The paradox of enrichment in an adaptive world

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Paradoxically, enrichment can destabilize a predator–prey food web. While adaptive dynamics can greatly influence the stability of interaction systems, few theoretical studies have examined the effect of the adaptive dynamics of interaction-related traits on the possibility of resolution of the paradox of enrichment. We consider the evolution of attack and defence traits of a predator and two prey species in a one predator–two prey system in which the predator practises optimal diet use. The results showed that optimal foraging alone cannot eliminate a pattern of destabilization with enrichment, but trait evolution of the predator or prey can change the pattern to one of stabilization, implying a possible resolution of the paradox of enrichment. Furthermore, trait evolution in all species can broaden the parameter range of stabilization. Importantly, rapid evolution can stabilize this system, but weaken its stability in the face of enrichment.

Keywords: paradox of enrichment; optimal foraging; evolution; stabilization; predator–prey

1. INTRODUCTION

Classical ecological theory suggests that enrichment destabilizes predator–prey systems, causing species extinction (Rosenzweig 1971). Resolution of this paradoxical prediction is a challenging theoretical problem in ecology. Many theoretical studies have proposed ways in which the paradox might be resolved theoretically (reviewed in Jensen & Ginzburg 2005). Although they capture the important aspects of the natural world, most of these studies assume fixed predator–prey interaction links (Gilpin 1975; Arditi & Ginzburg 1989; Kretzschmar *et al.* 1993; Abrams & Walters 1996; Arditi *et al.* 2004). This simplicity is analytically convenient, but these arguments ignore the flexible nature of the food webs.

Recent theoretical studies have reported that the adaptive nature of plasticity, such as optimal foraging, and the evolution of traits can stabilize species interaction systems (Kondoh 2003; Takimoto 2003; Yamauchi & Yamamura 2005; Kondoh 2007). Vos *et al.* (2004) and Mougi & Nishimura (2007) consider the plastic behaviour of the predator or prey, i.e. optimal foraging or an inducible defence, respectively, to stabilize a simple food web. Vos *et al.* (2004) demonstrated that inducible defence can resolve the paradox of enrichment in equilibrium dynamics. Mougi & Nishimura (2007) demonstrated that optimal foraging by the predator species can resolve the paradox of enrichment in non-equilibrium dynamics.

The diet utilization rule of the optimally foraging predator is based not only on the relative abundance of the prey species but also on the search and attack abilities of the predator and the hide and escape abilities of each prey species. If a foraging trait of the predator species and a defence trait of the prey species are the selection targets, then these traits *per se* might be evolvable. In this paper, we consider a predator's foraging trait and the preys' defence traits to be evolvable, and examine how the evolutionary dynamics of these traits influences the stability of

predator–prey population dynamics in the face of enrichment.

We use a familiar minimal predator–prey system that includes a flexible food-web link: a one predator–two prey system in which the predator practises optimal diet use (Fryxell & Lundberg 1994; Genkai-Kato & Yamamura 1999; Ma *et al.* 2003; Yamauchi & Yamamura 2005). In this system, we demonstrate that although evolution of a trait of either the predator (attack ability) or the prey (defence ability) magnifies the oscillation of population densities, such evolution can nevertheless resolve the paradox of enrichment in non-equilibrium dynamics. Furthermore, we demonstrate that the conditions for resolution of the paradox can be broadened if all species evolve, that is, in an adaptive world.

Finally, we show that rapid evolutionary speed is crucial to stabilize the system, as has been shown by previous studies (Kondoh 2003; Yamauchi & Yamamura 2005), but that, in the face of enrichment, it weakens the system's stability. In other words, slower trait evolution, which causes destabilization of the system when the basal resource supply is arbitrarily fixed, can increase the likelihood of stabilization in the face of enrichment. This result carries with it an important message about the concept of stability.

2. THE MODEL

(a) *Food-web dynamics*

We use a familiar one predator–two prey system in which the predator practises optimal foraging (Fryxell & Lundberg 1994; Genkai-Kato & Yamamura 1999; Ma *et al.* 2003; Yamauchi & Yamamura 2005). We consider the predator–prey system to be described by the following dynamics of the densities of the two prey species and the one predator species, denoted by X_i ($i = 1$ or 2) and Y, respectively,

$$\dot{X}_i = \left\{ r_i \left(1 - \frac{1}{K_i} \sum_{j \in \text{prey types}} \alpha_{ij} X_j \right) - \mu_i Y \right\} X_i, \qquad (2.1a)$$

$$\dot{Y} = \left(b \sum_{i \in \text{prey types}} g_i \mu_i X_i - d \right) Y, \tag{2.1b}$$

where

$$\mu_i = \frac{p_i a_i}{\left(1 + \sum_{i \in \text{prey types}} p_i h_i a_i X_i \right)}.$$

For the predator species, Y, term μ_i implies the instantaneous exploitation rate of prey species i, defined by a type 2 functional response; a_i is the search and attack efficiency for prey i; h_i is the handling time of prey i; g_i is the energy value of an individual of prey i; p_i ($0 \le p_i \le 1$) is the capture probability of an individual of prey species i given an encounter; b is the conversion efficiency, which relates the predator's birth rate to its prey consumption; and d is the death rate of the predator species. For prey i, α_{ij} 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 traditionally indicates the degree of enrichment (Rosenzweig 1971).

(b) *Optimal diet use*

We assume that the predator is an optimal forager and selects its diet in accordance with optimal diet utilization theory (Stephens & Krebs 1986). The predator determines the inclusion or exclusion of a prey species in 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 the handling time, h, upon an attack. The higher ranked prey species (species 1) is unconditionally included in the diet (i.e. $p_1 = 1$). Under perfect optimal foraging, the capture probability of an individual of the less profitable prey (species 2) given an encounter, p_2, equals 0 or 1, depending on whether the density of the more profitable prey X_1 is greater or less than the threshold density, $\hat{X}_1 (= g_2 / \{a_1 h_1 h_2 (g_1 / h_1 \ g_2 / h_2)\})$. If the density of the more profitable prey drops below a critical threshold (the menu change threshold), then the less profitable prey is also included in the diet ($p_2 = 1$). Otherwise, the less profitable prey is excluded from the diet ($p_2 = 0$). Inclusion or exclusion of the less profitable prey (i.e. menu variety) depends on the difference in the profitability between the prey items and the density of the more profitable prey (Stephens & Krebs 1986). This behavioural decision is optimal in terms of maximization of the long-term energy acquisition rate (Templeton & Lawlor 1981).

(c) *Evolution of attack and defence abilities*

We define ε_i, the attack ability of the predator with respect to prey i, and v_i, the defence ability of prey species i when attacked by the predator, each of which is independently quantified. We consider the evolution of either or both of the traits.

We assume that both traits influence the search/attack efficiency of the predator with regard to prey species i, a_i: $a_i = a_{\max} \varepsilon_i (1 - v_i)$, where $\sum_{i \in 1,2} \varepsilon_i = 1$ (trade-off between attack abilities) and $a_{\max}$ is the maximum search efficiency. The evolutionary dynamics of the attack and defence abilities are as follows (Matsuda *et al.* 1996; Kondoh 2003, 2007):

$$\frac{d\varepsilon_i}{dt} = \kappa_i \varepsilon_i \left(\frac{\delta F}{\delta \varepsilon_i} - \sum_{j \in 1,2} \varepsilon_j \frac{\delta F}{\delta \varepsilon_j} \right), \tag{2.2a}$$

$$\frac{dv_i}{dt} = \eta_i v_i (1 - v_i) \left(\frac{\delta G_i}{\delta v_i} \right), \tag{2.2b}$$

where F and G_i are the fitness functions of the predator and prey species, respectively, and are assumed to be equal to the *per capita* growth rate, i.e.

$$G_i = r_i \left(1 - \frac{1}{K} \sum_{k \in \text{prey types}} \alpha_{ik} X_k \right) - \mu_i Y, \tag{2.3a}$$

$$F = b \sum_{i \in \text{prey types}} g_i \mu_i X_i - d. \tag{2.3b}$$

As we mentioned above, we assume trade-off between attack abilities ($\sum_{i \in 1,2} \varepsilon_i = 1$). In defence abilities, we also assume trade-off, i.e. defence is costly and influences the intrinsic growth rate r_i, such that $r_i = r_{\max}(1 - v_i)$, where $r_{\max}$ is the maximum intrinsic growth rate. The term $v_i(1 - v_i)$ keeps the dynamics within $0 < v_i < 1$. κ_i and η_i are parameters that influence evolutionary speed, such as the additive genetic variance of the traits.

3. RESULTS

We examined how trait evolution influences the stability of the population densities of the predator–prey system and whether it can resolve the paradox of enrichment. In the system we analyse, local stability of the interior equilibrium changes from stable to unstable (oscillation) with increasing K, as Rosenzweig (1971) showed in his original model. In the wide range of parameter values that allow all of the species to coexist dynamically, the density of each species follows a complex cycle at large values of K. In the following analysis, we focus particularly on the non-equilibrium dynamics. For cases both with and without trait evolution, we conducted a sufficiently long simulation run, given the asymptotic behaviour of the traits and population dynamics, to allow us to evaluate the system stability in the face of enrichment. In no cases did the dynamics of all traits evolutionarily either converge to a fixed trait combination or diverge. We use the amplitude of population oscillations (difference between the maximum and minimum densities) as the stability index (the result is the same if minimum density is used as the stability index). We arbitrarily chose to examine the stability index of X_1, the higher ranked prey species, but the results would be the same regardless of the species chosen. Although we chose arbitrary parameter values in our investigations, we confirmed that our main result is robust when other parameter values are chosen.

(a) *Effect of trait evolution on stability and the paradox of enrichment*

The stability of the system is crucially influenced by the profitability of the less profitable prey, g_2/h_2. Genkai-Kato & Yamamura (1999) showed that when the profitability of the less profitable prey g_2/h_2 is 'inedible' or 'palatable' in their definition of the terminology (for the nominal designations, see appendix A), the amplitude of oscillation is larger than when it is 'unpalatable', and the paradox of enrichment cannot be resolved. Thus, we focused on stability in the parameter region of unpalatable prey.

As shown in figure 1, trait evolution increases the amplitude of oscillation in the parameter region close to the boundary between palatable and unpalatable, $d/$
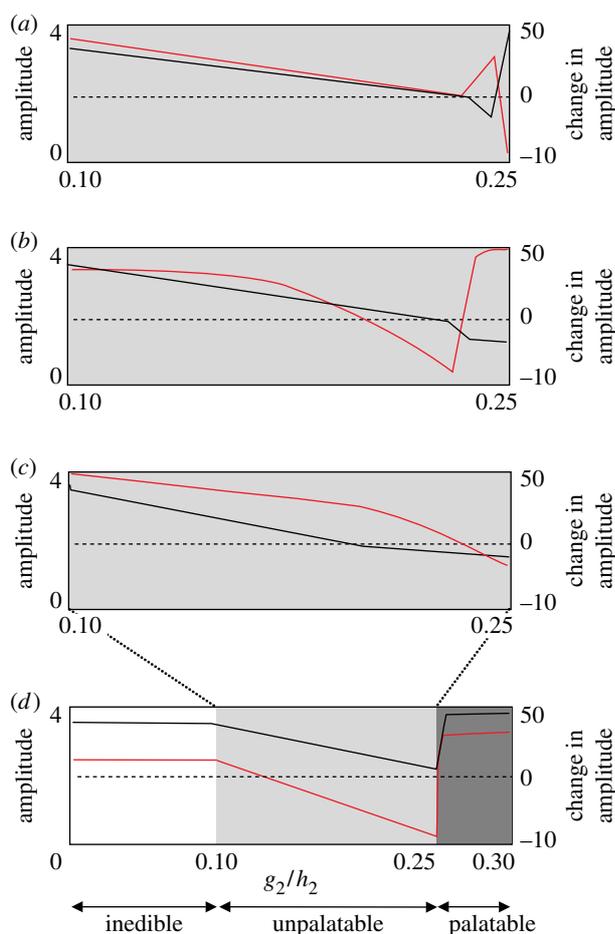
Figure 1. Stability–palatability relationship of the less profitable prey: (*a*) attack evolution, (*b*) defence evolution, (*c*) attack and defence evolution and (*d*) no evolution. The red lines represent the amplitude of oscillation of the more profitable prey ($K=5$). The black lines represent the magnitude of the change in the amplitude of oscillation of the more profitable prey that accompanies an increase in K from 5 to 50. The horizontal dotted lines represent the boundary between paradox and resolution (where the change in amplitude is 0). The paradox occurs above, and not below, the horizontal lines. The regions are categorized by the profitability of less profitable prey (see appendix A), indicated by variation in the shading in (*d*). In (*a*–*c*), the unpalatable region is the region of focus. The common parameter values used in the calculations are $\alpha_{12}=\alpha_{21}=0.1$, $r_1=r_2=0.25$ (or $r_{max}=0.25$), $g_1=g_2=0.5$, $b=1$, $d=0.25$ and $h_1=1$. The others are (*a*) $a_{max}=1$, $\kappa=0.1$, $\eta=0$, (*b*) $a_{max}=8$, $\kappa=0$, $\eta=0.25$, (*c*) $a_{max}=2.8$, $\kappa=0.3$, $\eta=0.1$ and (*d*) $a_1=a_2=1$, $\kappa=0$, η, $\kappa=0$. Note that we assume $\eta_1=\eta_2=\eta$ and $\kappa_1=\kappa_2=\kappa$. The initial values are $(X_1, X_2, Y, \varepsilon_1, \varepsilon_2, v_1, v_2) = (2, 2, 1, 0.1, 0.9, 0.1, 0.1)$. These arbitrary choices of parameter values do not influence our main result. We chose the values of a_{max}, η and κ in such a way that the range of resolution of the paradox of enrichment would be the broadest in each case. We confirmed that the main result did not change even if the same parameter values were used in all cases.

b (see appendix A), compared with the case of no evolution (compare *a*–*c* with *d* in figure 1). In the cases where the predator's attack ability or prey's defence abilities or both evolve, the amplitude of oscillation tends to be larger (figure 1*a*–*c*).

Next, we investigated the changes in amplitude with increasing K (i.e. checking for the paradox of enrichment). Interestingly, parameter regions in which the amplitudes

decrease with enrichment appear (figure 1*a*–*c*). In other words, the coupling of optimal foraging and evolution of predator's attack ability and/or prey's defence abilities can resolve the paradox of enrichment in non-equilibrium dynamics. In addition, the paradox is more likely to be resolved when the high stability caused by optimal foraging (where the amplitude is close to 0) is weakened by evolution of traits (compare figure 1*a*–*d*) and when all species evolve (figure 1*c*). In contrast, the paradox cannot be resolved when no species evolve even when the system is highly stable (figure 1*d*). Thus, these results suggest that although evolution of attack and/or defence abilities destabilizes stabilized food-web dynamics caused by optimal foraging behaviour on an ecological time scale, it can increase the stability of the system in the face of enrichment.

(b) *Effect of evolutionary speed on stability*
Next, we investigated how evolutionary speed, parametrized by κ_i and η_i, influences stability and the paradox of enrichment. Interestingly, we found that slow evolution destabilizes the system dramatically (both the amplitude of oscillation is increased) compared with a highly stable system in the absence of evolution (figures 1*d* and 2). In contrast, the amplitude of oscillation is smaller when the evolutionary speed is faster. This result is consistent with the previous findings that rapid evolution can stabilize the food web (Kondoh 2003; Yamauchi & Yamamura 2005). However, the paradox of enrichment is likely to be resolved when the evolutionary speed is relatively slower (figure 2).

In summary, the paradox of enrichment is likely to be resolved in non-equilibrium dynamics when any one of the following conditions is met: (i) when trait evolution destabilizes a flexible food web in which a predator practises optimal foraging, (ii) when all species evolve, and (iii) when the evolutionary speed is relatively slow.

4. DISCUSSION
In their theoretical study, Genkai-Kato & Yamamura (1999) suggested that a flexible one predator–two prey system in which the predator is an optimal forager mitigates the effect of the paradox pattern of enrichment. However, they did not show a pattern that resolved the paradox of enrichment (Mougi & Nishimura 2007). Recent theoretical and empirical studies of food-web stability have focused on evolutionary aspects (reviewed by Fussmann *et al.* 2007).

The present result shows that although evolution of predator's attack ability and/or prey's defence abilities can destabilize a stable one predator–two prey system with an optimal forager, surprisingly, it can also resolve the paradox of enrichment in non-equilibrium dynamics. In particular, if all species evolve or the evolutionary speed is slow, then the paradox is likely to be resolved. These results are interesting because we expect that the instability caused by evolution and a slow evolutionary speed to weaken the stability of system in the face of enrichment, but the opposite is true. Our results suggest two important things: (i) a faster evolutionary speed does not necessarily make a system stable in the face of enrichment and (ii) a relatively stable system (small
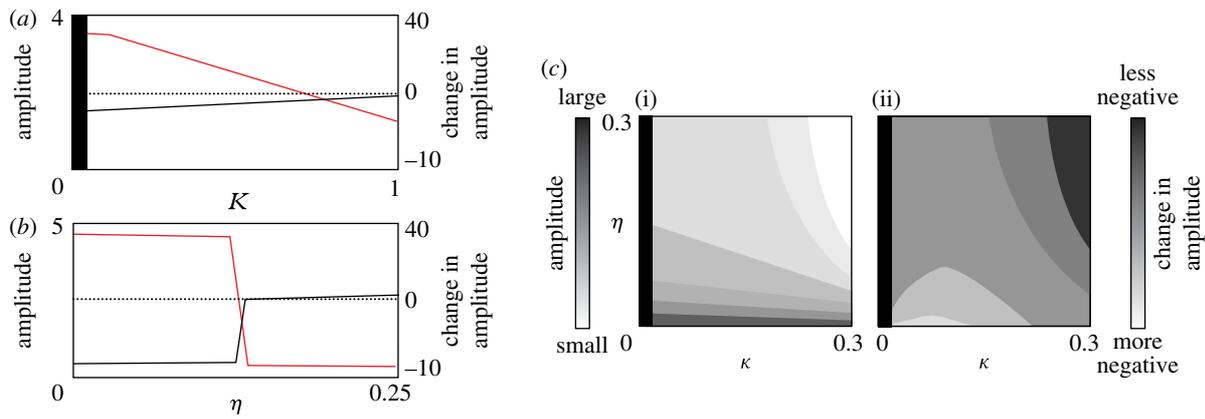
Figure 2. Stability–evolutionary speed relationship: (*a*) attack evolution, (*b*) defence evolution and (*c*) attack and defence evolution. In (*a*) and (*b*), the left and right vertical axes are the same as in figure 1. In (*c*), the contours reflect (i) the magnitude of the amplitude of oscillation (at $K=5$) and (ii) the change in amplitude that accompanies an increase in K from 5 to 50. Note that a decrease in amplitude accompanies the increase in K in all parameter regions (*c*(ii)). The black regions indicate regions where the species cannot coexist. The parameter values used in the calculations are the same as those used in figure 1 except for (*a*) $h_2=2.1$, (*b*) $h_2=2.3$ and (*c*) $h_2=2.2$.
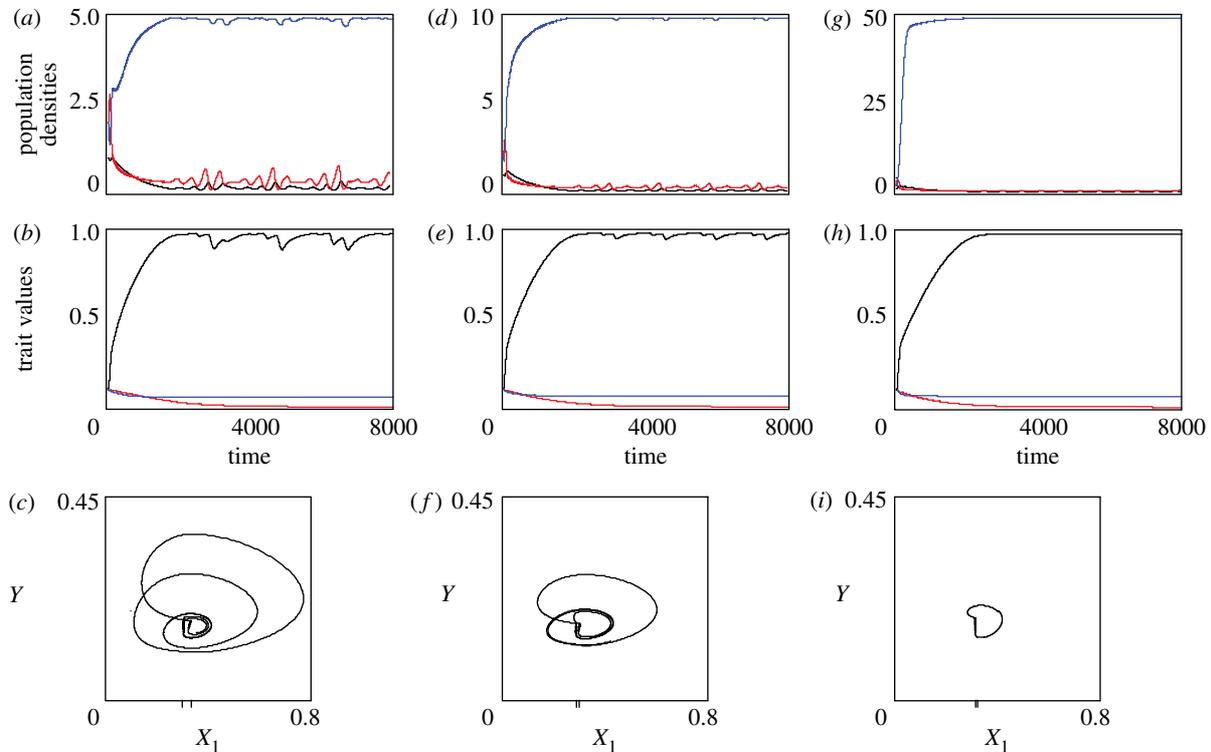

Figure 3. An example of population and trait dynamics in which the amplitude of oscillation decreases with enrichment in case that all species evolve. (*a,d,g*) The time-series behaviour of the population densities: red, X_1; blue, X_2; black, Y. (*b,e,h*) Time-series behaviour of the trait values: red, ε_1; blue, v_1; black, v_2 (ε_2 is not shown because simply $\varepsilon_2=1$ ε_1). (*c,f,i*) The asymptotic population dynamics behaviour in X_1–Y space with enrichment. The bars on horizontal axis represent the minimum and maximum values of the critical threshold $\hat{X}_1$(the critical threshold dynamically changes with changing values of attack and defence abilities). Note that enrichment (K) increases from left to right in the figures (from 5 to 10–50). The parameter values used in the calculations are $\alpha_{12}=\alpha_{21}=0.1$, $r_{max}=0.25$, $g_1=g_2=0.5$, $b=1$, $d=0.25$, $h_1=1$, $h_2=2.2$, $a_{max}=2.8$, $\kappa=0.15$ and $\eta=0.1$.

amplitude of oscillations and high minimum density) is not necessarily robust against enrichment.

Why is the population dynamics stabilized with enrichment? The pattern of population and traits dynamics with enrichment help us to understand the stabilization mechanism. Figure 3 shows a typical pattern of population and traits dynamics with enrichment in the case where all species can evolve. First, we explain the features of population dynamics in the system with only

optimal foraging. Optimal foraging can regulate the population oscillations and mitigate the destabilization with increasing enrichment at some level, although the paradox pattern does not disappear (Genkai-Kato & Yamamura 1999). When the less profitable prey is edible (the 'authors' term is unpalatable), the optimal forager can stop the decrease in the density of the more profitable prey at the critical threshold $\hat{X}_1$; therefore, the minimum density of the predator may become moderately higher,

resulting in a decrease in the amplitude of the density oscillations. However, this stability mechanism cannot stabilize the population oscillations with enrichment.

From the two features in our system, we can explain the stabilization mechanism with enrichment. First, in the system with optimal foraging and evolution of predator's attack ability and prey's defence abilities, evolution of higher attack ability to the more profitable prey (figure 3b) can decrease the density of the more profitable prey at a point below the critical threshold, $\hat{X}_1$, and break the stabilized system caused by optimal foraging, under a low enrichment (figure 3c; note that this destabilization cannot occur in the system without evolution). This is likely to be caused by slow evolution owing to its slow adaptive response to environmental changes. On the contrary, a fast evolution does not destabilize the system owing to its fast adaptive response to environmental changes. Second, in this system, the less profitable prey has higher density owing to low predation pressure and only its density dramatically increases with enrichment (figure 3a,d,g). In other words, the less profitable prey functions nicely as supplemental prey under higher enrichment. Thus, the degree of relaxation of predation pressure on the more profitable prey when the predator continues to use both prey species (or when the density of the more profitable prey decreases at a point below the critical threshold) is weaker under lower enrichment and stronger under higher enrichment. Owing to this reason, the system destabilized by slow evolution cannot be stabilized by optimal foraging with a weak stabilizing power when the enrichment is low, but can be stabilized by optimal foraging with a strong stabilizing power when the enrichment is higher. Such stabilizing mechanism raises the minimum density of the more profitable prey, which increases the minimum density of the predator itself, resulting in the smaller amplitude of population density oscillations under higher enrichment (figure 3c,f,i). In other words, the coupling of a destabilizing effect of slow traits evolution with a stabilizing effect of optimal foraging can change the effect of increasing prey density caused by enrichment on system stability from destabilization to stabilization.

We made no consideration of effect of defences on handling time. Vos et al. (2004) demonstrated that a change in g/h in defended prey relative to undefended prey could solve the paradox of enrichment in an equilibrium situation. In our system, the consideration of effect of defence on the handling time makes the situation more complex because the more profitable prey for the predator can dynamically change. Although the analysis of such situation is beyond this research focus, it would be an interesting future study.

Food-web links can change over time in response to several factors. Adaptive nature, such as plasticity and trait evolution, is one such factor. Kondoh (2003) demonstrated that the complexity–stability relationship can be positive in a flexible food web in which predators practise adaptive foraging through plasticity or evolution. In his study, evolutionary speed is a key parameter in the stability of food webs. A faster evolutionary speed (plasticity rather than evolution) makes a system more stable. Yamauchi & Yamamura (2005) also showed that a faster evolutionary rate in a defence trait is likely to stabilize a one predator–two prey system in which the predator practises optimal foraging. Our result is consistent with the results

of these studies. In the face of a change in productivity such as enrichment, however, this stability–evolutionary speed relationship does not hold. This is the new message for the argument of ecosystem stability.

Our study suggests that the concept of stability is never easy to grasp. A highly stable system in which the amplitudes of population oscillation are small and minimum densities are high might not be stable in the face of enrichment, whereas a relatively unstable system might stabilize in response to enrichment. Previously, Mougi & Nishimura (2007) reported qualitatively similar findings on stability, although the mechanism leading to stability in the face of enrichment was different. They theoretically demonstrated that a strong food-web link between a specialist predator and its prey, which destabilizes stable food webs when an optimally foraging generalist predator is part of the food web, is necessary for stability in the face of enrichment, i.e. for resolution of the paradox of enrichment (Mougi & Nishimura 2007; Mougi & Nishimura in press). This commonality suggests that a coupling of factors (traits evolution and optimal foraging or specialist and generalist predators), one of which causes instability and the other stability, is crucial for stability in the face of enrichment, and we propose that such a coupling represents a new stability mechanism.

APPENDIX A

We temporarily assumed that the prey species are ranked by predator j as $g_1/h_1 > g_2/h_2$. To facilitate comparison with the previous result of Genkai-Kato & Yamamura (1999), we figuratively call the status of the less profitable prey as a dietary item for predator j: inedible, if the minimum density of the more profitable prey (i.e. prey species 1) in a predator–prey oscillatory system consisting of the predator species and prey species 1, $X_1^{\min}$, is above the menu change threshold, $\hat{X}_1$ ($\hat{X}_1 < X_1^{\min}$), defined in the optimal diet; unpalatable, if the density of the more profitable prey is rarely less than $\hat{X}_1$ ($X_1^{\min} < \hat{X}_1 < X_1^{eq}$), where X_1^{eq} ($= d/\varepsilon_1(bg_1 - dh_1)$) is the equilibrium density of prey species 1 in a predator–prey oscillatory system consisting of the predator species and prey species 1; or palatable, if the density of the more profitable prey is frequently less than $\hat{X}_1$ ($X_1^{eq} < \hat{X}_1$), where $\hat{X}_1 = g_2/\{\varepsilon_1 h_1 h_2(g_1/h_1 - g_2/h_2)\}$. The marginal profitability of the less profitable prey between unpalatable and palatable ($\hat{X}_1 = X_1^{eq}$) is analytically defined as d/b.

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