

# Variant evolutionary trees under phenotypic variance

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## Abstract

Evolutionary branching, which is a coevolutionary phenomenon of the development of two or more distinctive traits from a single trait in a population, is the issue of recent studies on adaptive dynamics. In previous studies, it was revealed that trait variance is a minimum requirement for evolutionary branching, and that it does not play an important role in the formation of an evolutionary pattern of branching. Here we demonstrate that the trait evolution exhibits various evolutionary branching paths starting from an identical initial trait to different evolutionary terminus traits as determined by only changing the assumption of trait variance. The key feature of this phenomenon is the topological configuration of equilibria and the initial point in the manifold of dimorphism from which dimorphic branches develop. This suggests that the existing monomorphic or polymorphic set in a population is not a unique inevitable consequence of an identical initial phenotype.

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## 1. Introduction

Studies on adaptive evolutionary dynamics, which have recently been developed, emphasized on the process of phenotypic evolution by game interaction among trait individuals in an explicit life history or population dynamics scenarios with implicit concern about the supply of trait variance (Doebeli and Dieckmann, 2000; Doebeli and Ruxton, 1997; Geritz et al., 1998; Kisdi, 2002; Kisdi and Geritz, 2001; Law et al., 1997; Mathias et al., 2001). Some studies on adaptive evolutionary dynamics addressed the evolutionary process that generates dimorphism (more generally, polymorphism) via evolutionary branching from monomorphism (Dieckmann, 1997; Doebeli and Ruxton, 1997; Geritz et al., 1998; Kisdi, 1999). Convergence-stable but ESS-unstable evolutionary equilibrium generates branching (Christiansen, 1991; Geritz et al., 1998). The conditions and properties of the development of phenotypic branching were analysed (Christiansen, 1991; Geritz et al., 1998).

The evolution of phenotypes after branching exhibits a variety of patterns. In the simplest case, the branching trajectory converges to a stable dimorphic state (Doebeli and Ruxton, 1997; Geritz et al., 1998; Kisdi, 1999; Mathias et al., 2001). In some cases, one of the dimorphic morphs becomes extinct during branch development, and the extinction of one morph leads to the cyclical evolution of branching (Doebeli and Dieckmann, 2000; Doebeli and Ruxton, 1997; Kisdi, 1999; Kisdi et al., 2001) or stable monomorphism. (Kisdi, 1999). Generally, it is difficult to identify the mechanism underlying an evolutionary trajectory after branching, even though Geritz et al. (1998) presented a local stability analysis of polymorphism equilibrium (but see Dieckmann and Law, 1996; Geritz et al., 1999).

Quantitative genetics studies revealed that a phenotypic evolutionary trajectory varies depending on the genetic variance-covariance structure when there exist multiple peaks on an adaptive landscape (e.g., Price et al., 1993). In most previous studies on adaptive evolutionary branching, the trait variance is a minimum requirement and supplied under the assumption of the occurrence of rare mutations close to a common resident trait value. In some studies, an evolutionary trajectory was not confounded by the trait variance (Geritz et al., 1998; Kisdi, 1999). Here, we study

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divergent evolutionary trees primarily by searching for an evolutionary branching point, and demonstrate variant evolutionary branching trajectories under identical initial conditions with different trait variances in an adaptive evolutionary dynamics model. The model adopts no explicit assumptions of phenotype–genotype relationship, no interaction between heterospecifics, and no spatiotemporal environmental heterogeneity. Thus, variant evolutionary trajectories are caused only by the structure of the phenotypic game among trait individuals. Our central aims are to demonstrate the possibility of variant evolutionary paths in an adaptive evolutionary dynamics solely due to intraspecific game interaction, and to delineate the conditions under which alternative adaptive evolutionary branching paths will develop under the same initial conditions.

## 2. Adaptive dynamics

The model we investigate here is the cannibalism game. Cannibalism (intraspecific predation) is common among several taxonomic groups and has complex functions that work at any levels from individual fitness to community structure pattern (Claessen et al., 2000; Costantino et al., 1997; Crowley and Hopper, 1994; Cushing, 1991; Giray et al., 2001; Newman and Elgar, 1991; Tuomi et al., 1997; Wahlstrom et al., 2000). The trait of cannibalism has both positive and negative effects on energy acquisition and survival processes of the focal individual, assuming that cannibalism has a function of energy acquisition and the conspecific is less profitable than a heterospecific alternative, and heterospecific prey items are adequately abundant. (Nishimura and Hoshino, 1999). A low cannibalism rate is favored in terms of energy acquisition, but is not favored in terms of defense against intraspecific predation.

We consider the cannibalism rate,  $0 \leq u \leq 1$ , upon encounter with an opponent as a trait. The growth and survival of a focal individual are functions of not only the cannibalism rate of its own but also those of other members in the population. Suppose that the population consists of individuals with a set of traits,  $\mathbf{u} = (u_1, u_2, \dots | \Lambda)$ , where  $\Lambda$  is the frequency distribution of the traits ( $\sum \Lambda(u_i) = 1$ ). Growth and survival dynamics are described in the appendix. We define the fitness of a type- $u_i$  individual in a population as a function of  $\mathbf{u}$ ,  $W_{\mathbf{u}}(u_i) = l_i(T)B_i(T)$ , where  $l_i(T)$  is the survival probability and  $B_i(T)$  is the body size of a type- $u_i$  individual with an arbitrary terminal time  $T$ .

### 2.1. Directional evolution to a singular point and branching

We start with a case in which the population consists of a set of a single strategy,  $\mathbf{u} = (u | \Lambda)$  and  $\Lambda(u) = 1$ .

Suppose that a rare mutant  $u'$  emerges sufficiently close to the resident trait value, and the fitness of the rare mutant  $u'$  is  $W_{\mathbf{u}}(u')$ . A mutant strategy  $u'$  larger than  $u$  can invade the residents if the fitness gradient

$$\left. \frac{\partial W_{\mathbf{u}}(u')}{\partial u'} \right|_{u'=u}$$

is positive. On the contrary, if the gradient is negative, smaller mutants can invade the residents. If the condition

$$\left. \frac{\partial W_{\mathbf{u}^*}(u')}{\partial u'} \right|_{u'=u^*} = 0 \quad (1)$$

is satisfied at  $u = u^*$ ,  $u^*$  is called the “evolutionarily singular strategy” (Geritz et al., 1998). If the inequality

$$\left. \frac{\partial^2 W_{\mathbf{u}^*}(u')}{\partial u'^2} \right|_{u'=u^*} > \left. \frac{\partial^2 W_{\mathbf{u}^*}(u')}{\partial u'^2} \right|_{u'=u^*} \quad (2)$$

holds at the singular point, the directional evolution of a monomorphic population close to the point can approach the singular point (Eshel, 1983; Geritz et al., 1998; Taylor, 1989).

Furthermore, if the singular point satisfies the condition,

$$\left. \frac{\partial^2 W_{\mathbf{u}^*}(u')}{\partial u'^2} \right|_{u'=u^*} < 0,$$

any mutants occurring near the point cannot invade, and thus the singular point is evolutionarily stable (Maynard Smith, 1982). On the contrary, if the singular point satisfies the condition

$$\left. \frac{\partial^2 W_{\mathbf{u}^*}(u')}{\partial u'^2} \right|_{u'=u^*} > 0, \quad (3)$$

the singular point lacks evolutionary stability.

If the singular point  $u^*$  satisfies inequalities (2) and (3), an arbitrary monomorphic population near the point evolutionarily converges to the singular point, however, the population at the singular point is no longer stable and branching evolution further develops at that point (Christiansen, 1991; Geritz et al., 1998).

We conducted a global pairwise invasibility analysis of the cannibalism evolutionary system. The global pairwise invasibility map of a monomorphic population describes the relative fitness of a rare mutant with an arbitrary combination of mutant and resident types. Under the assumption that mutations are sufficiently infrequent that a mutant spreads or is excluded before the next mutant comes along, a monomorphic population evolves along the diagonal line and reaches one of the equilibrium points (e.g. see Ebenman et al., 1996; Kisdi and Meszina, 1993).

When neither the cost of cannibalism armament nor that of counterattack is assumed ( $\rho = 0$ ) (see the appendix), there exist three singular points (see Fig. 1(a)). An intermediate cannibalism rate does not evolve. The midequilibrium lacks convergence stability

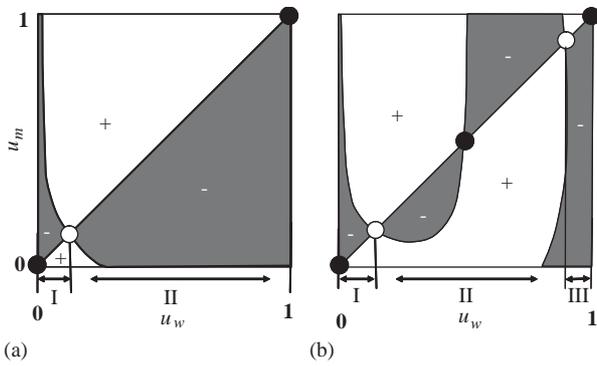


Fig. 1. Pairwise global invariability maps. The wild type's and mutant's strategies are denoted by  $u_w$  and  $u_m$ , respectively. The shaded area indicates combinations of  $u_w$  and  $u_m$  for which the mutant's relative fitness is lower than that of the wild type. Under the assumption that mutations are sufficiently infrequent that a mutant spreads or is excluded before the next mutant comes along, the strategies indicated by the open circles are convergence unstable, and the strategies indicated by solid circles are locally convergence stable. Regions labeled by Greek numbers indicate the basins of convergence stable attractors. (a) Case of no costs ( $\rho = 0$ ). Both boundary equilibria are evolutionarily stable. (b) Case of with costs ( $\rho = 1$ ). Both boundary equilibria are evolutionarily stable. The mid-convergence equilibrium lacks ESS stability, and thus is the branching point.

and both boundary equilibria are convergence and evolutionarily stable. When a resident population consists of individuals with higher cannibalism rates than the midsingular point, the maximum cannibalism rate evolves, even though a higher cannibalism rate suffers from the inefficiency of energy acquisition. In contrast, when a resident population consists of individuals with lower cannibalism rates, the non-cannibalism rate evolves, even though a lower cannibalism rate suffers from a high risk of predation by other cannibals.

When we assume the costs of cannibalism ( $\rho = 1$ ) (see the appendix), there exist five singular points, and the midsingular point satisfies the conditions of inequalities (2) and (3) (see Fig. 1(b)). An arbitrary monomorphic population in interval II converges to the midsingular point and the monomorphic population branches and gives rise to dimorphism at the singular point. In the following sections, we address the further development of the evolutionary path that reached the midsingular point shown in Fig. 1(b).

### 2.2. Evolution of dimorphism

Evolutionary branching gives rise to dimorphism from a monomorphic population at the singular point  $u^*$  by repeated invasions of mutants around the equilibrium strategy (Geritz et al., 1998). In several studies on adaptive dynamics, it is assumed that (1) mutant traits occur close to resident traits, and (2) evolution is mutation limited, that is, after occurrence of a mutation, the population reaches its equilibrium by

natural selection by the time the next mutant comes along (Ebenman et al., 1996; Geritz et al., 1998; Kisdi and Meszina, 1993). These assumptions are, however, not crucial requirements for the analysis of trait evolution. In the limit of infinitesimally small mutation steps, however, evolutionary branching does not occur (Geritz et al., 1998, p. 50). When we analyse about branching evolution, it should be assumed that mutants successively appear before the previous mutants reach their equilibrium and the trait variations distribute on the both sides of the branching singular point (e.g., Doebeli and Dieckmann, 2000; Doebeli and Ruxton, 1997; Geritz et al., 1998; Kisdi, 1999; Kisdi and Geritz, 2001; Kisdi et al., 2001).

To survey the evolution of a biramous branching tree, we assume that mutants would successively occur before natural selection completely fixates on a single trait. Assume that rare mutants emerge close to each trait value. We further assume that the variances of trait distributions are sufficiently small. Assuming a haploid organism, we apply the secondary theorem of natural selection (Robertson, 1968) to express the direction and intensity of phenotypic evolution. The evolutionary direction and the selection intensity of the two branching traits at time  $t$  are approximately given by the following equation under the assumption that the higher-order moments of trait distributions of  $u_1$  and  $u_2$  are negligibly small,

$$\mathbf{W}'_{\bar{\mathbf{u}}} = \begin{pmatrix} c_1 \sigma_1^2 \frac{\partial W_{\mathbf{u}}(u'_1)}{\partial u'_1} \Big|_{u'_1 = \bar{u}_1} \\ c_2 \sigma_2^2 \frac{\partial W_{\mathbf{u}}(u'_2)}{\partial u'_2} \Big|_{u'_2 = \bar{u}_2} \end{pmatrix}, \tag{4}$$

where  $\sigma_1^2$  and  $\sigma_2^2$  are the trait variances around the means at  $t$ , respectively, and  $c_1$  and  $c_2$  are positive constants. Fig. 2 shows the unit-vector field of  $\mathbf{W}'_{\bar{\mathbf{u}}}$  including the vector flows from the branching point given that  $c_1 \sigma_1^2 = c_2 \sigma_2^2$ .

When we assume that the magnitude of phenotypic variances is maintained by mutation-selection valance (Lande, 1976), a continuous approximation of the dynamics of the dimorphism development could be described as

$$\begin{pmatrix} \frac{d\bar{u}_1}{dt} \\ \frac{d\bar{u}_2}{dt} \end{pmatrix} = c \mathbf{W}'_{\bar{\mathbf{u}}}, \tag{5}$$

under the initial condition  $\bar{\mathbf{u}}(0) = (u_1^*, u_1^*)$  (branching point), where  $u_1^*$  is the singular point and  $c$  is a positive constant (see the analogous argument, Abrams et al., 1993; Lande, 1982). The vector field implies that there are three dimorphism equilibria (see Fig. 2). The midequilibrium point is a saddle point. The first and third equilibria from the left seem to be candidates for

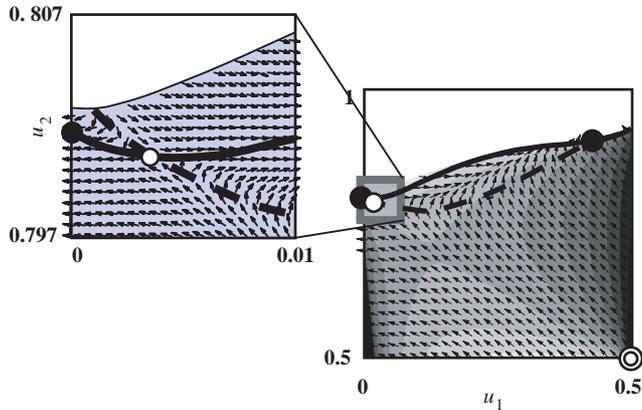


Fig. 2. Unit-vector field of dimorphism evolution from the branching point of Fig. 1(b) given by Eq. (4). The horizontal axis shows the lower trait values, and the vertical axis shows the higher trait values. The brightness of the shaded area indicates the equilibrium proportion of the higher trait values at the coordinates of the trait set. In completely white or black area, dimorphism is infeasible. The dashed line indicates

$$\left. \frac{\partial W_{\mathbf{u}}(u'_1)}{\partial u'_1} \right|_{u'_1=u_1} = 0,$$

and the solid line indicates

$$\left. \frac{\partial W_{\mathbf{u}}(u'_2)}{\partial u'_2} \right|_{u'_2=u_2} = 0.$$

Evolutionary branching starts at the double circles on the lower right corner,  $\mathbf{u}(0)$ . The solid and open circles show dimorphism equilibrium. The open circle is a saddle point and is not dynamically attainable from  $\mathbf{u}(0)$ . The equilibria indicated by solid circles are locally convergence stable.

the attainable convergence dimorphic equilibrium states from the branching point  $\mathbf{u}(0)$ . The l.h.s equilibrium state is infeasible via mutual invasion of mutant of either phenotype to the resident population of the other phenotype. If the equilibrium is attained, the attainment would be achieved via the evolution of the branching tree from the branching point. However, the feasible evolutionary pathway is non-trivial and it depends on the context beyond our assumptions.

### 2.3. Trait variance and development of biramous evolutionary tree

In the above argument, we implicitly stated that mutations are accumulated but phenotypic variances are sufficiently small. In the following, we argue the effect of the order of trait variances on evolutionary branching pathways.

Suppose that mutations are accumulated independently around the two trait values of residents,  $\bar{u}_1$  and  $\bar{u}_2$ , with the relative frequency of the existing traits. We define  $\pi_1(u_1)$  and  $\pi_2(u_2)$  to be the trait frequency distributions around the two resident strategies,  $\bar{u}_1$ , and  $\bar{u}_2$ , where the domains of  $u_1$  and  $u_2$  are not overlapping in both distributions.

We can predict the direction of the evolutionary change in the two trait distributions by weighting the gradient around the distributions

$$E[\mathbf{W}'] \approx \begin{pmatrix} \int \omega_{\mathbf{u}}(u_1) \pi_1(u_1) du_1 \\ \int \omega_{\mathbf{u}}(u_2) \pi_2(u_2) du_2 \end{pmatrix}, \tag{6}$$

where  $\omega_{\mathbf{u}}(u_i)$  is the  $i$ th element of Eq. (4) and the integrations are executed on the domains of  $\pi_1(u_1)$  and  $\pi_2(u_2)$  (see Abrams et al., 1993). Applying the Taylor expansion, the gradient around the resident strategy ( $\bar{u}_1$  or  $\bar{u}_2$ ) is

$$\begin{aligned} \omega_{\mathbf{u}}(u_i) \approx & \omega_{\mathbf{u}}(u_i)|_{u_i=\bar{u}_i} + (u_i - \bar{u}_i) \left. \frac{\partial \omega_{\mathbf{u}}(u_i)}{\partial u_i} \right|_{u_i=\bar{u}_i} \\ & + \frac{(u_i - \bar{u}_i)^2}{2} \left. \frac{\partial^2 \omega_{\mathbf{u}}(u_i)}{\partial u_i^2} \right|_{u_i=\bar{u}_i} + \dots \end{aligned} \tag{7}$$

$(i = 1 \text{ or } 2).$

Assume that terms higher than the second order can be neglected. The substitution of Eq. (7) into Eq. (6) under the condition that  $c_1 \sigma_1^2 = c_2 \sigma_2^2$  yields

$$\begin{aligned} E[\mathbf{W}']_{\mathbf{u}} \propto & \begin{pmatrix} \omega_{\mathbf{u}}(\bar{u}_1) \\ \omega_{\mathbf{u}}(\bar{u}_2) \end{pmatrix} + \frac{1}{2} \begin{pmatrix} \sigma_2^2 \left. \frac{\partial^2 \omega_{\mathbf{u}}(u_1)}{\partial u_1^2} \right|_{u_1=\bar{u}_1} \\ \sigma_1^2 \left. \frac{\partial^2 \omega_{\mathbf{u}}(u_2)}{\partial u_2^2} \right|_{u_2=\bar{u}_2} \end{pmatrix} \\ = & \mathbf{W}'_{\mathbf{u}} + \frac{1}{2} \begin{pmatrix} (\sigma^2)^2 \left. \frac{\partial^3 W_{\mathbf{u}}(u'_1)}{\partial u_1'^3} \right|_{u'_1=\bar{u}_1} \\ (\sigma^2)^2 \left. \frac{\partial^3 W_{\mathbf{u}}(u'_2)}{\partial u_2'^3} \right|_{u'_2=\bar{u}_2} \end{pmatrix}. \end{aligned} \tag{8}$$

The sign and magnitude of each element of  $E[\mathbf{W}']_{\mathbf{u}}$ , respectively, represent the expected direction and the intensity of the evolution at the sets of mean strategy trait values ( $\bar{u}_1, \bar{u}_2$ ) under the condition that the second power of the trait variances is not negligible. Fig. 3

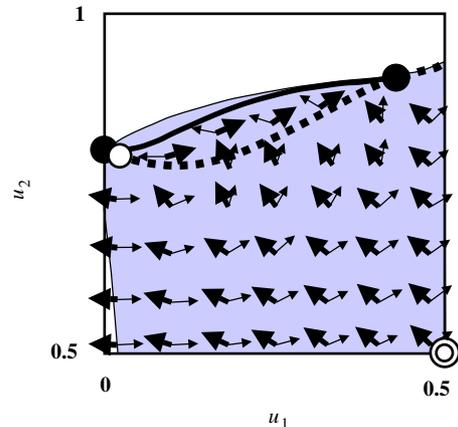


Fig. 3. Unit-vector fields of the two elements of Eq. (8),  $E[\mathbf{W}']_{\mathbf{u}}$ . The thick and thin vectors indicate the first and second elements of  $E[\mathbf{W}']_{\mathbf{u}}$  in Eq. (12), respectively.

shows the decomposition of the vector field of  $E[\mathbf{W}']_{\mathbf{u}}$  to the two elements of Eq. (8). According to the approximation, when the variance is sufficiently small, the second term of Eq. (8) vanishes and the vector field coincides with that in Fig. 2. As the trait variance increases, the vector field should be modified by the second component of Eq. (8), and the evolutionary pathway should move on the composite vector field of the two components.

#### 2.4. Variant evolutionary trees

In our example, the dimorphic population had three equilibrium points, two of which are locally convergence stable (solid circles in Fig. 2). Even though a preliminary examination of the composite vector field of Fig. 3 provides a qualitative prospect of the evolutionary pathway of branching, we have no explicit prospect whether the branching path reaches either of the convergence-stable points.

Trait variances are eroded by selection and supplied by new mutations. Trait variance is assumed to be maintained constant under a restricted condition (Lande, 1976), but this is not always guaranteed (Steppan et al., 2002; Turelli, 1988). Dieckmann and Law (1996, pp. 587–589) presented the general dynamical equation of the evolutionary system of trait distribution with explicit mechanisms of mutation and selection. They also presented the approximation of the mean evolutionary path of trait distribution. (Dieckmann and Law, 1996, pp. 592–595). Even though we have some approximation methods for analysing evolutionary dynamics that would be driven by selection and trait variance maintained by mutation accumulation, we have no substantial information about trait variances maintained throughout the evolutionary process.

We conducted numerical simulations of the evolutionary process to trace the evolutionary paths after branching. The possible domain of the strategy trait  $u \in (0, 1)$  was divided into  $1/\Delta u + 1$  equal intervals. The simulations start at the branching point ( $\mathbf{u} = (u^*)$  and  $A(u^*) = 1$ ). In the mutation process, mutants emerge from the resident at a rate of  $\delta m/2$  per unit density on either of the next intervals of both sides of the resident trait value. The mutation process generates a new trait vector and a trait frequency vector,  $\mathbf{u} = (u^* - \Delta u, u^*, u^* + \Delta u)$  and  $\mathbf{\Lambda} = (\delta m/2, 1 - \delta m, \delta m/2)$ , respectively. Each trait is selected according to the relative fitness. The frequency distribution,  $\mathbf{\Lambda}$ , of the next generation at birth with a fixed total population  $N$  is obtained by the consequence of the selection. If the frequency of a trait becomes lower than a certain threshold value, we evaluate the frequency of the trait individuals to be zero. The iterations of mutation and selection cycle describe the adaptive evolutionary dynamics. Trait variances are maintained according to

the mutant supply and selection rules. We changed the value of  $\Delta u$  while keeping other parameters unchanged. Even though we cannot control the actual within-branch trait variances under a mutation supply and the selection regime in the simulation, the additive variance generated from a certain trait individual per generation is proportional to  $\delta m \Delta u^2$  without selection, which implicitly indicates the source of trait variance.

Fig. 4 shows branching evolutionary trajectories for different  $\delta m \Delta u^2$  values. For a negligibly small magnitude of  $\delta m \Delta u^2$ , the biramous tree evolved to the l.h.s equilibrium point (tr1 in Fig. 4(a)). The l.h.s equilibrium point,  $\tilde{\mathbf{u}} = (\tilde{u}_1, \tilde{u}_2)$  is infeasible via direct mutual invasion of mutant of either phenotype to the resident population of the other phenotype. The equilibrium is attainable only by the evolution of the branching pathway. For non-negligible but small  $\delta m \Delta u^2$ , the evolutionary trajectory is sensitive to drift (tr2 and tr3 of Fig. 4(b)). Determining which of the two convergence-stable points the trajectory reaches is a matter of chance (see also Geritz et al., 1998, pp. 46–48). As  $\delta m \Delta u^2$  increases, the terminus of the biramous trajectory develops in between the two convergence equilibrium points (tr4 and tr5 in Figs. 4(c) and (d)).

Even though we do not explicitly evaluate the effect of selection on the trait variance in each branch through the simulation runs, the magnitude of the source of variation,  $\delta m \Delta u^2$ , changes the evolutionary pathways of branches. The numerical simulations qualitatively provide the same implication as shown in Fig. 3, which is drawn based on Eq. (8) given that  $c_1 \sigma_1^2 = c_2 \sigma_2^2$ . The paths from the branching point (double circles on the lower right corner of each map in Fig. 4) tended to lean toward the clockwise direction due to the thin vector field component in Fig. 3 as the maintained trait variance increases (see also Fig. 3). As the path passes across the lower isocline (dashed lines in Fig. 4), the thin vector component shown in Fig. 3 induces the path toward the counterclockwise direction.

The entire evolutionary trees depending on the levels of  $\delta m \Delta u^2$  are shown in Fig. 5. The result of the numerical simulation with the smallest  $\delta m \Delta u^2$  would give the evolutionary consequence provided under the mutation-limited scenario. In such a case, the evolutionary trajectory reaches the leftmost convergence-stable equilibrium point as shown in Fig. 2 and dimorphism is stabilized. Apparently, the evolutionary trees exhibit three distinct types: (1) fixation of dimorphism, one is the minimum and the other is an interior value, (2) a Red Queen evolution with the extinction of a low trait value, and (3) fixation of monomorphism of the maximum trait value via triramous branch evolution.

For a non-negligible but small trait variance, Red Queen evolution occurs because biramous trajectories evolve to the upper boundary of the dimorphism

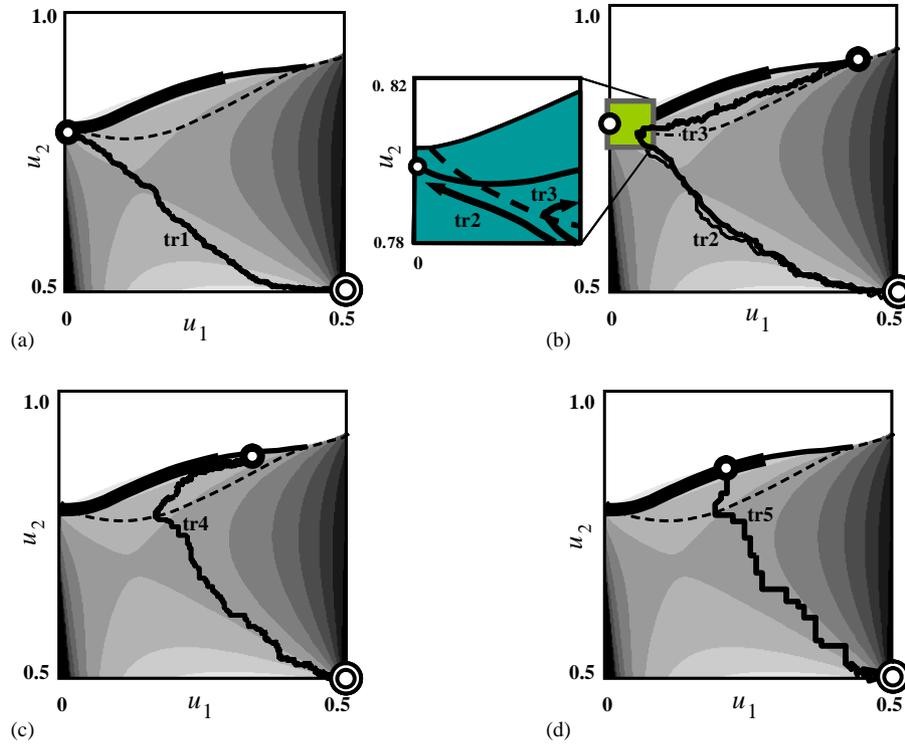


Fig. 4. Evolutionary trajectories of biramous tree for different trait variances. Development of biramous evolutionary branching starts at the double circles on the lower right corner. The open circles denote the developmental end of the biramous tree. On the thick solid line, conditions

$$\frac{\partial W_{\mathbf{u}}(u'_2)}{\partial u'_2} \Big|_{u'_2=u_2} = 0 \quad \text{and} \quad \frac{\partial^2 W_{\mathbf{u}}(u'_2)}{\partial u'^2_2} \Big|_{u'_2=u_2} > 0$$

hold, and thus, the biramous tree on the thick line has a possibility of further branching at higher trait values. The thin solid line that satisfies condition

$$\frac{\partial W_{\mathbf{u}}(u'_2)}{\partial u'_2} \Big|_{u'_2=u_2} = 0$$

is located along the boundary of the protected dimorphism. Orders of trait variances supplied are (a)  $\delta m \Delta u^2 = 1 \times 10^{-8}$ , (b)  $\delta m \Delta u^2 = 4 \times 10^{-8}$ , (c)  $\delta m \Delta u^2 = 2.5 \times 10^{-7}$ , and (d)  $\delta m \Delta u^2 = 1 \times 10^{-6}$ , where  $\delta m = 0.01$ . The evolutionary trajectories are denoted “tr1” to “tr5” depending on the corresponding trait variance.

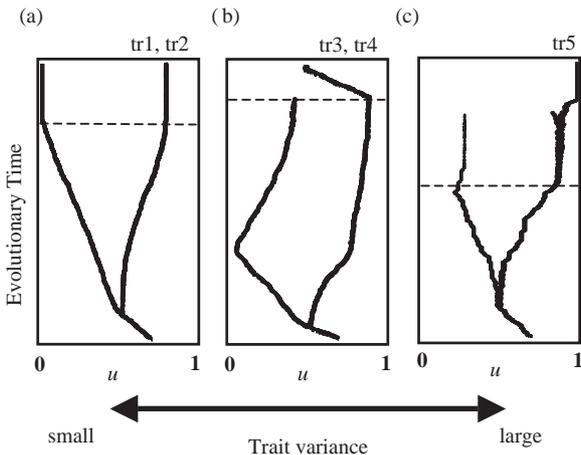


Fig. 5. Classification of development of evolutionary trees. The actual evolutionary trees drawn on each panel are tr1, tr3, and tr5. The evolutionary time scale in each panel is arbitrary. On the horizontal dashed lines, the biramous branches reach the corresponding open circle in Fig. 4.

manifold on which the frequency of the lower trait becomes zero. Thus, the branch of the lower trait becomes extinct, and the surviving higher trait remains in the basin of the branching point (region II in Fig. 1(b), tr3 and tr4 in Fig. 5(b)). Red Queen evolution by a similar mechanism had also been reported by Kisdi et al. (2001).

When trait variance is sufficiently large, the second variance occurs at the higher trait branch because the endpoint of the biramous trajectory reaches the zero isocline of  $u_2$  that satisfies the ESS-instability of  $u_2$  at the point on the isocline (see tr5 in Figs. 4(d) and 5(c)). After triramous branching, the population cannot reach an internal evolutionary stable point in the higher-order manifold of a possible polymorphism, but reaches the boundary of the manifold. The collapse of the triramous tree reduces the tree to its monomorphous form (tr5 in Fig. 5(c)). The surviving branch is in the basin of the monomorphism attractor (III in Fig. 1(b)). The

triramous tree (tr5 in Fig. 5(c)) begins from a monomorphism in the basin of the branching point (II in Fig. 1(b)) and jumps to the other basin of stable monomorphism (III in Fig. 1(b)). The inversion of the basins of the monomorphic trait by this mechanism had also been demonstrated by Kisdi (1999, Fig. 6, pp. 158).

### 3. Discussion

Evolutionary branching has been found in a number of studies on adaptive evolutionary dynamics that treated numerous ecological situations (Dieckmann, 1997; Doebeli and Ruxton, 1997; Geritz et al., 1998; Kisdi, 1999; Mathias et al., 2001). However, further branching from a biramous tree and the stability of a multiramous tree could not be easily analysed (Geritz et al., 1998, see also Geritz et al., 1999, pp. 43, 47). Evolutionary branching reaches a fixed state in some cases (Doebeli and Dieckmann, 2000; Doebeli and Ruxton, 1997; Geritz et al., 1998; Kisdi, 1999; Mathias and Kisdi, 2002; Mathias et al., 2001). When the population dynamics process is explicitly incorporated to an adaptive dynamics model, cyclical or more complicated adaptive dynamics occur (Doebeli and Dieckmann, 2000; Doebeli and Ruxton, 1997). Particularly, traits of the predator and prey exhibit cyclical evolutions associated with population dynamics (Doebeli and Dieckmann, 2000). Variant evolutionary consequences have been known in quantitative genetics studies, in which the adaptive landscape is not a function of the traits of population members (Lewontin and White, 1960; Price et al., 1993).

Our model incorporates neither explicit population dynamics, genetic architecture, nor environmental stochasticity. We demonstrated the generation of variant biramous trees and the subsequent trajectories in evolutionary adaptive dynamics with an identical initial trait population. Various trajectories are generated for different levels of trait variance. The properties (attractor or repeller) and the locations of equilibria, and the initial point of the trajectory of the biramous tree in the dimorphism manifold are the conditions necessary for inducing such variant trees. Even though we demonstrated variant trajectories in the biramous process, the variant evolutionary trajectories are also possible in the higher-order-branching tree, if the topological configuration satisfies such conditions. This suggests that the existing monomorphic or polymorphic set in a population is not a unique inevitable consequence of an identical initial phenotype.

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### Appendix

We consider the cannibalism rate,  $0 \leq u \leq 1$ , upon encounter with an opponent as the evolutionary trait. We assume a simple encounter scenario of a type- $u_i$  focal individual with a type- $u_j$  individual. Both individuals try to eat their opponent with probability  $u_i u_j$  at the time of encounter. Then, the probability that either individual cannibalizes the opponent is  $\frac{1}{2} u_i u_j$ . The type- $u_i$  individual tries to eat the type- $u_j$  individual that does not try to cannibalize the type- $u_i$  individual with a probability  $u_i(1 - u_j)$ , and thus the type- $u_i$  individual cannibalizes the type- $u_j$  individual, and vice versa. Summing up all possible events, the probability that the type- $u_i$  individual eats the type- $u_j$  individual is  $\zeta(u_i, u_j) = \frac{1}{2} u_i u_j + u_i(1 - u_j)$ , and the probability that the type- $u_i$  individual is eaten by the type- $u_j$  individual is  $\xi(u_i, u_j) = \frac{1}{2} u_i u_j + u_j(1 - u_i)$ .

Let  $A(u_j)$  be the relative frequency of a type- $u_j$  individual at birth,  $N$  the total population number at birth, and  $l(u_j, t)$  the survival probability of a type- $u_j$  individual at  $t$ . The instantaneous encounter rate of a focal individual with a type- $u_j$  individual at time  $t$  is  $aNA(u_j)l(u_j, t)$ , where  $a$  is the encounter coefficient of conspecific individuals. We can define the instantaneous encounter rate of a type- $u_j$  'prey', and the instantaneous encounter rate of a type- $u_j$  'predator' for the focal type- $u_i$  individual at time  $t$  as

$$\eta(u_i, u_j, t) = \kappa \zeta(u_i, u_j), \quad (\text{A.1})$$

$$\gamma(u_i, u_j, t) = \kappa \xi(u_i, u_j), \quad (\text{A.2})$$

respectively, where  $\kappa = aNA(u_j)l(u_j, t)$ .

We designate  $B_i(u_i, t)$  as the size and  $l_i(u_i, t)$  as the survival probability of a type- $u_i$  individual at time  $t$ . We assume that the growth and survival trajectories of a type- $u_i$  individual are described by

$$\frac{dB_i}{dt} = g \left( \frac{\sum_j \eta(u_i, u_j, t) e_1 + \lambda e_2}{1 + \sum_j \eta(u_i, u_j, t) h_1 + \lambda h_2} \right) B_i, \quad (\text{A.3})$$

$$\frac{dl_i}{dt} = - \left[ \frac{1}{B_i} \left( \mu + \frac{b}{\lambda + \sum_j \eta(u_i, u_j, t)} \right) + \sum_j \gamma(u_i, u_j, t) \right] l_i. \quad (\text{A.4})$$

The fraction in the parentheses of Eq. (A.3) indicates the net energy gain per unit time per unit body size, where  $e_1$  and  $e_2$  are energy intakes, and  $h_1$  and  $h_2$  are handling times for conspecific victims and heterospecific preys, respectively,  $\lambda$  is a constant of the instantaneous encounter rate of the heterospecific prey, and  $g$  is a positive constant. The term in the brackets of Eq. (A.4) indicate the instantaneous death rate, which has three components. The first term,  $\mu$ , in the brackets indicates the hazard of predation by a heterospecific predator.

The second term represents the hazard of starvation that is proportional to the expected waiting time for successive encounters with a prey. Assuming that the encounters occur by a Poisson process, the expected waiting time for successive events is reciprocally proportional to the sum of instantaneous rates (i.e. the fraction term in parentheses). Both the factors are inversely proportional to body size. The last terms in the brackets indicate the hazard of intraspecific predation (cannibalism).

We assume that  $e_1$  and  $h_1$  are basically proportional to the size of the cannibalized individual. However, the net energy gain should be discounted due to energy costs incurred using the cannibalism armament of the focal individual and the counterattack by the prey. Suppose that the type- $u_i$  focal individual cannibalizes a type- $u_j$  opponent. A high cannibalism rate of a cannibal implies high cannibalism armament cost, while a high cannibalism rate of an opponent implies that the protagonist incurs a high counterattack cost. Assume function  $\phi(u_i, u_j)$  that is a non-increasing function of  $u_i$  and  $u_j$ , and  $\phi(0, 0) = 1$ .  $\phi$  is a monotonically decreasing function of  $u_i$  and  $u_j$ . The net intake energy and handling time for a type- $u_i$  cannibal dealing with a type- $u_j$  prey are  $e_1 = \phi(u_i, u_j)B(u_j, t)$  and  $h_1 = \beta B(u_j, t)$ , respectively, where  $\beta$  is a handling time parameter. We assume an arbitrary descriptive function,  $\phi(u_i, u_j) = e^{-\rho u_i u_j^{\theta}}$ , that satisfies the properties of  $\phi$ , where  $\rho = 0$  (for no costs) or 1 (for with costs). We define the fitness of type- $u_i$  individual in a population as

$$W_{\mathbf{u}}(u_i) = l_i(T)B_i(T), \quad (\text{A.5})$$

where  $T$  is an arbitrary terminal time of fitness evaluation.

In numerical simulations, the parameter values for the numerical analysis are  $\mu = 15$ ,  $\lambda = 3$ ,  $\beta = 1$ ,  $\theta = 1.5$ ,  $a = 1$ ,  $N = 1000$ ,  $b = 0.1$ ,  $g = 5$ ,  $e_2 = 1.5$ ,  $h_2 = 1$ , and  $T = 1$ . Here, we assume that a conspecifics ( $e_1/h_1 = \phi/\beta = \phi \leq 1$ ) is an inferior prey compared with a heterospecifics ( $e_2/h_2 = 1.5$ ), and that the inclusion of conspecifics into the diet decreases energy intake rate ( $e_1/h_1 < \lambda e_2/(1 + \lambda h_2)$ ). This assumption had positive (e.g. survival among intraspecific predation) and negative (energy acquisition rate) effects on cannibalism evolution (Nishimura and Hoshino, 1999).

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