

Evolution of life-history traits collapses competitive coexistence

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Abstract

Trade-offs between competitive ability and the other life-history traits are considered to be a major mechanism of competitive coexistence. Many theoretical studies have demonstrated the robustness of such a coexistence mechanism ecologically; however, it is unknown whether the coexistence is robust evolutionarily. Here, we report that evolution of life-history traits not directly related to competition, such as longevity, and predator avoidance, easily collapses competitive coexistence in several competition systems: spatially structured, and predator-mediated two-species competition systems. In addition, we found that a superior competitor can be excluded by an inferior one by common mechanisms among the models. Our results suggest that ecological competitive coexistence due to a life-history trait trade-off balance may not be balanced on an evolutionary timescale, that is, it may be evolutionarily fragile.

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1. Introduction

Competition has been spotlighted as a key species interaction that determines species coexistence and exclusion on an ecological timescale (Lotka, 1925; Gause, 1934; MacArthur, 1972; May, 1972). In general, competing species can coexist when interspecific competition is weak (Lotka, 1925; Gause, 1934). Nevertheless, even when interspecific competitive interaction is strong, coexistence frequently occurs in a natural community. In this context, a trade-off of life-history traits has been the focus of attention as the mechanism explaining this species coexistence (Hutchinson, 1957; Tilman, 1982; Kneitel and Chase, 2004). Life-history traits of an inferior competitor that are advantageous compared with those of the superior competitor, such as the reproductive, migration and predator resistance abilities, mitigate the exclusion effect of the inferior competitor by the superior one (Levins and Culver, 1971; Armstrong, 1979; Levin and Rees, 2002). Even if the coexistence mechanism is ecologically robust,

however, whether the trade-off balance is evolutionarily robust is an open question (Geritz et al., 1999).

Competitive interaction has also attracted much attention as the driving force of the evolution of 'competitive traits' (MacArthur and Levins, 1967; Matsuda and Abrams, 1994; Law et al., 1997; Doebeli and Dieckmann, 2000; Kisdi and Geritz, 2001). Intense interspecific competition may exert selection pressure on interference and exploitative competition traits, such as body or beak size, of either or both competing species (Brown and Wilson, 1956; Law et al., 1997). Coevolution of the competitive traits of the interacting species may cause character divergence and resulting coexistence (MacArthur and Levins, 1967; May and MacArthur, 1972; Roughgarden, 1972; Slatkin, 1980; Taper and Case, 1985) or cause parallel evolution, convergence, evolutionary cycles, or extinction of one species (Law et al., 1997; Geritz et al., 1999; Kisdi and Geritz, 2001). These theoretical studies have envisaged a competitive trait such as body size as the evolvable trait under an evolutionary scenario of competitive interaction. However, life-history traits (e.g., maturation, colonization, migration, and predator avoidance) other than competitive ability, which have been assumed to be merely a cost of the evolution of competitive traits

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(Matsuda and Abrams, 1994; Law et al., 1997; Geritz et al., 1999; Kisdi and Geritz, 2001), can evolve in a similar fashion (Gyllenberg and Parvinen, 2001; Webb, 2003). In a single population or in antagonistic interaction systems, evolution of life-history traits can cause extinction (Gyllenberg and Parvinen, 2001; Webb, 2003). From this viewpoint, the consequence of the evolution of such life-history traits may influence competitive interaction among species in unexpected ways.

Previously, we demonstrated that the ecological coexistence of competing species accomplished by a balance between competitive abilities and other life-history traits can be easily collapsed evolutionarily by the evolution of a life-history trait other than competitive ability driven by competitive interaction between species (Mougi and Nishimura, 2006). The major emphasis of this earlier work was that the ecological coexistence of competing species by ‘a life-history trait trade-off’ (Hutchinson, 1957; Levins and Culver, 1971; Armstrong, 1979; Tilman, 1982; Kneitel and Chase, 2004) might easily collapse via the evolution of ‘a life-history trait not directly related to exploitative or interference competition’. However, this result might depend on the specific model structure (Mougi and Nishimura, 2006 considered evolution of the maturation rate in a stage-structured competition system).

In this paper, we demonstrate that the evolutionary collapse of competitive coexistence can easily occur with evolving a life-history trait not directly related to exploitative or interference competition in various ecological scenarios involving competitive interaction, and argue that our previous result (Mougi and Nishimura, 2006) can be generalized. We describe ecological scenarios involving stage-structured (Mougi and Nishimura, 2006), spatially structured, and predator-mediated two-species competition systems, which we present as examples of competitive coexistence by a life-history trait trade-off. These models are largely different systems reflecting various competition scenarios; thus, similar results in all three models highlight a general theory. Our additional purpose is to understand the common features leading to evolutionary collapse in a variety of ecological situations. In this context, we suggest that the classic mechanism explaining the coexistence of competing species, a life-history trait trade-off, may be fragile with respect to evolution of life-history traits not directly related to competitive ability.

2. Model

As examples, we employ two interspecific competition models, both of which explicitly describe a different aspect of the complex life histories of the competing species. In the first model, we consider the evolution of the mortality rate (longevity) in a familiar spatially structured competition system. In the second model, we consider the evolution of the predator avoidance rate in a one predator–two competing prey system.

In both models, we concentrate on a particular type of competitive relationship known as dominance competition ($\alpha_{12} < \alpha_{21} \leq 1$ in model 1 and $\alpha_{12} < 1 < \alpha_{21}$ in model 2, where α_{ij} are the competition coefficients of the j th species to i th species), where the superior competitor species 1 (hereinafter referred to as “superior”) enjoys dominance over the inferior competitor species 2 (hereinafter referred to as “inferior”) in the competitive interaction, and on an ecological scenario in which the two species coexist owing to a balance between their competitive abilities and their other life-history traits (i.e., a life-history traits trade-off mechanism). Note that the ecological coexistence is due to the interspecific trade-off between competitive ability and the synthetic trait of other two life-history traits. The classical coexistence scenario assumes the coexistence due to the trade-off between two traits (e.g., competitive ability and colonization ability). However this assumption is for the mathematical simplicity, a life-history parameter involves a number of traits (Yu and Wilson, 2001).

We incorporate the evolution of the life-history traits, mortality rate, and predator avoidance rate, into each competition system by using an adaptive dynamics framework (Dieckmann, 1997; Geritz et al., 1998). In order to realize the trait evolution process, we first define the invasion fitness of a rare mutant $W(\hat{v}, v)$ with trait \hat{v} , which is slightly different from trait v of the resident population of each competing species. We assume that the expected rate of sequences of phenotypic substitution is proportional to the mutation-generating process (Dieckmann, 1997) and the selection gradient $(\partial W(\hat{v}, v)/\partial \hat{v})\hat{v} = v$ (the derivative of invasion fitness with respect to the value of the mutated trait), which reflects the intensity and direction of the selection acting on the trait (Geritz et al., 1998) (see Appendix A), and we describe the evolutionary trajectory of the life-history traits according to the sequences of phenotypic substitution (Dieckmann and Law, 1996).

3. Ecological competition systems

3.1. Model 1: Spatially structured competition system

We use a classical patch-occupancy model, which is widely used in biology (Nowak and May, 1994), and particularly in community ecology (Levins and Culver, 1971; Hastings, 1980; Nee and May, 1992; Tilman, 1994; Calcagno et al., 2006). Consider a local community characterized by many discrete patches connected by migration and colonization events. We assume that no fully asymmetric local competition occurs in an individual patch, and that there is no preemptive effect (dominance competition or displacement competition). We focus on the relationships among competitive ability, mortality rate, and colonization rate that affect ecological coexistence. The mortality rate (longevity) of each species is the focal evolutionary trait.

The implicit spatial two-species competition system is described by the following equations:

$$\begin{aligned} \dot{N}_i = & c_i N_i \left(1 - \sum_{j \in \{1,2\}} N_j \right) - m_i N_i \\ & + c_i N_i \sum_{j \neq i} N_j \alpha_{ji} - N_i \sum_{j \neq i} c_j N_j \alpha_{ij}, \end{aligned} \quad (1)$$

where N_i is the proportion of sites occupied by the i th species ($i \in \{1,2\}$). c_i is the colonization rate into an empty patch, and m_i is the mortality rate. α_{ij} and α_{ji} are the competition coefficients of the j th species relative to the i th species and vice versa. The right-hand terms imply colonization of empty sites through pure scramble competition (first term), local death (second term), and colonization of occupied sites (third term, patches gained by displacing other species; fourth term, patches lost by being displaced by other species). We assume a colonization–mortality trade-off, that is, $c_i (= c(m_i))$ is an increasing function of m_i (see Fig. 1 for details of each specific function).

3.2. Model 2: One predator–two competing prey system

Consider two competing species and their one shared predator species. Similar systems have been the subject of many theoretical and empirical studies (Paine, 1966; Leibold, 1996; Grover, 1995; Genkai-Kato and Yamamura, 2000). We focus on the relationships among competitive ability, predation avoidance ability, and fecundity that affect ecological coexistence. The predator avoidance rate in each competing species is the focal evolutionary trait in the competitive interaction.

The ecological dynamics reflecting this scenario is described by the following equations:

$$\dot{N}_i = (b_i - o_i P) N_i, \quad (2a)$$

$$\dot{P} = \left(k \sum_{j \in \{1,2\}} g_j o_j N_j - d \right) P, \quad (2b)$$

where N_i is the density of i th competing species, and P is the density of the shared predator. b_i is the per capita birth rate of each species, which is characterized by intra- and interspecific competition; that is, $b_i = b_{0i} (1 - \sum_{j \in \{1,2\}} \alpha_{ij} N_j / K_i)$. b_{0i} is the intrinsic birth rate, K_i is the carrying capacity of i th species and α_{ij} are the competition coefficients of the j th species to i th species ($\alpha_{ii} = 1$). $o_i = a_i / (1 + \sum_{j \in \{1,2\}} a_j h_j N_j)$ is the consumption speed of one individual of the j th prey species by an individual predator given a prey density of (N_i, N_j) (Kretzschmar et al., 1993; Grover, 1995), where a_i is the predator’s encounter efficiency with prey species i , which we treat as a characteristic of the prey, namely, the predator avoidance rate. We assume that the higher the predator avoidance rate, the lower the value of parameter a_i . In addition, we assume that the carrying capacity of the

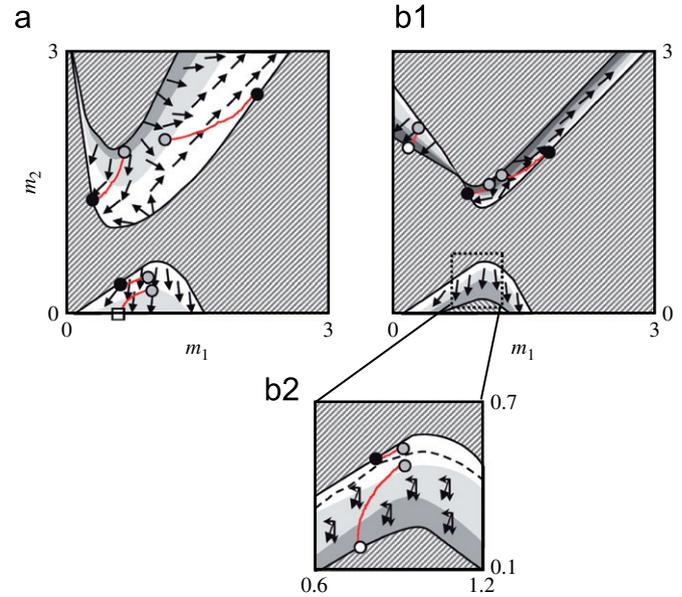


Fig. 1. Model 1. Selection and evolution of m_1 and m_2 on the ecological equilibrium states in m_1 – m_2 space: (a) strong dominance competition, $\alpha_{12} = 0.05$, $\alpha_{21} = 0.95$; (b) weak dominance competition, $\alpha_{12} = 0.3$, $\alpha_{21} = 0.7$. We adopt a trade-off function $c(m_i) = c_{0i} \exp(\mu_i m_i)$ in these examples. c_{0i} is the baseline colonization rate and μ is intensity of the trade-off between the mortality rate and the colonization rate. In both (a) and (b), $c_{01} = c_{02} = 0.4$, $\mu_1 = \mu_2 = 1$. In regions other than the hatched area, both species stably coexist. (The hatched areas represent the trivial equilibrium state.) Shaded contours indicate the proportion of the superior competitor’s population density relative to the total population of both species. The lighter the contour, the higher the superior species’ abundance. The arrows show the unit selection gradient vector fields based on the relative magnitudes and signs of the invasion fitness of the mortality rates of each species. The red trajectories connecting circles show the numerical evolutionary simulation results. The simulation starts at the gray circles and terminates at the time when either species becomes extinct, where the white and black circles represent the extinction of the superior and inferior species, respectively. (b2) is the enlargement of the indicated portion of (b1). If needed, we show the component vectors of the synthetic vectors of the fitness gradients. The dashed line indicates the separatrix, above which the evolutionary trajectory leads to extinction of the inferior species and below which the trajectory leads to extinction of the superior species. The white square represents the termination point where two species coexist.

prey is a decreasing function of the predator avoidance rate (see figure legend for details of a specific function). k is the conversion efficiency of consumed prey into the predator’s reproduction rate, g_i is the energy value of an individual of prey species i , and h_i is the handling time for prey species i . d is the predator death rate. We assume here that the predation is described by a type 2 functional response.

3.3. Ecological coexistence

Ecological stable coexistence is accomplished by attainment of a compensatory balance among life-history traits and competitive ability between species. In all models, ecological stable coexistence is possible if the

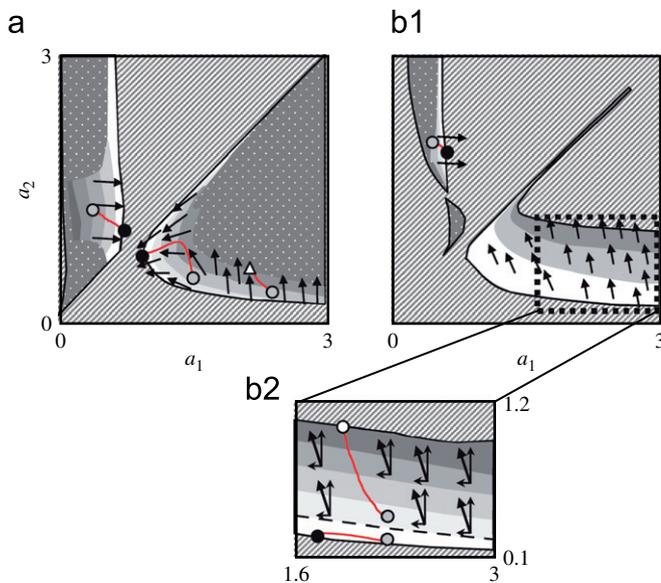


Fig. 2. Model 2. Selection and evolution of a_1 and a_2 on the ecological equilibrium states in a_1 – a_2 space: (a) strong dominance competition, $\alpha_{12} = 0.1$, $\alpha_{21} = 1.1$; (b) weak dominance competition, $\alpha_{12} = 0.9$, $\alpha_{21} = 1.1$. We adopt a linear trade-off function $K(a_i) = K_{0i} + \varepsilon_i a_i$ in these examples. K_{0i} is the baseline carrying capacity and ε is intensity of the trade-off between the predator avoidance rate and the carrying capacity. In both (a) and (b), $k = 1$, $g_1 = 1.1$, $g_2 = 0.8$, $h_1 = 0.1$, $h_2 = 1.1$, $b_{01} = b_{02} = 1$, $K_{01} = K_{02} = 0.01$, $\varepsilon_1 = \varepsilon_2 = 1.2$, and $d = 0.3$. Note that we adopt $g_1 > g_2$ and $h_1 < h_2$, which mean that the superior competitor is preferred by the predator over the inferior competitor, because we want to highlight the result visually (the main results are not influenced even if these parameters are symmetrical between two species (see Appendix A and B)). The dotted regions are regions of unstable coexistence, where the densities in the system oscillate. The white triangle represents the termination point where both species enter a region of unstable equilibrium. Other information is the same as in Fig. 1.

focal life-history trait value of one competing species is considerably higher or considerably lower than that of the other competing species (coexistence regions above (CRA) and below (CRB) the 45° line from zero in Figs. 1 and 2).

In model 1, ecological stable coexistence is possible if the superior competitor has a higher mortality rate, which results in a sufficiently higher mortality rate to cancel out the advantage of the higher colonization ability (CRA in Figs. 1a and b), or a lower mortality rate, which results in a sufficiently lower colonization ability to cancel out the advantage of the lower mortality (CRB in Figs. 1 and b), compared with the inferior. In model 2, coexistence is possible if the superior has a sufficiently lower predator avoidance rate to cancel out a resulting higher carrying capacity (CRB in Figs. 2a and b), or a sufficiently higher predator avoidance rate, which results in a lower carrying capacity (CRA in Figs. 2a and b) compared with the inferior. In such coexistence regions of the focal evolutionary trait values, how do the life-history traits, mortality rate and predator avoidance rate, evolve in a spatially structured, and a one predator–two competing prey system, respectively?

3.4. Evolution of the life-history traits and the collapse of stable coexistence

We investigate how the life-history traits evolve in each competitive interaction system, and how trait evolution affects the coexistence of the two competing species.

We first analyze the direction and intensity of selection acting on the life-history trait by evaluating the magnitude and sign of the selection gradient in the competing species, $(\partial W_i(\hat{v}_i, v_i)/\partial \hat{v}_i)\hat{v}_i = v_i$ (see Appendix A for details of the fitness functions and an analysis of the invasive potential of a mutant). Figs. 1 and 2 show the unit vector fields based on the relative magnitude and sign of the fitness gradient for the life-history trait values of two species superimposed on the ecological equilibrium conditions on the trait values plane for models 1–2, respectively.

It is clear that most of the selection gradient vectors of both species trend toward the extinction region in all models (see Appendix B for the proof). In all models, the selection gradient vectors trend toward extinction of the inferior in a wide parameter space when the competition effect of the inferior on the superior is very low, that is, when there is strong dominance competition (Figs. 1a and 2a; a low $\alpha_{12} (\ll 1)$). If the dominance competition relationship is weak (Figs. 1b and 2b; a high $\alpha_{12} (< 1)$), however, the selection gradient vectors trend toward extinction of the superior under certain initial conditions (see Figs. 1b and 2b).

The evolutionary simulations whose trajectories initiate from any of the parameter sets in the ecological coexistence regions are shown in each figure (see Appendix C for details of the evolutionary simulations). The trajectories of trait evolution reflect the trends of the selection gradient vectors. This result suggests that ecological coexistence due to a balance between competitive ability and other life-history traits can collapse on an evolutionary timescale (see Appendix B). The relaxation of the shape of trade-off functions (we used specific functions as example in the figures) does not destroy our main results.

3.5. Mechanism of evolutionary extinction

We examine how and why the evolution of life-history traits balancing with competitive ability in an ecological equilibrium collapses the coexistence, leading to destabilization or extinction of either species.

The ecological state (stable coexistence, destabilizing fluctuation, or exclusion of either species) is determined on the evolvable traits space of both species. The key factors dictating trait evolution resulting in destabilization or species extinction are the evolutionary directions, determined by the selection gradient, and the relative evolutionary speeds, determined by both the selection gradient and the mutation supply of the traits, in the competing species, without incorporating the genetic covariance structure among the focal trait and other traits in each species.

Population densities at ecological equilibrium are the driving force of the selection intensity that determines the selection gradients via intra- and interspecific competition. The densities also determine the fecundity via intra- and interspecific competition. Assuming that the occurrence rate of a mutant per newborn is the same among the species (we assume that the mutation rate per newborn is unity, with an arbitrarily small unit), the mutation supply is determined by the fecundity and the number of reproducing individuals in each species at ecological equilibrium.

In the common mathematical terminology used in the three different models, the evolutionary trajectory of the trait evolution is expressed as

$$\frac{\partial v_i}{\partial t} \propto \tilde{b}_i \cdot \tilde{N}_i^* \cdot \left. \frac{\partial W_i(\hat{v}_i, v_i)}{\partial \hat{v}_i} \right|_{\hat{v}_i=v_i}, \quad (3)$$

where \tilde{b}_i is the fertility of a reproducing individual, and $(\partial W_i(\hat{v}_i, v_i)/\partial \hat{v}_i)|_{\hat{v}_i=v_i}$ is the selection gradient of the i th species given a certain combination of evolvable traits and the resulting densities at ecological equilibrium, and \tilde{N}_i^* is the effective number of reproducing individuals of the i th species at ecological equilibrium.

We can understand the pattern of the evolutionary trajectories shown in each figure by reference to two factors, mutation supply and selection gradient: the higher the mutation supply rate and/or the greater the effect of the selection gradient, the faster the evolutionary speed. In other words, evolutionary speed can be fast or slow, depending on the combination of these two factors. This implies that the selection gradient effect reflects the coevolutionary trajectory as long as the selective force is not hampered by the inverse effect of the relative mutation supply rate. The inverse effect occurs when one species that suffers intense selection has a low occurrence rate of a mutant due to a low effective density of reproductive individuals and another species that suffers weak selection has a high occurrence rate of the mutant due to a high effective density of reproductive individuals (e.g., see the upper trajectory in Fig. 1b and the lower trajectories in Fig. 2b).

In the coevolutionary trajectory, extinction of one species occurs with the rapid evolution of the trait in the opposite species. Since the mutant with a higher fitness than the resident can invade the resident population, the viability of the individuals with respect to survival and fecundity continues to be improved until the mutation supply or the selection pressure vanishes. In the parameter regions for coexistence in each system, selection pressures on each species never vanish simultaneously during trait evolution. Hence, the evolutionary trajectories move past the coexistence parameters region during coevolution. In other words, rapid evolution of one species increases its equilibrium density with a rapid improvement in individual viability and drives another species into extinction before selection pressures on both species vanish.

Selection intensity represents the rate at which mutants replace the resident population. A species that suffers

intense selection is replaced at a higher rate by a mutant with higher survival, higher fecundity, and/or a shorter generation time than the resident, and vice versa.

The viability components of the invading mutant, that is, its survival, fecundity, and generation time, change, depending on the direction of selection on the evolvable trait (Appendix A). Not all the viability components of the invading mutant can be improved as a result of the trade-off between life-history traits. Since the coexisting competing species have antithetical trait values for balancing asymmetric competitive abilities, selection pressures on the evolvable traits influence changes in the viability components differently. The speed at which a resident is replaced by a mutant in each species can be fast or slow depending on the combinations of the life-history traits, the competitive abilities of the species, and the directions of selection on the traits.

4. Conclusion

We demonstrated that the evolution of life-history traits not directly related to competition via intra- and interspecific competitive interaction can potentially collapse competitive coexistence maintained by the life-history traits' balance in various types of competition systems (see also Mougi and Nishimura, 2006). Ecologically stable competitive coexistence requires antithetical life-history traits between competing species to offset their asymmetric competitive abilities (Hutchinson, 1957; Tilman, 1982; Kneitel and Chase, 2004). However, the presence of such antithetical life-history traits between species may result in a reversal of the relative intensity and/or direction of selection on the evolvable life-history traits and in the relative evolutionary speed of change of the traits, eventually leading to extinction of one species owing to the faster evolution of the other species. In addition, the evolution of life-history traits may have unexpected evolutionary consequences. In all models, it could be predicted that the superior competitor might be driven to extinction by rapid trait evolution in the inferior competitor. The results are less susceptible to the shape of trade-off functions. On the other hand, we know that the evolutionary stable coexistence can be possible in a model (Mougi and Nishimura, 2006) if we largely relax the symmetry of several parameters. In the present models, some relaxation of the symmetry of parameters also can make the evolutionary stable coexistence. However, at least under the symmetrical parameters among species (i.e., closely related species), our results show that ecologically stable competitive coexistence is fragile on an evolutionary timescale (Appendix B).

The models analyzed in this paper were spatially structured, and predator-mediated two-species competition systems, and the model in our previous study was a stage-structured one (Mougi and Nishimura, 2006). These ecological scenarios cover the essential processes necessary for understanding species interaction in a natural

community (Levins and Culver, 1971; Leibold, 1996; Amarasekare, 2004). Although each model describes a specific system that largely differs from the other two, reflecting a specific competition scenario, the similarity of results among all models implies a general theory, which we expect will stimulate further investigation of other ecological scenarios.

We must refer to the assumptions of our models. A recent theoretical study considered one predator–two prey system with defense evolution of prey species (Yamauchi and Yamamura, 2005). Although this model and our model 2 are similar, the main results of each study are quite different. Their model predicts evolutionary stable coexistence, in contrast, our model does not. They (we) assumed (1) no (complete) separation of timescales between the dynamics of population and traits evolution, (2) no direct (direct) interspecific competition between the prey species, (3) a cost of evolutionary trait included into growth rate (carrying capacity), and (4) a predator that practices optimal foraging (a fixed foraging). In particular, we focus on the first two main assumptions. First, the problem in timescales between the population and evolutionary dynamics is important (Abrams, 2001). The result of Yamauchi and Yamamura (2005) may reflect the consequences of species interactions on an ecological timescale rather than evolutionary timescale (Yoshida et al., 2003), in contrast our result reflects that on an evolutionary timescale. Second, the type of interspecific competition between the prey species is also important. In our models, a coexistence balance due to the interspecific trade-off between competitive ability (of direct interspecific competition) and the synthetic trait of other two life-history traits is a key assumption, and evolution of the life-history traits other than competitive ability collapses the balance. However, Yamauchi and Yamamura assumed no direct interspecific competition between prey species. This suggests that evolution of defenses can lead to a coexistence balance due to the interspecific trade-off between two life-history traits (defense and growth). Future study needs to examine the relative importance between evolution of direct and indirect competitive traits. In addition, we did not consider evolutionary dynamics under oscillating population in model 2, although the consideration would not influence our main result unless coevolutionary cycle leads to evolutionary cyclic coexistence (Dercole et al., 2006).

The classical theoretical studies on trait evolution driven by competition are studies of character displacement (MacArthur and Levins, 1967; May and MacArthur, 1972; Roughgarden, 1972; Slatkin, 1980; Taper and Case, 1985). In these studies, the evolving trait is a competitive one, such as body size or beak size, which directly influences the competition. In general, coevolution of competitive traits leads to coexistence as a result of character displacement; however, recent studies have shown that character evolution can be convergent or in parallel rather than divergent, and have suggested that evolutionary

coexistence may be unlikely to occur (Roughgarden, 1983; Taper and Case, 1985; Matsuda and Abrams, 1994; Abrams, 1996; Law et al., 1997; Geritz et al., 1999; Kisd and Liu, 2006). For example, Geritz et al. (1999) showed that competitive coexistence by a competition–colonization trade-off can be collapsed through evolution of a competitive trait (seed size) under some conditions. In addition, we showed that evolution of life-history traits not directly related to competition which has been forgotten by above studies can easily collapse competitive coexistence maintained by the life-history traits' balance. In this context, we suggest that the classical coexistence mechanism, “the life-history traits trade-off” may be evolutionarily fragile.

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Appendix A. Fitness function and analysis of the selection gradient

In the following analyses, we assume the symmetry of all parameters except for the evolving parameters and the competition coefficients.

In order to visualize the invasive potential of a mutated trait of a life-history parameter, we evaluate whether the mutant can invade the resident population by determining the local fitness gradient,

$$\left. \frac{\partial W_i(\hat{v}_i, v_i)}{\partial \hat{v}_i} \right|_{\hat{v}_i=v_i}, \quad (\text{A.1})$$

If the gradient is positive, then mutants with a higher rate of change in a life-history parameter than that of the resident population can invade that population, and, similarly, if it is negative, then those with a lower rate than that of the resident population can invade that population. If it is zero, the selection pressure vanishes and the point defined as evolutionary singularity is a candidate of evolutionary end point (Geritz et al., 1998).

A.1. Model 1

We adopt per capita growth rate as fitness. A mutant's fitness is given by

$$W_i(\hat{m}_i, m_i) = c_i(\hat{m}_i) \left(1 - \sum_{j \in 1,2} N_j^* \right) - \hat{m}_i + c_i(\hat{m}_i) \sum_{j \neq i} N_j^* \alpha_{ji} - \sum_{j \neq i} c_j N_j^* \alpha_{ij}. \quad (\text{A.2})$$

The condition that a mutant with a higher mortality rate strategy will be able to invade the resident population of

species i , $\partial W_i(\hat{m}_i, m_i)/\partial \hat{a}_{ij} > 0$, is

$$c'(m_i) > 1 / \left\{ \left(1 - \sum_{j \in 1,2} N_j^* \right) + \alpha_{ji} N_j^* \right\}, \quad (\text{A.3})$$

where $c'(m_i) = \partial c(m_i)/\partial m_i > 0$. The term $1 - \sum_{j \in 1,2} N_j^*$ (> 0) equals $(-m_i + m_j - c_i \alpha_{ij} + c_j \alpha_{ji}) / (c_j(1 - \alpha_{ij}) - c_i(1 - \alpha_{ji}))$. Inequality (A.3) implies that a mutant with a higher mortality rate strategy (higher m_i) can invade if the proportion of a patch occupied by species i is lower and that occupied by species j is higher; conversely, a mutant with a lower mortality rate strategy (lower m_i) can invade if the conditions are reversed.

A.2. Model 2

We adopt per capita growth rate as fitness. The mutant fitness is given by

$$W_i(\hat{a}_i, a_i) = b_i(N_1^*, N_2^*) - \hat{a}_i(N_1^*, N_2^*, P^*), \quad (\text{A.4})$$

where $b_i(N_1^*, N_2^*) = b_{0i}(1 - \sum_{j \in 1,2} \alpha_{ij} N_j^* / K(\hat{a}_i))$, $\hat{a}_i(N_1^*, N_2^*, P^*) = \hat{a}_i P^* (1 + \sum_{j \in 1,2} a_j h_j N_j^*)$.

The condition that a mutant with a lower predator avoidance rate strategy will be able to invade the resident population of species i , $\partial W_i(\hat{a}_i, a_i)/\partial \hat{a}_i > 0$, is

$$K'(a_i) > \frac{P^*}{b_{0i}} \frac{1}{Q} \frac{K(a_i)^2}{H_i}, \quad (\text{A.5})$$

where $H_i = \sum_{j \in 1,2} \alpha_{ij} N_j^*$ and $Q = 1 + \sum_{j \in 1,2} a_j h_j N_j^*$. Note that there are no differences between the competing species with respect to the parameters, b_{0i} , $K'(a_i) = \partial K(a_i)/\partial a_i$ (> 0), P^* , and Q . Whether the fitness gradient shows a larger value than zero depends largely on the magnitude of the last term on the right-hand side of Eq. (A.5), $K(a_i)^2/H_i$, because its effect is squared ($K(a_i)^2$). Thus, if the value of a_i is higher, then the right-hand side of Eq. (A.5) has a larger value because of the larger value of $K(a_i)^2/H_i$; in contrast, if the value of a_i is lower, the right-hand side of Eq. (A.5) has a smaller value because of the smaller value of $K(a_i)^2/H_i$. In other words, condition (A.5) means that a mutant with a lower predator avoidance strategy (higher a_i) can invade if the resident has a higher predator avoidance strategy (lower a_i); conversely, a mutant with a higher predator avoidance strategy can invade if the resident has a lower predator avoidance strategy.

Appendix B. Proof of evolutionary extinction

We examine whether ecological competitive coexistence is possible when the selection gradients of both competing species simultaneously vanish (evolutionary singularity (Geritz et al., 1998)) to show that evolutionary extinction always occurs under the condition of dominance competition.

B.1. Model 1

We focus on the special case in which the selection gradients of both competing species, $(\partial W_i(\hat{m}_i, m_i)/\partial \hat{m}_i)\hat{m}_i = m_i$ equal zero. Then,

$$\alpha_{12} = \frac{1 - (1 - N_1^* - N_2^*)c'}{N_1^*c'}, \quad (\text{B.1})$$

$$\alpha_{21} = \frac{1 - (1 - N_1^* - N_2^*)c'}{N_2^*c'}, \quad (\text{B.2})$$

where $c' = \partial c(m_i)/\partial m_i > 0$ and N_i^* is equilibrium density at a singular point. Under the dominance condition, the inequality $\alpha_{12} < \alpha_{21} \leq 1$ must be true. Thus,

$$N_2^* < N_1^* \leq 1 - \frac{1}{c'}. \quad (\text{B.3})$$

Furthermore, since $N_1^* + N_2^* < 1$,

$$\frac{(\alpha_{21} + \alpha_{12})(c' - 1)}{\alpha_{12}(-1 + \alpha_{21}) - \alpha_{21}} > c'. \quad (\text{B.4})$$

Notice that the denominator on the left-hand side is negative and the right-hand side is positive. Thus $c' < 1$ is a necessary condition for Eq. (B.4) to be true. However, $N_i^* < 0$ is a necessary condition for Eq. (B.3) to be true, implying that evolutionary coexistence is impossible under dominance competition.

B.2. Model 2

We focus on the special case in which the selection gradients of both competing species, $(\partial W_i(\hat{a}_i, a_i)/\partial \hat{a}_i)\hat{a}_i = a_i$ equal to zero. Then,

$$N_1^* = A(K_1^2 - K_2^2 \alpha_{12}), \quad (\text{B.5})$$

$$N_2^* = A(K_2^2 - K_1^2 \alpha_{21}), \quad (\text{B.6})$$

where $A = P^*/(b_{0i}Q(1 - \alpha_{12}\alpha_{21})K') > 0$ (because we focus on the case where two competing species can coexist ($\alpha_{12}\alpha_{21} < 1$)) and $K_i = K(a_i)$. If two competing species coexist evolutionarily ($N_1^* > 0$ and $N_2^* > 0$) under the dominance condition ($\alpha_{12} < 1 < \alpha_{21}$), the following condition must be met,

$$\alpha_{12} < \left(\frac{K_1(a_1)}{K_2(a_2)} \right)^2 < 1/\alpha_{21} < 1. \quad (\text{B.7})$$

In the case $a_1 \geq a_2 (K_1 \geq K_2)$, the condition (B.7) is not met, implying that evolutionary coexistence is impossible. In the case $a_1 < a_2 (K_1 < K_2)$, however, the evolutionary coexistence may occur under extremely narrow parameter spaces ($a_1 \approx a_2 (K_1 \approx K_2)$).

Appendix C. Evolutionary simulation

We describe the evolutionary dynamics by numerical simulations. We assume that evolution is strictly mutation-limited (i.e., a new mutant enters only when the resident

population has reached a stationary state). If we assume that ecological and evolutionary processes operate on different timescales, then the rates of change of traits are given by $u_i \tilde{b}_i N_i^* (\partial W_i(\hat{v}_i, v_i) / \partial \hat{v}_i) \hat{v}_i = v_i$ ($i = 1$ or 2) (Dieckmann and Law, 1996). \hat{b}_i is the fertility of a reproducing individual, and \tilde{N}_i^* is the effective number of reproducing individuals of the i th species at ecological equilibrium. We iteratively replace a trait of the resident population of either species by a mutant trait with probabilities proportional to the magnitude of $u_i \tilde{b}_i \tilde{N}_i^* (\partial W_i(\hat{v}_i, v_i) / \partial \hat{v}_i)_{\hat{v}_i=v_i} / \sum_{j \in X, T} u_j \tilde{b}_j \tilde{N}_j^* (\partial W_j(\hat{v}_j, v_j) / \partial \hat{v}_j)_{\hat{v}_j=v_j}$, given the situation that the mutant emerges, thus making the time dimension implicit. In the simulations, we set the mutation rate u_i to unity.

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