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# A resolution of the paradox of enrichment

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## Abstract

Theoretical studies have shown a paradoxical destabilizing response of predator–prey ecosystems to enrichment, but there is the gap between the intuitive view of nature and this theoretical prediction. We studied a minimal predator–prey system (a two predator–two prey system) in which the paradox of enrichment pattern can vanish; the destabilization with enrichment is reversed, leading to stabilization (a decrease in the amplitude of oscillation of population densities). For resolution of the paradox, two conditions must be met: (1) the same prey species must be preferred as a dietary item by both predator species, creating the potential for high exploitative competition between the predator species, and (2), while both predators are assumed to select their diet in accordance with optimal diet utilization theory, one predator must be a specialist and the other a generalist. In this system, the presence of a less profitable prey species can cause the increase in population oscillation amplitudes associated with increasing enrichment to be suppressed via the optimal diet utilization of the generalist predator. The resulting stabilization is explained by the mitigating effect of the less profitable prey showing better population growth with increasing enrichment on the destabilization underlying the specialist predator and prey relation, thus resolving the paradox of enrichment.

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## 1. Introduction

Ecosystem stability is a central issue in ecology. In an analysis of six different mathematical models, Rosenzweig (1971) found that in one predator–one prey systems destabilization occurred as the resource supply for the prey species increased (enrichment). He named this phenomenon the “paradox of enrichment”. Since McAllister et al. (1972) challenged the extrapolation of this theoretical analysis to natural ecosystems, the universality of the paradox in more complicated mathematical models and in real interactions among species has been debated (Luckinbill, 1974; Riebesell 1974; Arditi and Ginzburg, 1989; McCauley and Murdoch, 1990; Yodzis and Innes, 1992; Kretzschmar et al., 1993; Abrams and Roth, 1994; Grover, 1995; Jansen, 1995; Abrams and Walters, 1996; McCann and Hastings, 1997; Kirk, 1998; Genkai-Kato and Yamamura, 1999;

McCauley et al., 1999; Holyoak, 2000; Persson et al., 2001; Verschoor et al., 2004; Vos et al., 2004; Steiner et al., 2005).

Most of these theoretical studies followed the original analytical approach of Rosenzweig (1971), who had performed a local stability analysis of an equilibrium state, to support or resolve the paradox of enrichment (e.g., Gilpin, 1972; Kretzschmar et al., 1993; Abrams and Walters, 1996; Murdoch et al., 1998; Vos et al., 2004). Genkai-Kato and Yamamura (1999), however, tackled the problem by considering species interaction in terms of non-equilibrium dynamics. Even though non-equilibrium dynamics analyses have no general power to determine stability conditions, such analyses are well suited to empirical dynamics data (e.g., McCauley and Murdoch, 1990; McCauley et al., 1999), and the dynamics of multispecies interaction systems in particular (Huisman and Weissing, 1999; Vandermeer et al., 2006).

In this study, we examined the effect of enrichment on stability of a two predator–two prey system in which the predators practice optimal diet utilization between more

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profitable and less profitable prey, and in which intra- and interspecific exploitative competition occurs in the area of diet. We compare our model with that of Genkai-Kato and Yamamura (1999), who modeled a one predator–two prey system in which the predator exhibits optimal foraging behavior between more profitable and less profitable prey, and analyzed the non-equilibrium dynamics of the limit cycle to investigate the mechanism resolving the paradox of enrichment (hereafter, we refer to this one predator–two prey system model of Kato and Yamamura as KYM). They operationally classified the dietary quality of the less profitable prey type as “inedible,” “unpalatable,” or “palatable” (see below). Even though in their system the amplitude of the oscillation of population densities was enhanced (i.e., the system was destabilized) with increasing enrichment, they found that the destabilizing trend was minimized when the less profitable prey was unpalatable, suggesting a possible resolution of the paradox of enrichment. However, their statement claiming that the paradox of enrichment was resolved is not accurate, because the amplitude of the oscillation still increased with increasing enrichment.

Here, we report a real resolution of the paradox of enrichment (stabilization with enrichment) in non-equilibrium dynamics, a new finding, and present its mechanism. In particular, we emphasize that the addition of another predator species into a KYM-type model implies an increase in exploitative competition, which introduces the additional concept of predator strategy, namely, whether a predator is a generalist or a specialist. These additional concepts not found in KYM allow us to identify a mechanism for the resolution of the paradox of enrichment.

## 2. The model

### 2.1. Population dynamics: a two predator–two prey system

Consider the following dynamics of the densities of two prey species and two predator species, denoted by  $X_i$  ( $i = 1$  or  $2$ ) and  $Y_j$  ( $j = 1$  or  $2$ ), respectively,

$$\dot{X}_i = \left\{ r_i \left( 1 - \frac{1}{K_i} \sum_{k \in \text{prey types}} \alpha_{ik} X_k \right) - \sum_{j \in \text{predator types}} \mu_{ji} Y_j \right\} X_i, \quad (1a)$$

$$\dot{Y}_j = \left( b_j \sum_{i \in \text{prey types}} g_{ji} \mu_{ji} X_i - d_j \right) Y_j \quad (1b)$$

where  $\mu_{ji} = p_{ji} \varepsilon_{ji} / (1 + \sum_{i \in \text{preys}} p_{ji} h_{ji} \varepsilon_{ji} X_i)$ . For predator species  $j$ , term  $\mu_{ji}$  implies the instantaneous exploitation rate of prey species  $i$ , defined by a type 2 functional response;  $\varepsilon_{ji}$  is the searching efficiency for prey  $i$ ;  $h_{ji}$  is the handling time of prey  $i$ ;  $g_{ji}$  is the energy value of an individual of prey  $i$ ; and  $p_{ji}$  ( $0 \leq p_{ji} \leq 1$ ) is the capture probability of an individual of prey species  $i$  given an encounter.  $b_j$  is the conversion efficiency, which relates the predator’s birth rate to prey

consumption, and  $d_j$  is the death rate of predator species  $j$ . For prey  $i$ ,  $\alpha_{ik}$  are the intra- and interspecific competition coefficients ( $\alpha_{ii} = 1$ );  $r_i$  is the per capita prey growth rate; and  $K_i$  is the carrying capacity of the prey, which indicates the degree of enrichment. For simplicity, we assume identical values of the parameters  $b$ ,  $d$ ,  $r$ ,  $g$ ,  $\varepsilon$ , and  $K$  among predators and/or prey, but relaxation of this assumption does not influence our story. This predator–prey community, in which at most four species are involved, potentially leads to cyclic or chaotic behavior of the density of each species.

### 2.2. Optimal diet use

We assume that the predators are optimal foragers and select their diet in accordance with optimal diet utilization theory (Stephens and Krebs, 1986). Each predator determines the inclusion or exclusion of a prey species on its diet on the basis of the prey’s profitability in order to maximize its net rate of energy intake while foraging. Profitability of prey items is ranked according to the net energy gain,  $g$ , relative to handling time,  $h$ , upon an attack. The higher ranked prey species is unconditionally included in the diet (i.e.,  $p = 1$ ). If the density of the more profitable prey drops below a critical threshold (the menu change threshold), the less profitable prey is also included in the diet ( $p = 1$ ). Otherwise, the less profitable prey is excluded from the diet ( $p = 0$ ). Inclusion or exclusion of the less profitable prey (i.e., menu variety) depends on the difference in profitability between the prey items and the density of the more profitable prey (Stephens and Krebs, 1986).

### 2.3. Status of the less profitable prey in the menu

Given that prey profitability is fixed, the menu variety of each predator is affected by the population dynamics of the more profitable prey. System Eqs. (1a) and (1b) do not behave statically, and the density of the more profitable prey also oscillates; thus, the menu list of each predator may change along with the dynamics of the system.

Here, we temporarily assume that the prey species are ranked by predator  $j$  as  $g_{j1}/h_{j1} > g_{j2}/h_{j2}$ . We term the status of the less profitable prey as a dietary item for predator  $j$  figuratively as (1) “inedible” if the minimum density of the more profitable prey (i.e., prey species 1) in a predator–prey oscillatory system consisting of predator species  $j$  (1 or 2) and prey species 1,  $X_{j1}^{\min}$ , is above the menu change threshold,  $X_{j1}^{ct}$  ( $X_{j1}^{ct} < X_{j1}^{\min}$ ), defined in the optimal diet; (2) “unpalatable” if the density of the more profitable prey is rarely less than  $X_{j1}^{ct}$  ( $X_{j1}^{\min} < X_{j1}^{ct} < X_{j1}^{eq}$ ), where  $X_{j1}^{eq}$  ( $= d/\varepsilon_{j1}(bg_{j1} - dh_{j1})$ ) is the equilibrium density of prey species 1 in a predator–prey oscillatory system consisting of predator species  $j$  (1 or 2) and prey species 1; or (3) “palatable” if the density of the more profitable prey is frequently less than  $X_{j1}^{ct}$  ( $X_{j1}^{eq} < X_{j1}^{ct}$ ), where  $X_{j1}^{ct} = g_{j2}/\{e_{j1}h_{j1}h_{j2}(g_{j1}/h_{j1} - g_{j2}/h_{j2})\}$  (after Genkai-Kato and Yamamura, 1999). The marginal profitability of the less

profitable prey between unpalatable and palatable ( $X_{j1}^{ct} = X_{j1}^{cq}$ ) is analytically defined as  $d/b$ .

### 3. Results

In the wide range of parameter values that allow all of the species to coexist, the density of each species follows a complex cycle for large values of  $K$ . The stability of equilibrium changes from stable to unstable (oscillation) with increasing  $K$ . All of the species can coexist regardless of the stability of equilibrium except in lower values of  $K$ . We focus on non-equilibrium dynamics and examine how the oscillation changes with increasing  $K$ . With a sufficiently long simulation run, we obtained asymptotic behavior, allowing us to evaluate system stability in non-equilibrium states. We considered the amplitude of oscillation (difference between the maximum and minimum densities) to be the stability index for each species. Since the trends of the changes in the stability index with a change in  $K$  were identical for all species, we arbitrarily chose the stability index of  $X_1$  to evaluate the paradox of enrichment. We numerically surveyed the behavior of the amplitude for various possible combinations of the carrying capacity of the prey,  $K$  ( $K$  is identical among prey), and prey profitability for each predator,  $g/h_{ji}$ . First, for certain sets of parameters, we found that the amplitude of the oscillations became smaller with increasing enrichment; that is, the paradox was truly resolved (Fig. 1). This decreasing pattern of the amplitude is kept in the non-

equilibrium range of  $K$  and the amplitude ultimately becomes a fixed size for larger values of  $K$ .

For resolution of the paradox, two conditions must be met: (1) the same prey species must be ranked higher as a dietary item by both predator species, creating the potential for high exploitative competition between the predator species, and (2) the less profitable prey species must be inedible, or unpalatable and close to inedible, to one predator (predator species 2) and unpalatable close to palatable to the other (predator species 1) (see Fig. 2). The first condition is not intuitively convincing. However, we rationally speculated that the paradox is not resolved when a two predator–two prey system has food web structures different from those of the first condition because such a system would consist of a loose coupling of the KYM and Rosenzweig models, neither of which resolves the paradox. In a long-term population dynamics cycle, predator species 1, has a euryphagous phase (utilizing both prey species) and a stenophagous phase (utilizing solely the profitable prey species), depending on the density change of the profitable prey. In contrast, predator species 2, rarely or never eats the less profitable prey during a long-term population dynamics cycle. Therefore, the second condition for resolution of the paradox can be paraphrased by describing one predator (predator 1) as a generalist and the other (predator 2) as a specialist. In addition, the stabilizing trend with increasing enrichment is enhanced when the specialist predator is a good hunter, that is, when the handling time ( $h_{ji}$ ) involved in capturing the prey is short (see Fig. 2b, c).

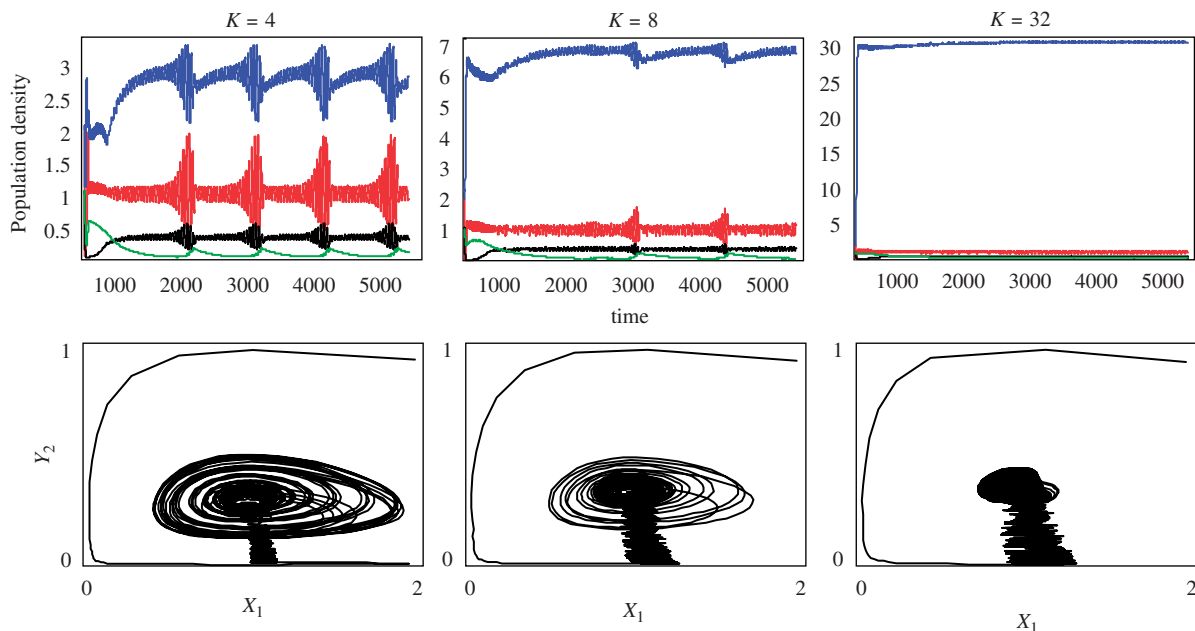


Fig. 1. An example of population density dynamics in which the amplitude of oscillation decreases with increasing enrichment. The upper panels show the time-series behavior of the population densities of four species,  $X_1$  (red),  $X_2$  (blue),  $Y_1$  (green), and  $Y_2$  (black). The lower panels show the dynamics in the  $X_1$ – $Y_2$  space for each value of  $K$  in the upper panels. The parameter values used in the calculations are  $\alpha_{12} = 0.5$ ,  $\alpha_{21} = 0.1$ ,  $\varepsilon = 1$ ,  $b = 1$ ,  $d = 0.25$ ,  $r = 0.25$ ,  $g = 0.5$ ,  $h_{11} = 1$ ,  $h_{12} = 2$ ,  $h_{21} = 0.9$ , and  $h_{22} = 25$ . Note that enrichment increases from left to right in the figure (we have assumed that the magnitude of the carrying capacity ( $K$ ) of the prey indicates the degree of enrichment). The maximum amplitude of population oscillation ( $X_1$ ) decreased from 1.67 to 1.05 to 0.36 when  $K$  was increased from 4 to 8 to 32, respectively (the other species also showed similar decreasing pattern of the amplitude of population oscillations). The amplitude was also decreasing for intermediate values of  $K$ .

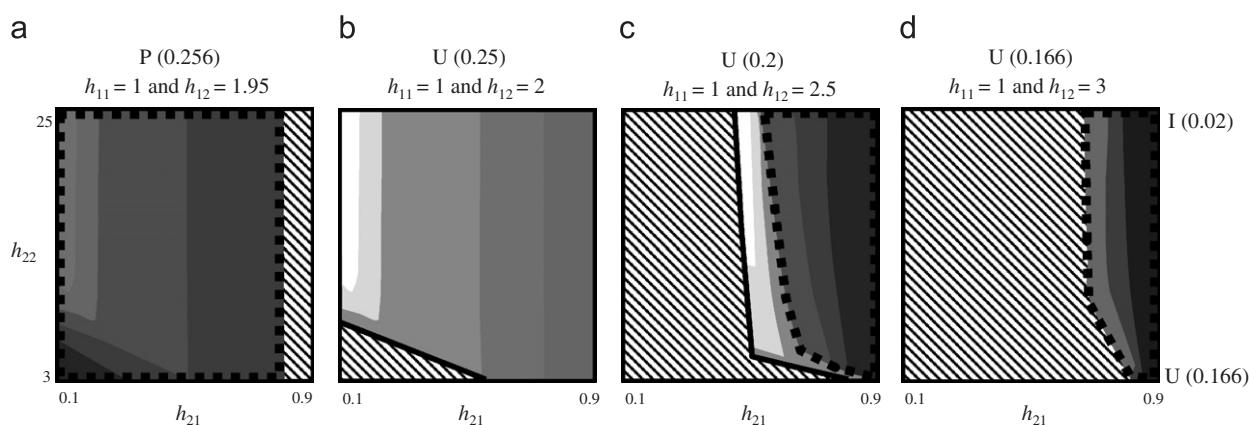


Fig. 2. Change in the amplitude of oscillation with increasing enrichment (evaluated for  $K$  from 8 to 32) in the  $h_{21}$ – $h_{22}$  space. Panels (a)–(d) differ according to the dietary worth of the less profitable prey species to predator species 1. The values of  $P$ ,  $U$ , and  $I$ , shown outside of the panels, represent the profitability of the less profitable prey for the predators ( $g/h_{j2}$ ), where  $P$  implies palatable,  $U$  unpalatable, and  $I$  inedible. Those above the panels apply to predator species 1, and those on the right side of rightmost panel apply to predator species 2. The profitability for predator 1 in (b) is the boundary between unpalatable and palatable ( $g/h_{j2} = d/b$ ). In each panel, the hatched area represents the non-persistent region, in which at least one of the four species cannot exist. The area surrounded by the dashed line represents the region in which a paradox of enrichment exists (the change in the amplitude of oscillation with increasing  $K$  is positive). The shades of gray within this region show the degree of destabilization with increasing enrichment (the darker the shade, the higher the degree of destabilization). The remaining area outside of the dashed lines, represents the region in which the paradox of enrichment is resolved (the change in the amplitude of oscillation with increasing  $K$  is negative). The relative brightness of the region represents the degree of stabilization with increasing enrichment (the lighter the shading, the higher the degree of stabilization). Parameters, except for  $h_{ji}$ , are the same as those in Fig. 1.

### 3.1. Mechanism for resolution of the paradox of enrichment

To determine the mechanism by which the paradox of enrichment is resolved in the two predator–two prey system, we first analyzed in detail the behavior of the dynamics when the paradox is resolved. The analysis of this complex behavior, although time-consuming, is required to understand how the system becomes stabilized with enrichment. Next, we compared the dynamics behavior for different values of  $K$  to attain our end goal, understanding of the mechanism by which stabilization is achieved with enrichment.

#### 3.1.1. Behavior of the dynamics when the paradox of enrichment is resolved

We summarize the behavior of the dynamics when the paradox of enrichment is resolved by showing a typical time series over one cycle period (Fig. 3a). This dynamics behavior has the following key features. First, densities of the specialist predator ( $Y_2$ ) and its prey ( $X_1$ ) follow short cycles with a  $\pi/2$  phase lag, the pattern exhibited by a typical predator–prey cycle. This  $Y_2$ – $X_1$  cycle generates antiphase (a phase lag of approximately  $\pi$ ) cycles between the competing prey species ( $X_1$  and  $X_2$ ) (see Fig. 3c). Second, densities of the generalist predator ( $Y_1$ ) and of the less profitable prey ( $X_2$ ) show long antiphase cycles ( $\pi$  phase lag) (see Fig. 3a (ii) and (iii)). Third, during the decreasing phase of the long cycle of  $Y_1$  (phase 3, shown in Fig. 3a), the short cycles of  $Y_2$  and  $X_1$  have small amplitudes. Fourth, the initial increasing phase of  $Y_1$  in the long cycle is associated with an increase in the amplitudes of the short cycles of  $Y_2$  and  $X_1$  (phase 1, shown in Fig. 3a). Finally, the increase of  $Y_1$  in the long

cycle ceases (a maximum is reached), which is associated with damping of the magnitudes of the short cycles of  $X_1$ ,  $X_2$  and  $Y_2$  (phase 2, shown in Fig. 3a).

These descriptions of the features of the dynamics behavior are rather superficial. Next, we explain the mechanisms that link the short- and long-cycle dynamics.

**3.1.1.1. Short-cycle dynamics.** In one period of the short cycle of the more profitable prey ( $X_1$ ), the generalist predator ( $Y_1$ ) enjoys a high density of the more profitable prey when  $X_{11}^{ct} < X_1$ , and the result is an increase in its own density ( $0 < dY_1/dt$ ). When  $X_1 < X_{11}^{ct}$ , in contrast, because of the low density of the more profitable prey, the generalist predator utilizes the less profitable prey as well, resulting in a decrease of  $Y_1$  ( $dY_1/dt < 0$ ). This pattern is consistent during the short cycles of density changes. The long-cycle trend, increasing or decreasing, of  $Y_1$  is determined by whether  $dY_1/dt$  values are dominantly positive or negative through the short cycle, which depends on the relative length of the periods with  $X_{11}^{ct} < X_1$  and  $X_1 < X_{11}^{ct}$ . Note that the sign inversion of  $dY_1/dt$  occurs rigorously at the boundary  $X_{11}^{ct}$  only when  $X_{11}^{ct} = d/b$ .

**3.1.1.2. Long-cycle dynamics.** We explain the three phases (1–3 in Fig. 3a, b) of the long-cycle dynamics in sequence. For convenience, let us consider an initial state in which the generalist predator is rare (low value of  $Y_1$ ).

**Phase 1:** When the density of the generalist predator ( $Y_1$ ) is low (bottom of the “bottle” in Fig. 3b), predation pressure on the less profitable prey is relaxed, and the prey species enjoys a relatively high density during this part of the long cycle (see the densities around the open triangles in Fig. 3a (ii), (iii)). For the generalist predator, this high

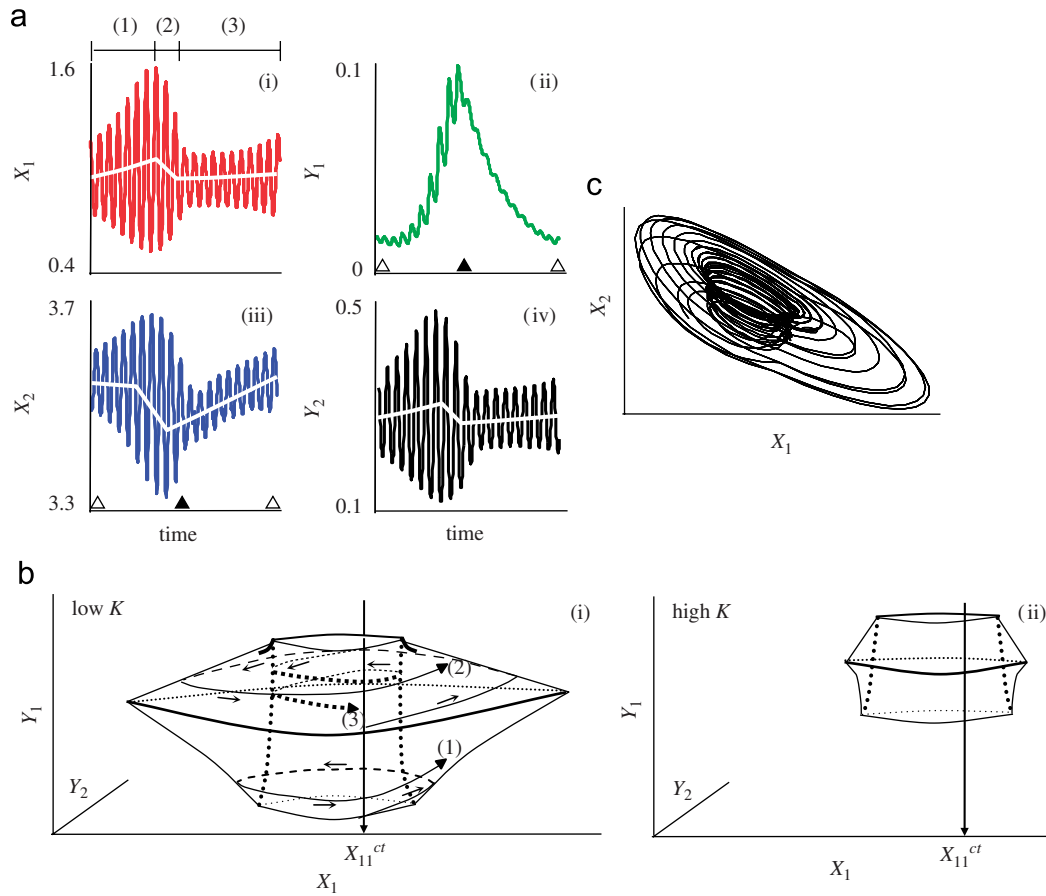


Fig. 3. Underlying mechanisms that generate system stabilization with increasing enrichment. (a) Typical time-series behaviors of the four populations in one long-cycle period in the case that the paradox is resolved. The white lines in (i), (iii), and (iv) show the long-cycle trend. The filled and open triangles indicate the points where  $Y_1$  reaches a maximum and minimum, respectively. The numbers in parentheses above panel (i) show long-cycle phases, described in (b). (b) The schematic three-dimensional phase trajectory in  $X_1$ - $Y_1$ - $Y_2$  space (drawn from (a)). The left (i) and right (ii) figures are the cases where  $K$  is relatively low and high, respectively. The trajectory spirals up around the outside of the bottle shape, reaches the top of the bottle, and then spirals downward around the inner tube. The numbered trajectories (see arrows) in (i) correspond to the phases of one cycle period, shown in (a). For trajectories 1 and 2, the solid lines show the trajectories on the front of the outer bottle, and the dashed lines show them around the back of the bottle. For trajectory 3, the thick dotted line shows the trajectory on the near side of the inner tube, and the thin dotted line shows it on back side of the tube. We described the dynamics trajectories with time progression only for low  $K$  because they do not change with changes in the value of  $K$ . (c) A two-dimensional phase trajectory plot in  $X_1$ - $X_2$  space. Note that the phase relationship between the population densities of the two prey species is very close to antiphase.

density of the less profitable prey leads to a constant increase in the generalist predator's density, given the short-cycle oscillation of the density of both prey species in this phase.

During the initial increasing phase of the long cycle of the generalist predator, the more profitable prey receives an indirect benefit from the generalist predator, because the increasing density of the generalist predator depresses the density of the less profitable prey, resulting in a relaxation of interspecific competition between prey species (see the long-cycle trends of  $X_1$  and  $X_2$  in phase 1, shown in Fig. 3a). Thus, the short-cycle maximum of  $X_1$  increases during this portion of the long cycle. However, the more profitable prey also suffers a direct negative effect as a result of the increasing density of the generalist predator, causing the short-cycle minimum of  $X_1$  to decrease. These two antithetical effects enlarge the amplitude of the short cycles of  $X_1$ , and, consequently, that of the short cycles of  $Y_2$  (see trajectory 1 in Fig. 3b).

**Phase 2:** When the generalist predator attains an intermediate density in the increasing phase of its long cycle, the density of the more profitable prey ( $X_1$ ) in the long cycle begins to decrease, owing to the higher predation pressure from both predator species. The density of the generalist predator ( $Y_1$ ) continues to increase in the long cycle because the generalist predator is exploiting both prey species (see the long-cycle trends of  $X_1$ ,  $X_2$ , and  $Y_1$  during phase 2, Fig. 3a).

During this phase, the following mechanisms decrease the amplitude of the short cycle of  $X_1$ . When  $X_{11}^{ct} < X_1$ , the increasing density of  $Y_1$  suppresses the maximum short-cycle value of  $X_1$ . Thus, it suppresses the increase of  $Y_2$ , resulting in an increase in the minimum value of  $X_1$ . As a result, when  $X_1 < X_{11}^{ct}$ , the generalist predator need not utilize the less profitable prey as much as before, causing enhancement of interspecific competition between the prey species; thus, the maximum value of  $X_1$  further reduces.

These effects shrink the amplitude of the short cycles of  $X_1$  and  $Y_2$  (see trajectory 2 in Fig. 3b).

*Phase 3:* At a high density of the generalist predator ( $Y_1$ ) in its long cycle, densities of the more profitable prey ( $X_1$ ) are well suppressed and  $dY_1/dt$  no longer maintains a positive value on average during short cycles. Therefore, the density of the generalist predator enters the decreasing phase of its long cycle (see trajectory 3 in Fig. 3b). During this phase, the system is most stable.

During the decreasing phase of the generalist predator in its long cycle, both prey species experience a release from predation pressure by the generalist predator, and the density of the less profitable prey increases fairly steeply. The increasing densities of the less profitable prey species eventually stop the decline of the generalist's density, which then begins to increase again (return to phase 1).

### 3.1.2. The system is stabilized with enrichment

Here, we explain the mechanism by which the paradox of enrichment is resolved in this system. We begin by comparing how the features of the dynamics behavior differ for different values of the enrichment parameter,  $K$ . The dynamics trajectories over time basically do not differ for different values of  $K$  (see Fig. 3b); however, the shape of the “bottle” depicting these trajectories in  $X_1$ – $Y_1$ – $Y_2$  space differs obviously between low and high  $K$  (Fig. 3b). In particular, when  $K$  is high, the outer frame of the bottle is smaller. This means that higher enrichment causes the amplitudes of the short cycles to decrease. The answer to the main question, why the system stabilizes with enrichment, lies in the explanation of the cause of this difference.

The key species for the generalist predator is the less profitable prey, whose density is always higher than that of the other prey species (see Fig. 1). Under continuous predation by both predators, the more profitable prey would never receive the benefit of enrichment. In contrast, the less profitable prey unilaterally gains the benefit of an increase in enrichment. Since the predators appraise the less profitable prey as unpalatable ( $Y_1$ ) or inedible ( $Y_2$ ), both predators reduce the density of its competitor prey species, allowing the less profitable prey to benefit from the enrichment; thus, it attains a higher density with enrichment.

As a result, the less profitable prey functions as a stable supplemental prey resource for the generalist predator, and the predation pressure of the generalist predator on the more profitable prey is relaxed whenever the less profitable prey is being utilized as supplemental prey. The degree to which predation pressure on the more profitable prey is relaxed is enhanced with enrichment, because the higher the enrichment, the higher the density of the less profitable prey becomes. The enhanced relaxation of predation pressure on the more profitable prey thus raises its minimum density on average (compare (i) and (ii) in Fig. 3b). Consequently, the minimum densities of the predator species are maintained at a higher level on average. Furthermore, the increase in enrichment effectively in-

creases the impact of interspecific competition between the less profitable and more profitable prey species, because high predation pressure from the two predators on the more profitable prey decreases its maximum density. This results in a lower maximum density of the generalist predator because it can no longer make as much use of the more profitable prey. As a result, the oscillations in all of their populations reduce with enrichment.

## 4. Discussion

In the original Rosenzweig model (one predator–one prey systems) (Rosenzweig 1971), increasing the potential maximum prey density by enrichment destabilizes predator–prey systems. In the KYM system (Genkai-Kato and Yamamura, 1999), which involves one generalist optimal forager, one more profitable prey species, and another less profitable prey species, although enrichment increases the potential maxima of the prey densities, it increases the density of the less profitable prey species unilaterally. This increasing density of the less profitable prey with enrichment tends to suppress the amplitude of the oscillation of the predator–more profitable prey cycle. However, the amplitude is insufficiently suppressed to resolve the paradox of enrichment because it continues to increase with enrichment. This continued increase is because the predator population spends most of its time in a stenophagous phase (it tends to utilize only the more profitable prey) in the population dynamics cycle. Thus, the food web structures of the predator–prey interaction are homologous to those of the Rosenzweig model, which shows the paradox of enrichment.

In our two predator–two prey system, the predator–prey relationship between the specialist predator and its prey species (species 1) is the primary generator of the short cycles, which are subject to the paradox of enrichment in the Rosenzweig model. Structurally, our model system is a composite of the Rosenzweig system and the KYM system. In our system, higher enrichment can decrease the amplitudes of the short cycles. Our analysis showed that the composite effects of the two models altering the amplitudes of the predator–prey oscillations that occur with enrichment can truly resolve the paradox of enrichment.

Interestingly, we found that the prey exploited by the specialist and the more profitable prey of the generalist must be the same (prey species 1) when the paradox of enrichment is resolved. This pattern results in high exploitative competition for utilization of the shared prey species between the two predator species. This exploitative competition has several effects. First, it causes the less profitable prey to function as a stable supplemental prey resource for the generalist predator. As a result, optimal foraging by the generalist predator has a stabilizing effect. In addition, this effect is the strongest when the generalist considers the less profitable prey to be unpalatable, which is suggested by the results of the study of Genkai-Kato and

Yamamura (1999) (see Fig. 2). Second, it means that the presence of the specialist predator can decrease the density of the more profitable prey to a point lower than the menu change threshold of the generalist predator. Third, it effectively suppresses the increase in the more profitable prey, because of high predation pressure from the two predators and high interspecific competition between two prey species, with the second species maintaining higher density. In what follows, we explain why the paradox is resolved by showing how these exploitative competition effects act on the population dynamics with increasing enrichment. Note that the latter two effects are not found in the KYM system.

The less profitable prey (prey species 2) causes the predation pressure of the generalist predator on the shared more profitable prey species (prey species 1) to be relaxed whenever the less profitable prey is being utilized as supplemental prey. This relaxation of predation pressure on the more profitable prey is enhanced with enrichment, thus raising the minimum density of the more profitable prey on average. Consequently, the minimum densities of both predator species are maintained at a higher level on average. Furthermore, the increase in enrichment effectively increases the impact of interspecific competition from the less profitable prey on the more profitable prey because of the high predation pressure from the two predators on the more profitable prey, which decreases the maximum density of the more profitable prey. As a result, the oscillations in all of their populations reduce with enrichment.

We emphasize that our results show that the minimum density values of all populations increase with increasing enrichment, which is not observed in the KYM system (see Genkai-Kato and Yamamura, 1999). In summary, in our system, stabilization is accomplished in the face of enrichment from two perspectives: the amplitude of oscillation is decreased, and the minimum population densities of all species are increased.

Several theoretical studies on the paradox of enrichment have focused on within-trophic level heterogeneity of prey types (e.g., Kretzschmar et al., 1993; Vos et al., 2004). These studies show that the difference in profitability of preys,  $g/h$ , is important for the local stability of equilibrium and resolution of the paradox of enrichment in one predator–two prey systems. The same is true of our model, however, our result additionally shows that within-trophic level heterogeneity of predator types is important for the stability (of non-equilibrium dynamics) and resolution of the paradox of enrichment. In other words, these findings may suggest that the biodiversity is important for the stability of ecosystem.

The many theoretical studies on the paradox of enrichment have explored only a single aspect of a real complex ecosystem, in particular, predator–prey interaction. In simple model ecosystems, the paradox of enrichment may exist (Rosenzweig, 1971; Abrams and Roth, 1994; Genkai-Kato and Yamamura, 1999). However,

optimal behavior prevents this pattern to some degree (Genkai-Kato and Yamamura, 1999). Moreover, our result shows that not only optimal behavior but also the dynamic-food web structures of complex interactions among species contributes to the stability of the system (Kondoh, 2003) and have the ability to resolve the paradox of enrichment. Future research will clarify the relationship between topological features of interaction linkages and stability in a multispecies food-web system in response to enrichment, and determine whether our findings presented in this study have universal applicability.

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