < \beta \text{ and } 0 < \alpha < 1. \quad (\text{case III})$$

Note that  $v'_{\text{inf}}$  is described in Ineq. 10, and that  $v_{\text{inf}}$  and/or  $v_{\text{sup}}$  for cases I, II, and III are specified in Ineqs. 16, 12, and 13, respectively, in terms of the competition coefficients.

The upper-boundedness of the viability parameter  $v < v_{\text{sup}}$  is by definition  $b_0\gamma^2/c^2 < v_{\text{sup}}$ , which can be rearranged as

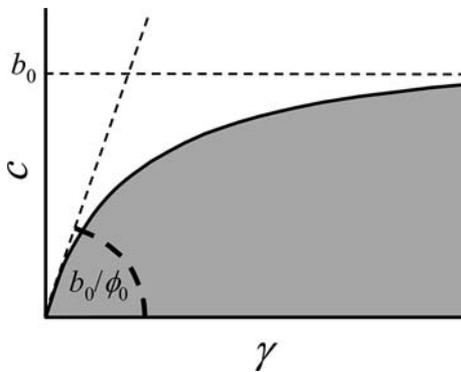
$$\gamma \sqrt{b_0/v_{\text{sup}}} < c. \quad (17)$$

Similarly, the lower-boundedness of the viability parameter,  $v_{\text{inf}} < v$ , can be rearranged as

$$c < \gamma \sqrt{b_0/v_{\text{inf}}}. \quad (18)$$

The values of  $\gamma$  and  $c$  for given values of  $b_0$  and  $\phi_0$  that result in a value of  $v$  allowing a nontrivial equilibrium to be biologically feasible and to stabilize are shown in Fig. 2.

For case I, stable coexistence tends to be easily established via merely a large value of viability, achieved by a high maturation rate, a high birth rate, and low adult and juvenile mortality rates (see Fig. 2a). For cases II and III, in contrast, stable coexistence tends to be



**Fig. 1** Ineq. 9 is rearranged as  $c < b_0\gamma/(\gamma + \phi_0)$ . Values of  $\gamma$  and  $c$  that allow persistence of the population for given values of  $b_0$  and  $\phi_0$  are shown (shaded area). The curved line is the hyperbola  $b_0\gamma/(\gamma + \phi_0)$  whose slope at the origin is  $b_0/\phi_0$ . See the text for details

established for a very narrow range of viability values achieved by very narrow ranges of values for maturation rates, birth rate, and mortality rates (see Fig. 2b, c). This implies that the sets of life-history parameters required for stable coexistence are restricted when interspecific competition for either or both species at either or both stages is high. For these cases, if

$$\phi_0 > \sqrt{b_0 v_{\text{sup}}} \quad (19)$$

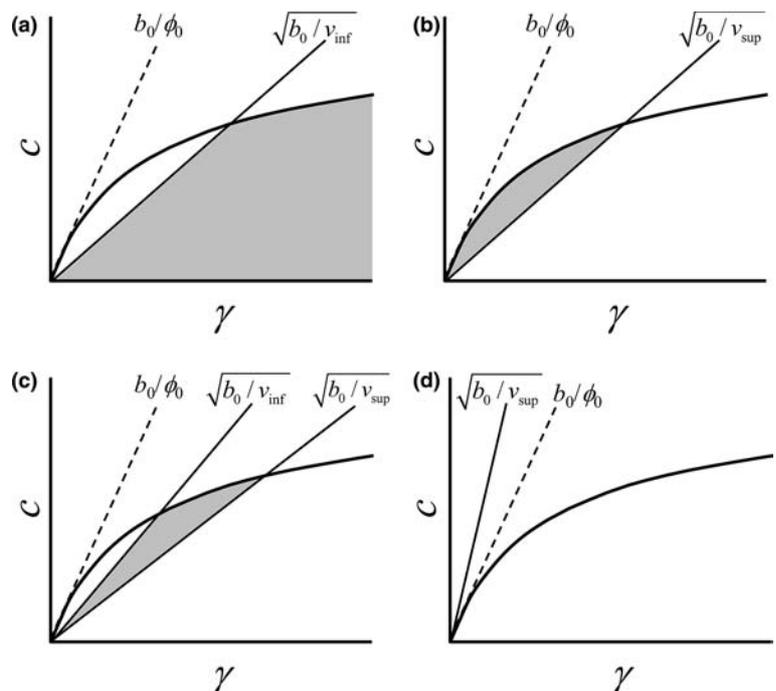
holds, even though higher values of  $\gamma$  and lower values of  $c$  permit the persistence condition of each population, coexistence is either impossible or unstable (see Fig. 2d).

### Biological implications

The classic, unstructured Lotka-Volterra competition model demonstrates that stable coexistence of two species cannot be expected except when interspecific competition is less than intraspecific competition. We can confirm that our model also behaves identically to the unstructured model in the extreme case where the maturation rate is infinite. Under this condition, the stability/instability of the coexistence is determined by the competitive relationships at the adult stage, irrespective of competitive relationships at the juvenile stage.

The model presented here suggests that (1) stability of coexistence depends on the magnitude of the synthetic individual viability parameter, and (2) the boundaries of the viability parameter stabilizing the coexistence reflect within-stage competitive relationships at each stage. The viability parameter  $v$  is the composite of the life-history parameters characterizing the stage-structured system: maturation rate  $\gamma$ , adult mortality rate  $c$ , and intrinsic

**Fig. 2** Shaded areas show values of  $\gamma$  and  $c$  that allow coexistence and stability of coexistence for given values of  $b_0$  and  $\phi_0$ , with certain upper and/or lower boundaries of the viability parameter,  $v_{\text{inf}}$  and  $v_{\text{sup}}$ , required for a certain set of parameters  $\alpha$ ,  $\beta$ ,  $\alpha'$ , and  $\beta'$ . **a**, **b**, and **c** correspond to cases I, II, and III. **d** is a particular instance of case II or III in which coexistence is unstable or impossible for any value of  $\gamma$  and  $c$ . See the text for details



birth rate  $b_0$ . Thus, we can rationalize the mechanisms of stable coexistence in terms of life-history characteristics.

*Refuge* Notice that the equilibrium ratio of the adult density to the juvenile density of each species is  $\gamma/c$  (refer to Appendix 1). This implies that a higher maturation rate, which gives  $1 < \gamma/c$ , leads to a higher density at the adult stage compared to the density at the juvenile stage, and a lower maturation rate, which gives  $\gamma/c < 1$ , leads to a lower density at the adult stage compared to the density at the juvenile stage. The behavior of the whole system therefore is dominated by the mechanism of interspecific competition at the dominant stage.

When interspecific competition is intense at the juvenile stage and weak at the adult stage, species interaction during the juvenile stage tends to destabilize and during the adult stage tends to stabilize coexistence in the whole system. In this case, the adult stage can be seen to have a refuge effect in that it counteracts the destabilization mechanism at the juvenile stage. When the maturation rate is high, while keeping  $1 < \gamma/c$ , both species tend to enjoy a long adult period, in which the stabilizing mechanism is embedded, compared with the juvenile period, and, consequently, the whole system achieves stable coexistence.

In contrast, when interspecific competition is intense at the adult stage and weak at the juvenile stage, species interaction during the adult stage tends to destabilize and during the juvenile stage tends to stabilize coexistence in the whole system. The juvenile stage can be seen to have a refuge effect in that it counteracts the destabilization mechanism at the adult stage. When the maturation rate is low, while keeping  $\gamma/c < 1$ , both species tends to enjoy a long juvenile period in which the stabilizing mechanism is embedded, compared with the adult period, and consequently, the whole system achieves stable coexistence.

Two-patch two-competing-species models with interpatch migrations (Levin 1974; Nishimura and Kishida 2001; Amarasekare 2004) have similar topological configurations of model structure to our stage-structured competition model. The adult and juvenile stages in our model correspond to the two patches, and maturation and birth processes correspond to migrations between the patches. In two-patch models, stable coexistence of the competing species is accomplished partly by refuge patch effects via certain migration rates between patches when a destabilizing competition effect is embedded in either or both patches (Levin 1974; Nishimura and Kishida 2001; Amarasekare 2004). Our stage-structured model is analogous to the patch models (Levin 1974; Nishimura and Kishida 2001; Amarasekare 2004) in that refuge effects lead to stable coexistence with sufficiently low migration rates. However, a complete source-sink structure of our model (wherein the adult stage is the source patch and the juvenile stage is only a sink patch) provides a unique mechanism for stable coexistence.

*Underactivity* Suppose again the case that interspecific competition is intense at the adult stage and weak at the juvenile stage. For the juvenile stage to provide a refuge requires a low maturation rate. However, a high maturation rate that leads to higher density at the adult stage still permits stable coexistence if the intrinsic birth rate is low. The allowable maximum maturation rate is

The allowable maximum maturation rate is  $1/2 \left( -\phi_0 + \sqrt{4cv_{\text{sup}} + \phi_0^2} \right)$  (see Appendix 5). For a

high maturation rate  $\gamma$ , the required minimum intrinsic birth rate for population persistence is  $c(\gamma + \phi_0)/\gamma$ . Even if the ratio of adult density to juvenile density is high, implying that the adult stage, which destabilizes the whole system, is dominant, when the intrinsic juvenile mortality rate  $\phi_0$  is low, coexistence is stabilized by a low birth rate, which causes both species to be underactive.

*Overcoming the destabilizing effect* When the interspecific competition is weak at the adult stage and intense at the juvenile stage, in contrast, for the adult stage to have a refuge effect requires a high maturation rate. However, a low maturation rate that leads to a higher density at the juvenile stage still permits stable coexistence if the intrinsic birth rate is high. A higher birth rate increases both the adult and juvenile densities and keeps the ratio of the densities constant. Higher juvenile densities as well as higher total densities seem to destabilize coexistence. Despite this destabilizing effect, that is, despite higher densities of juveniles of both species, the absolute higher densities of adults of both species caused by the high birth rate overcomes the destabilizing effect.

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## Conclusion

Theoretical studies on exclusion and coexistence of competing species regard competition coefficients as fundamental synthetic parameters that implicitly reflect the competing processes. These synthetic parameters or competition coefficients incorporate the life-history characteristics of the competing species, linking them to the niche concept and allowing analysis of the conditions of exclusion or coexistence (Lotka 1925; MacArthur and Levins 1967). Even in a multiple age-structured competition model, the conditions of stable coexistence have been discussed with reference to competition coefficients, and in this regard, the model is qualitatively the same as a simple no-age-structured model (Travis et al. 1980).

Competitive interaction between species with stage-structured life cycles offers a different perspective on exclusion or coexistence. In this case, exclusion or coexistence of the competing species is determined not only by the competition per se but also by the characteristics of the life-cycle stages. The individual viability parameter, comprising the intrinsic birth rate, the intrinsic adult death rate, and the maturation rate, plays a key role, linking the adult and juvenile life stages. For a

single-species dynamic system, high individual viability facilitates the persistence of the population, whereas low individual viability does not. On the other hand, our analysis demonstrated that both a particular competitive relation between competing species and an appropriate individual viability are necessary for two species to coexist stably, even though individual viability must be high to maintain the population of each species. However, the viability that is necessary for the populations to persist must satisfy the conditions that stabilize the equilibrium in a given competitive relation as well. When adult inter-specific competition is greater than intraspecific competition in either or both species, the necessary individual viability for the equilibrium to be stable is an intermediate value. We identified the patterns of the competitive relations and the life-history characteristics necessary for stable coexistence and elucidated the stability mechanism from the perspective of both the concept of refuge and the performance of the birth process.

Here, we focused primarily on the conditions necessary for stable coexistence. The fate of competition in cases of unstable equilibrium is also of interest, but was not presented in detail in this paper. In some cases, we can deduce the fate of competition exclusion solely via combinations of competition coefficients at each life stage. In other cases, however, the fate of competition exclusion depends on the value of the viability parameter as well. For instance, when there is asymmetric inter-specific competition at one stage and antagonistic asymmetric competition at the other stage, competitive outcomes depend on whether the competition at either stage is emphasized through the value of the viability parameter. This also suggests that the life-history characteristics, as links between life stages, significantly affect the competitive interaction and its consequences for species with a complex life cycle.

We formulated an analytically tractable model by making several assumptions: (1) segregation of inter-specific competition between stages; (2) incorporation of density-dependent processes into particular life-history processes, that is, birth and juvenile mortality; (3) identical life-history parameters among species; (4) a linear density-dependence function; (5) fixed life-history parameters. We chose the simplest assumptions among the plausible and realistic alternatives in the interest of parsimony to analyze the effects of interspecific competition and stage structure per se on stable coexistence.

The concepts of ontogenetic niche shift and life-history segregation (Werner and Gilliam 1984) support the first assumption. To minimally incorporate density-dependent processes into essential parts of the model, we made the second assumption that density dependence operates via birth and juvenile-mortality processes. We are confident that relaxation of the third and fourth assumptions would have little influence on our results. The fifth assumption excludes evolutionary changes in life-history parameters. Whether coexistence is maintained on an evolutionary timescale by natural selection acting on the life-history parameters must be

investigated. It is possible that the evolution of life-history traits leads to different competitive outcomes from those determined without taking into account the evolutionary process (manuscript in preparation).

There is some empirical evidence of reciprocal competitive abilities in the developmental stages of coexisting competing species with complex life cycles (Walls 1990; Mores et al. 1999). Some scientists have postulated that such antagonism in competitive abilities may sustain coexistence of species by achieving a balanced interaction in which one species is competitively superior in the juvenile environment and the other species has a competitive advantage in the adult environment (Istock 1966; Zwolfer 1971; Schroder 1974; Briggs 1993; Holt and Polis 1997; Amarasekare 2000a, b, 2003). However, our analysis demonstrates that coexistence is supported not only by the competitive relation but also by certain life-history characteristics inherent in complex life cycles. In other words, coexistence might readily collapse as a result of shifts in individual viability via a change in any related factor, even though two species potentially have a competitive relation that supports stable coexistence.

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## Appendix 1

The nontrivial equilibrium values of Eqs. 6a–d are

$$X^* = \frac{(\gamma/c^2)\{b_0\gamma - c(\gamma + \phi_0)\}\{b_0\gamma^2(-1 + \alpha) - c^2(1 - \alpha')\}}{v^2(-1 + \alpha\beta) + v(-2 + \alpha\beta' + \alpha'\beta) + c^2(-1 + \alpha'\beta')} \quad (20)$$

$$x^* = \frac{(1/c)\{b_0\gamma - c(\gamma + \phi_0)\}\{b_0\gamma^2(-1 + \alpha) - c^2(1 - \alpha')\}}{v^2(-1 + \alpha\beta) + v(-2 + \alpha\beta' + \alpha'\beta) + c^2(-1 + \alpha'\beta')} \quad (21)$$

$$Y^* = \frac{(\gamma/c^2)\{b_0\gamma - c(\gamma + \phi_0)\}\{b_0\gamma^2(-1 + \beta) - c^2(1 - \beta')\}}{v^2(-1 + \alpha\beta) + v(-2 + \alpha\beta' + \alpha'\beta) + c^2(-1 + \alpha'\beta')} \quad (23)$$

and

$$y^* = \frac{(1/c)\{b_0\gamma - c(\gamma + \phi_0)\}\{b_0\gamma^2(-1 + \beta) - c^2(1 - \beta')\}}{v^2(-1 + \alpha\beta) + v(-2 + \alpha\beta' + \alpha'\beta) + c^2(-1 + \alpha'\beta')}, \quad (24)$$

where  $v = b_0\gamma^2/c^2$ .

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## Appendix 2

Biological feasibility of the equilibrium population densities is satisfied when the fractions  $C_1/B$  and  $C_2/B$  in

Eqs. 7a and b are positive, given that the persistence condition in Ineq. 9 holds. The necessary condition for the equilibrium to be positive is either of the following:

Case 1:

$$v(-1 + \alpha) > 1 - \alpha' \quad (25a)$$

$$v(-1 + \beta) > 1 - \beta' \quad (25b)$$

$$(-1 + \alpha\beta)v^2 + (-2 + \alpha\beta' + \alpha'\beta)v + (-1 + \alpha'\beta') > 0, \quad (25c)$$

Case 2:

$$v(-1 + \alpha) < 1 - \alpha' \quad (26a)$$

$$v(-1 + \beta) < 1 - \beta' \quad (26b)$$

$$(-1 + \alpha\beta)v^2 + (-2 + \alpha\beta' + \alpha'\beta)v + (-1 + \alpha'\beta') < 0. \quad (26c)$$

We verified that if Ineqs. 25a and 25b are satisfied, Ineq. 25c is necessarily satisfied and if Ineqs. 26a and 26b are satisfied, Ineq. 26c is necessarily satisfied. Therefore, the necessary condition for the equilibrium to be positive is reduced to: Ineqs. 25a and 25b in case 1, and Ineqs. 26a and 26b in case 2.

### Appendix 3

We chose a set of values of parameters,  $\alpha$ ,  $\beta$ ,  $\alpha'$ ,  $\beta'$ ,  $v$ , and  $\phi_0$ , and judged whether the set of parameters is classified into either of the conditions of positive interior equilibrium, i.e., case 1 or 2 in Appendix 2. If the parameters set satisfied case 1 or 2, we designed  $b_0$ ,  $\gamma$ , and  $c$  for the given value of  $v$ . Then, we get a set of values of parameters,  $\alpha$ ,  $\beta$ ,  $\alpha'$ ,  $\beta'$ ,  $\phi_0$ ,  $b_0$ ,  $\gamma$ , and  $c$ . For the set of parameters and the equilibrium values (Appendix 1), the dominant eigenvalue associated with the 4×4 Jacobian matrix

$$J = \begin{pmatrix} -c & \gamma & & \\ -b_0X^* + b_0(1 - X^* - \alpha Y^*) & -x^* - \gamma - \phi_0 - x^* - \alpha'y^* & & \\ 0 & 0 & & \\ -b_0\beta Y^* & -\beta'y^* & & \\ 0 & 0 & & \\ -b_0\alpha X^* & -\alpha'x^* & & \\ -c & \gamma & & \\ -b_0Y^* + b_0(1 - Y^* - \beta X^*) & -y^* - \gamma - \phi_0 - y^* - \beta'x^* & & \end{pmatrix},$$

which is acquired by the linearized system of Eqs. 6a–d, is evaluated at the equilibrium point. We repeated this procedure systematically for various combinations of the parameters, and inductively confirmed that the equilibrium is stable for the sets of parameters belonging to case 1.

### Appendix 4

The partial analysis of the local stability of the equilibrium is constrained,  $x = (c/\gamma)X$  and  $y = (c/\gamma)Y$ , by the direction of perturbations of each species being restricted on each line. With this constraint, we can describe the dynamic equations of both species only by the adult populations, denoted as  $F_X(X, Y)$  and  $F_Y(X, Y)$ , respectively. The Jacobean matrix of the linearized system of  $F_X$  and  $F_Y$  in the state of a nontrivial equilibrium was obtained, and then we found the eigenvalues,  $-A$  and  $C_1C_2A^2/B$  (these variables are as defined in Eqs. 7a and b). Because we consider that  $A$  is positive (thus,  $-A < 0$ ), stability is determined only by the sign of the latter eigenvalue. Therefore, the stability condition is reduced to

$$\frac{C_1C_2}{B} < 0. \quad (27a)$$

Now, since we consider that equilibrium is positive (that is, Eqs. 7a, b are both positive),  $C_1$  and  $C_2$  have same sign. Therefore,  $B$  must be negative for stability, and, consequently,  $C_1$  and  $C_2$  are both negative. Thus, the stability conditions are again reduced to

$$C_1 < 0, C_2 < 0. \quad (27b)$$

### Appendix 5

When the interspecific competition is intense at the adult stage and weak at the juvenile stage, the condition of stable coexistence is

$$\frac{\gamma(\gamma + \phi_0)}{c} < \frac{b_0\gamma^2}{c^2} < v_{\text{sup}}. \quad (28a)$$

Rearrangement of the inequality in terms of  $b_0$  leads to the following:

$$\frac{c(\gamma + \phi_0)}{\gamma} < b_0 < \left(\frac{c}{\gamma}\right)^2 v_{\text{sup}}. \quad (28b)$$

Then, the allowable maximum maturation rate while keeping a positive interval of  $b_0$  in Ineq. 28b is obtained by solving the equality,

$$\frac{c(\gamma + \phi_0)}{\gamma} = \frac{c^2}{\gamma^2} v_{\text{sup}}. \quad (28c)$$

Considering  $\gamma > 0$ , the allowable maximum maturation rate is

$$\gamma_{\text{sup}} = \frac{1}{2} \left( -\phi_0 + \sqrt{4cv_{\text{sup}} + \phi_0^2} \right). \quad (28d)$$

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