

Effects of evolutionary changes in prey use on the relationship between food web complexity and stability

Wakako Yamaguchi · Michio Kondoh ·
Masakado Kawata

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Abstract The relationship between food web complexity and stability has been the subject of a long-standing debate in ecology. Although rapid changes in the food web structure through adaptive foraging behavior can confer stability to complex food webs, as reported by Kondoh (Science 299:1388–1391, 2003), the exact mechanisms behind this adaptation have not been specified in previous studies; thus, the applicability of such predictions to real ecosystems remains unclear. One mechanism of adaptive foraging is evolutionary change in genetically determined prey use. We constructed individual-based models of evolution of prey use by predators assuming explicit population genetics processes, and examined how this evolution affects the stability (i.e., the proportion of species that persist) of the food web and whether the complexity of the food web increased the stability of the prey–predator system. The analysis showed that the stability of food webs decreased with increasing complexity regardless of evolution of prey use by predators. The effects of evolution on stability differed depending on the assumptions made regarding genetic control of prey use. The probabilities of species extinctions were associated with the establishment

or loss of trophic interactions via evolution of the predator, indicating a clear link between structural changes in the food web and community stability.

Keywords Community stability · Food web evolution · Individual-based model · Prey–predator system · Trophic interaction

Introduction

The relationship between food web complexity and stability has been the subject of a long-standing debate in ecology (MacArthur 1955; May 1972; McCann 2000; Ives and Carpenter 2007). May (1972) presented a simple mathematical model that demonstrated that increasing complexity destabilizes food webs. Thereafter, several empirical studies have attempted to examine the complexity (e.g., the number of species and connectance) of natural food webs on the basis of the assumption that, if complex food webs are unstable, existing food webs should be simple (e.g., Winemiller et al. 2001; Pascual and Dunne 2006). A recent study (Banasek-Richter et al. 2009) indicated that larger food webs had more connectance with weak trophic interactions and that all the analyzed existing food webs would be highly unstable and should collapse according to May's (1972) criteria. Further, Jiang and Pu (2009) showed that positive relationships between diversity and temporal stability could be found in multitrophic communities. Thus, contrary to the predictions based on the simple mathematical model, complex food webs that support a large number of interactive species can exist stably in nature. To explain the stability of complex food webs, several theories have been proposed. Some studies have suggested that food web architecture is an important

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W. Yamaguchi (✉) · M. Kawata
Department of Ecology and Evolutionary Biology,
Graduate School of Life Sciences, Tohoku University,
Aoba, Sendai, Miyagi 980-8578, Japan
e-mail: wakako-y@mail.tains.tohoku.ac.jp

M. Kondoh
Department of Environmental Solution Technology,
Faculty of Science and Technology, Ryukoku University,
Seta Oe-cho, Kyoto, Japan

determinant of the stability of food webs in nature (Solé and Montoya 2001; Neutel et al. 2002).

Flexibility in trophic interactions arising from the adaptation of organisms provides a potential explanation for the stability of complex food webs. It is known that adaptation is critical to food web dynamics (Abrams 2000). Adaptive changes in traits that affect prey–predator interaction strength have important effects on the relationship between food web complexity and stability. Kondoh (2003) constructed an adaptive dynamics model assuming adaptive foraging by consumers. In this model, consumers can change their food items optimally with sufficient rapidity, resulting in “flexibility” in the food web structure. This induces rapid food web reconstruction when a disturbance occurs and allows complex food webs with many potential resources to stabilize (Kondoh 2003).

One mechanism of such adaptive change is evolution. Recently, many studies have reported the genetic bases of traits that affect prey–predator interaction strength, as well as the evolution of such traits in several organisms (Filchak et al. 2000; Hawthorne and Via 2001; McBride 2007; Ohshima 2008). Theoretical studies of prey–predator systems have shown that adaptations in predator foraging strategies or prey defense strategies may affect prey–predator dynamics (Matsuda et al. 1996; Abrams 2000; Kondoh 2003; Yamauchi and Yamamura 2005). However, these studies did not assume explicit population genetics processes, such as adequate mutation rates, genetic drift, and mating. For example, Kondoh (2003) showed that a rapid adaptive shift in food items increased the stability of complex food webs, but he did not explicitly assume a genetic basis for the adaptive changes. The assumptions underlying adaptive dynamics did not consider appropriate evolutionary processes, and the conclusions based on adaptive dynamics are valid only under some conditions (Waxman and Gavrilets 2005). In several studies, quantitative genetic models have been used (e.g., Yamauchi and Yamamura 2005), but these models assumed fixed genetic variances and did not reproduce the patterns predicted by more mechanistic models that assumed explicit multilocus trait determination (Nuismer and Doebeli 2004). A number of recent studies have incorporated individual-based models or simulations of digital organisms to examine the evolution of complex food webs (e.g., Christensen et al. 2002; Anderson and Jensen 2005; Sevim and Rikvold 2005; Bell 2007; Laird and Jensen 2007; Rikvold 2007). These models included population genetics processes; however, most (e.g., Anderson and Jensen 2005; Sevim and Rikvold 2005; Bell 2007; Laird and Jensen 2007; Rikvold 2007) assumed asexual reproduction, in which the definitions of species are arbitrary and the change of gene frequencies within a species cannot be represented. Thus, there have been no theoretical studies on prey–predator food web evolution that

take into consideration appropriate population genetic processes. Appropriate evolutionary models should consider not only evolutionary changes through natural selection but also various constraints on adaptive changes (e.g., non-adaptive changes owing to genetic drift and the lack of genetic variations). These factors can be accounted for in explicit population genetic models.

The purpose of this study was to examine how evolution of prey use by predators affects community stability and whether complexity of the food web increases stability of the prey–predator system, using an individual-based model that assumes explicit population genetics processes for evolution of prey use. As an index of the stability of the prey–predator system, we measured the percentage of species that persisted for a given length of time. One of the goals of this paper was to determine whether the results of Kondoh (2003) are supported when explicit population genetics processes are assumed in the evolution of predator foraging. Thus, we followed the definitions of food web stability used in Kondoh (2003). In the present model, a locus determines the use of one food item for an individual predator; therefore, allele frequency change would lead to changes in the food web structure by varying the use of prey by predators. Using this model, the probability of the extinction of predator populations was simulated in food webs with various initial conditions for species richness and connectance. We also discuss factors that promote or disturb the stability of food web structures.

Model

Outline of the model

Consider a two-trophic-level food web comprising S species with the same number of predators and prey at the initial conditions. Over 2,000 generations, some species become extinct (i.e., the population size became zero) through interactions among the populations. The population dynamics of the predators and interactions between the prey and predators were simulated using an individual-based model, while the population dynamics of the prey were simulated using the Lotka–Volterra equation. Predator individuals each have a set of loci that determine whether or not they consume a prey species. Initially, all the individuals of a species consume the same diet, because the alleles at each locus are constant within a species. Over multiple generations, mutations on individual gametes can alter the food items of the offspring. When an allele resulting from a mutation increases in frequency to a certain level of the population, the diet of the species is assumed to change, resulting in addition or loss of food web links between species. The number of offspring produced by a predator increases with food consumption.

Thus, the allele frequency can increase if individuals having the allele have higher fitness due to greater food acquisition. However, simultaneously, genetic drift affects allele frequency, especially when the population size is small. In addition, the fate of a newly occurring mutation is influenced by genetic drift.

Construction of the initial food webs

In this study, the effects of the complexity of the food web (i.e., initial species richness and connectance) were examined. In the initial food webs, any given pair of predator and prey species was randomly connected with probability C , as follows: connectance $C = L/S^2$, where L is the realized number of links and $(S - 1)/S^2 \leq C \leq 0.25$. Food webs having species without any interactions or with multiple compartments were not included.

Population dynamics

Predators were defined as diploid hermaphrodites that reproduce sexually and whose generations do not overlap. The population size of predator species i at time $t + 1$, $P_i(t + 1)$, was calculated as the sum of the number of offspring. The number of offspring produced by a randomly chosen pair was based on the sum of the fitness of the two parents. Individual fitness was calculated as the number of prey the predator individual consumed multiplied by the conversion rate. Thus, the total number of offspring produced by the population was given by:

$$P_i(t + 1) = \sum_{k \in \text{individual}} e_i \sum_{j \in \text{prey}} f_{ij} a_{ikj} N_j(t)$$

where e_i is the conversion rate of predator species i , f_{ij} is the foraging efficiency of predator species i on prey species j , a_{ikj} is the foraging effort of individual k of predator species i allocated to prey species j , and $N_j(t)$ is the population size of prey species j at time t . The foraging efficiency f_{ij} was assumed to differ among prey species and was set to a uniform random number with average = f and range = f_r . a_{ikj} is the inverse of the number of prey species the individual k consumes, with $\sum_{j \in \text{prey}} a_{ikj} = 1$; e.g., if a predator consumes 3 prey species, $a_{ikj} = 0.333$.

The population size of prey species j at time $t + 1$ was determined by density-dependent growth and the number of prey consumed by predators. Thus, the number of individuals at time $t + 1$ was given by:

$$N_j(t + 1) = N_j(t) + r_j N_j(t) \left(1 - \frac{N_j(t)}{K} \right) - \sum_{i \in \text{predator}} \sum_{k \in \text{individual}} f_{ij} a_{ikj} N_j(t)$$

where r_j is the intrinsic growth rate of prey species j and K is the carrying capacity, which was assumed to be equal among prey species.

Prey consumption by predators

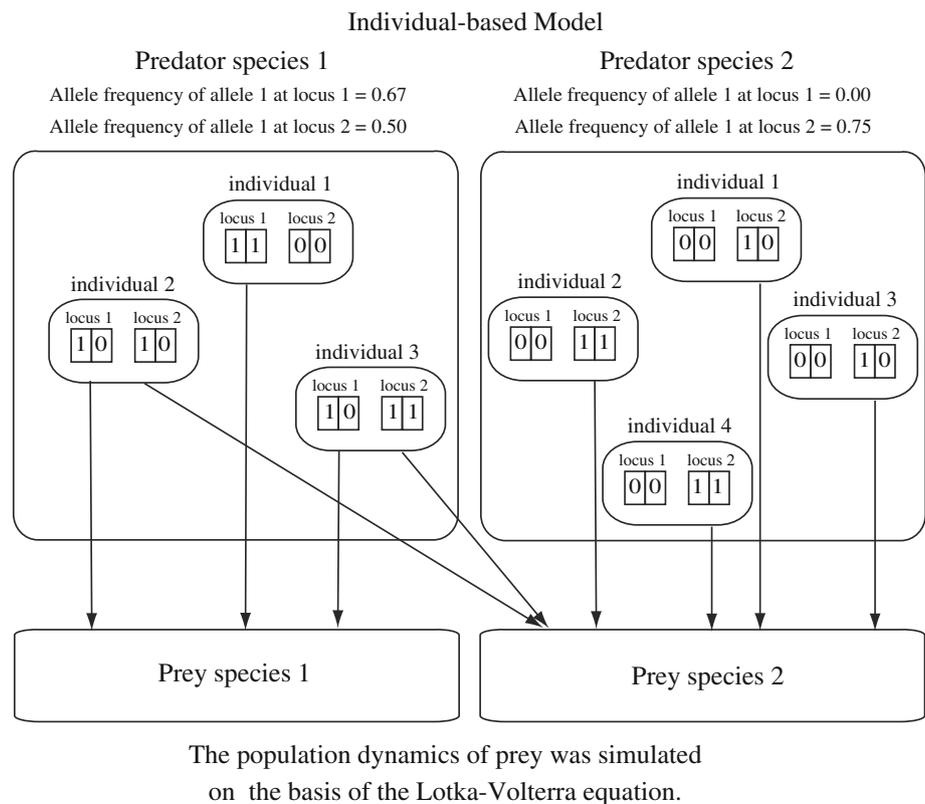
Whether or not each predator individual consumes a given prey species j was determined by a unique locus G_j . Thus, each predator initially had the same number of loci as the number of prey species. Each locus G_j had two alleles, 1 and 0. This assumption is not unrealistic when the genetic basis of the prey use of several organisms is considered. For example, the African finch *Pyrenestes* exhibits a polymorphism in bill size resulting from a single locus, and this polymorphism produces differences in diet and feeding performance (Smith 1993). In the leaf-mining moth *Acrocercops transecta*, a single-locus, two-allele system determines the ability of the larvae to use a host and the host preference of the ovipositing female (Ohshima 2008). We utilized two models with differing genetic assumptions, the dominant-loci model and the recessive-loci model. In the dominant-loci model, an individual with a genotype of either 11 or 10 at G_j consumes prey j ; in the recessive-loci model, only an individual with a genotype of 11 does so. Mutations were assumed to occur at a rate of μ , resulting in a change from allele 1 to 0 or allele 0 to 1, with the same probability.

To examine the effects of changes in linkage patterns on the extinction of species, we analyzed the addition or loss of links between predator and prey species. In the dominant-loci model, we considered that a link was added when the frequency of allele 1 at a locus increased from 0 to ≥ 0.1 and that a link was lost when the frequency decreased from 1.0 to < 0.1 . The value of 0.1 was rather arbitrary; however, we performed simulations applying different values, such as 0.05, and the same results were obtained. In the recessive-loci model, a link was added when the frequency of allele 1 at a locus increased from 0 to ≥ 0.43 , and a link was lost when the frequency decreased from 1.0 to < 0.43 . The value of 0.43 was used because the percentage of individuals that can consume the prey at this level in the recessive-loci model (p = allele 1 frequency at the locus = 0.43, p^2 = 0.19) is nearly the same as that in the dominant-loci model when 0.1 is used (q = allele 0 frequency at the locus, p = 0.1; percentage of individuals that can consume the prey = $p^2 + 2pq$ = 0.19). This portion of the model is shown in Fig. 1.

Colonization and settlement of the model community

Local communities often intermingle and may be initiated by species that randomly disperse into local communities (Holyoak et al. 2005). Considering this, we assumed that prey and predator species randomly colonized vacant habitat in the

Fig. 1 Schematic illustration of a two-predator–two-prey food web for the dominant-loci model. Predator species 1 and 2 have 3 and 4 individuals, respectively. The *arrow* indicates that a predator individual consumes a prey species. An individual predator with genotype 11 or 10 at locus 1 (or 2) consumes prey species 1 (or 2). In this example, links exist between predator species 1 and prey species 1 and 2, and between predator species 2 and prey species 2



initial stage of the model. Predator species may become extinct shortly after the introduction of new species because of the interactions produced by the combination of the introduced species and relatively rapid evolution of prey use. The settled species subsequently interact with each other and may become extinct due to evolution of prey use. Therefore, to detect the effects of evolution on stability of the food web (i.e., the percentage of species that survive), we focused on two stages of community dynamics: the colonization stage (0–500th generations) and the settlement stage (500–2,000th generations) (see also the “[Simulations and results](#)”).

We constructed three models. The first was a model in which the consumption of prey by predators evolved due to mutations (Evolution model), while the second was a model in which it did not because mutations did not occur (Non-Evolution model). The third was a model in which the Non-Evolution model changed to the Evolution model (Non-to-Evolution model). In this model, mutations were allowed after the 500th generation.

Stability of the prey-predator system

As an index of the stability of the prey–predator system, we measured the percentage of the species that persisted for a given time, as in Kondoh (2003). Considering the two stages of community formation, i.e., the colonization and settlement stages, our definition of stability is meaningful.

Examining stability during the colonization stage is important, because recent studies have proposed that diversity in local communities is largely influenced by dispersal from regional communities (e.g., Hubble 2001; Ricklefs 2007). During this stage, the definition of stability used in the present study is nearly the same as the percentage of species that become extinct after an invasion. The settlement stage reflects the situation where species in relatively isolated communities interact with each other, and their persistence depends on both prey–predator and competitive interactions and on evolution of prey use. In this case, our definition is similar to the probability that communities move toward a new equilibrium after pulse perturbation of evolution of prey use.

Table 1 summarizes the parameters used in our model. Parameter values were selected from the region near the center of the parameter space in which at least one predator species persisted for 2,000 generations.

Simulations and results

Effects of evolution of prey use on the complexity–stability relationship

To investigate the relationship between complexity (initial species richness and connectance) and stability in the prey–

Table 1 Symbols, definitions, and parameter values

Symbol	Definition	Value
S	Species richness	4, 6, or 8
C	Connectance	0–0.25
e_i	Conversion rate	0.2
f	Average of foraging efficiency	0.0001
f_r	Range of foraging efficiency	0.00004
μ	Mutation rate	10^{-5}
r_j	Intrinsic growth rate	2.0
K	Carrying capacity	100,000
$P_i(0)$	Initial predator population size	5,000
$N_j(0)$	Initial prey population size	50,000
h	Magnitude of the cost of generalization	0.1

predator system and the effects of evolution of prey use on this relationship, computer simulations were carried out for 2,000 generations for food webs with species richness $S = 4, 6,$ and 8 and all possible connectances. For food webs with a given species richness and connectance, links were randomly constructed, and simulations with the same complexity of food webs were repeated 70 times for both the Evolution model and the Non-Evolution model.

The stability (i.e., percentage of species that survived) decreased with increasing species richness and connectance in all of the models, regardless of the inclusion of evolution or genetic assumptions regarding prey use (Fig. 2a, b). The effects of evolution of prey use by predators on the stability of the food webs varied according to the genetic assumptions governing prey use. For the dominant-loci model, the stability of the Evolution model was significantly lower than that of the Non-Evolution model when the connectance was low, while differences in stability between the two models became nonsignificant when the connectance was high (Fig. 2a). On the other hand, for the recessive-loci model, significant negative effects of evolution on stability were observed only for high species richness and low connectance (Fig. 2b). At high connectance, stability increased slightly with evolution over time, although the effect was not significant (Fig. 2b). The same results were obtained when we used other parameter values for the conversion rate (e_i), the average and range of the foraging efficiency (f and f_r , respectively), intrinsic growth rate (r_j), carrying capacity (K), and initial predator and prey population size ($P_i(0)$ and $N_j(0)$, respectively) than those used in this simulation (Table 1) (data not shown).

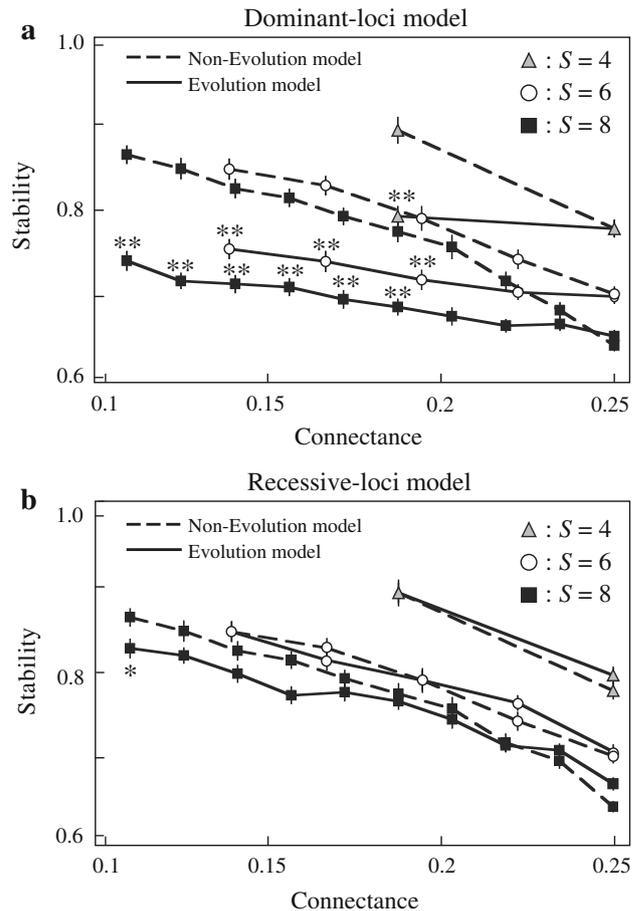


Fig. 2 The relationship between stability and species richness and connectance over 2,000 generations for the Non-Evolution model and the Evolution model. Seventy replicate simulations were used to measure stability. S indicates species richness at the initial conditions. Vertical lines indicate the standard error range. **a** Dominant-loci model; differences in stability between the Evolution model and the Non-Evolution model, GLM, family = binomial, link = logit: $P = 0.00137$ for $S = 4$ and $C = 0.188$; $P = 1.0$ for $S = 4$ and $C = 0.25$; $P < 0.001$ for $S = 6$ and $C = 0.139$; $P = 0.00202$ for $S = 6$ and $C = 0.167$; $P < 0.001$ for $S = 6$ and $C = 0.194$; $P = 0.217$ for $S = 6$ and $C = 0.222$; $P = 0.940$ for $S = 6$ and $C = 0.25$; $P < 0.001$ for $S = 8$ and $C < 0.186$; $P = 0.00291$ for $S = 8$ and $C = 0.203$; $P = 0.0608$ for $S = 8$ and $C = 0.219$; $P = 0.305$ for $S = 8$ and $C = 0.234$; $P = 0.707$ for $S = 8$ and $C = 0.25$. **b** Recessive-loci model; differences in stability between the Evolution model and the Non-Evolution model: $P = 1.0$ for $S = 4$ and $C = 0.188$; $P = 0.606$ for $S = 4$ and $C = 0.25$; $P = 1.0$ for $S = 6$ and $C = 0.139$; $P = 0.589$ for $S = 6$ and $C = 0.167$; $P = 0.193$ for $S = 6$ and $C = 0.194$; $P = 0.471$ for $S = 6$ and $C = 0.222$; $P = 0.880$ for $S = 6$ and $C = 0.25$; $P = 0.019$ for $S = 8$ and $C = 0.109$; $P = 0.199$ for $S = 8$ and $C = 0.125$; $P = 0.252$ for $S = 8$ and $C = 0.141$; $P = 0.0898$ for $S = 8$ and $C = 0.156$; $P = 0.513$ for $S = 8$ and $C = 0.172$; $P = 0.722$ for $S = 8$ and $C = 0.188$; $P = 0.629$ for $S = 8$ and $C = 0.203$; $P = 0.741$ for $S = 8$ and $C = 0.219$; $P = 0.647$ for $S = 8$ and $C = 0.234$; $P = 0.345$ for $S = 8$ and $C = 0.25$

Effects of evolution of prey use on species extinctions

During the colonization stage, food webs may not be static, as the persistence of populations may depend on the initial selection of randomly assembled species. However, during the settlement stage, extinction rarely occurred after the 500th generation in the Non-Evolution model (Fig. 3); thus, the food webs stabilized when evolution was not assumed. During the colonization stage, comparison of the Non-Evolution model and the Evolution model showed extinctions resulting both from evolution and from the compositions and linkages among species in the initial food webs. During the settlement stage, comparison between the Non-Evolution model and the Non-to-Evolution model were used to detect the effects of evolution. Simulations were performed for 2,000 generations for food webs with species richness $S = 8$ and connectance $C = 0.125$ or 0.234 , and repeated 100 times.

The effects of evolution on extinctions differed depending on the stage of community formation, initial connectance, and genetic assumptions (Fig. 3); the statistical results are shown in Table 2. The number of species rapidly decreased until the 500th generation (i.e., the colonization stage) and thereafter, zero or one species became extinct until the 1,000th generation (i.e., the early period of the settlement stage) (Fig. 3a, b). Figure 3a shows the change over time in the average number of species for the dominant-loci model. At low connectance ($C = 0.125$), the average number of extinct species in the models with evolution (Evolution model during the colonization stage and Non-to-Evolution model during the settlement stage) was significantly larger than that in the model without evolution (Non-Evolution model) during both the colonization and settlement stages (Fig. 3a; Table 2). At high connectance ($C = 0.234$), a significantly larger number of species became extinct when evolution was assumed than when evolution was not assumed during the settlement stage, but there was no significant difference during the colonization stage (Fig. 3a; Table 2).

Figure 3b shows the change over time in the average number of species in the recessive-loci model. At low connectance ($C = 0.125$), a larger number of extinct species was observed in the model with evolution than without evolution during the settlement stage, but this was not observed during the colonization stage (Table 2). At high connectance ($C = 0.234$), there was no significant difference in the number of extinct species between the models with and without evolution during either the settlement or colonization stage, although the average number of extinct species in the Non-Evolution model was slightly larger than that in the Evolution model in the colonization stage (Fig. 3b; Table 2).

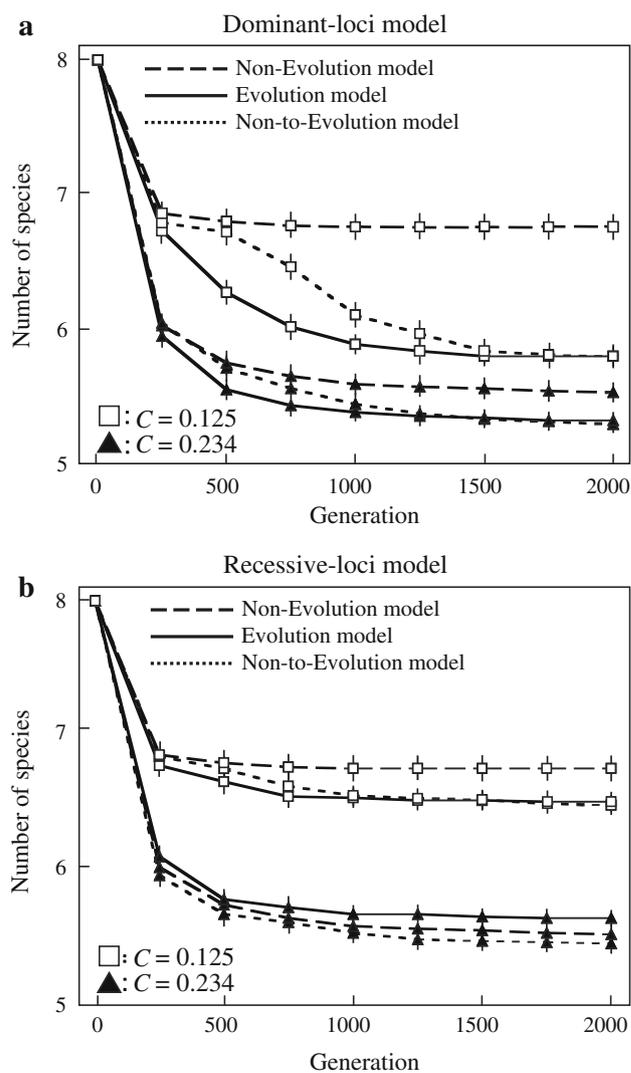


Fig. 3 Changes in the average number of species over 2,000 generations for the Evolution model, Non-Evolution model, and Non-to-Evolution model. **a** Dominant-loci model and **b** recessive-loci model. The simulations were conducted 100 times. The initial species richness was 8 and C indicates the initial connectance. Vertical lines indicate the standard error range

The effects of linkage changes in the food web on species extinctions during the settlement stage

The effects of evolution of prey use on species extinctions during the settlement stage were examined by comparison of the Non-to-Evolution model and the Evolution model. To examine the effects of changes in linkage patterns on the extinctions of species discussed above, the number of added and lost links between prey and predator species was counted during the 500–2,000th generations in the Non-to-Evolution model ($S = 8$, $C = 0.125$ or 0.234). The results of the simulation runs can be classified into four cases in which only link additions (A), only link losses (L),

Table 2 Summary of the effects of evolution on extinctions and their putative causes

	Colonization stage	Settlement stage
Dominant-loci model		
Low connectance ($C = 0.125$)	No. of extinct species	No. of extinct species
	Evolution model 1.74 Non-Evolution model 1.21 ($P = 0.007$) Putative causes: Link addition frequently occurred and caused extinction in the Evolution model (Fig. 5a)	Non-to-Evolution model 0.93 Non-Evolution model 0.04 ($P = 0.001$) Putative causes: Link addition frequently occurred and caused extinction in the Non-to-Evolution model (Fig. 4a)
High connectance ($C = 0.234$)	No. of extinct species	No. of extinct species
	Evolution model 2.47 Non-Evolution model 2.27 ($P = 0.151$) Putative causes: Infrequent link additions increased extinctions in the Evolution model, whereas the initial food web structure (Non-link-change food web) increased extinction in both the Evolution and Non-Evolution models (Fig. 5b)	Non-to-Evolution model 0.42 Non-Evolution model 0.22 ($P = 0.009$) Putative causes: Link addition caused extinction in the Non-to-Evolution model (Fig. 4b)
Recessive-loci model		
Low connectance ($C = 0.125$)	No. of extinct species	No. of extinct species
	Evolution model 1.35 Non-Evolution model 1.21 ($P = 0.255$) Putative causes: Link losses occurred at a high frequency and there were increased extinctions in the Evolution model, whereas the initial food web structure (Non-link-change food web) increased extinctions in both the Evolution and Non-Evolution models (Fig. 5c)	Non-to-Evolution model 0.27 Non-Evolution model 0.15 ($P < 0.001$) Putative causes: Link addition accompanied by link losses caused extinction in the Non-to-Evolution model (Fig. 4c)
High connectance ($C = 0.234$)	No. of extinct species	No. of extinct species
	Evolution model 2.23 Non-Evolution model 2.27 ($P = 0.956$) Putative causes: Link losses occurred at a high frequency and there were decreased extinctions in the Evolution model, whereas the initial food web structure (Non-link-change food web) increased extinctions in both the Evolution and Non-Evolution models (Fig. 5d)	Non-to-Evolution model 0.22 Non-Evolution model 0.22 ($P = 1.0$) Putative causes: Extinction occurred infrequently in both the Non-Evolution and Non-to-Evolution models (Fig. 4d)

The numbers of extinct species were compared between the Evolution and Non-Evolution models in the colonization stage, and between the Non-to-Evolution and Non-Evolution models in the settlement stage (Fig. 3a, b). Generalized Linear Models were used for the statistical comparison (family = binomial, link = logit)

both link additions and losses ($L + A$), or no link changes (N) were observed. The frequency of each case among 100 simulation runs was determined. The average number of extinct species was also determined for each case for these models and the Non-Evolution model.

For the dominant-loci model, most of the evolutionary changes were link additions (A) (Fig. 4a, b). Link additions (A) through evolution occurred more frequently at low connectance than that at high connectance (Fig. 4a, b). The average number of extinct species was larger for the simulation runs in which link additions (A) were observed than for those in which changes in the linkage pattern were not observed (N) (Fig. 4a, b; GLM, family = binomial, link = logit, $P = 0.020$ and $P < 0.001$, respectively).

In the recessive-loci model, most of the evolutionary changes were link losses (L) (Fig. 4c, d). There were no significant differences in the average number of extinct

species between the simulation runs in which link losses (L) were observed and those in which changes were not observed (N) (Fig. 4c, d; $P = 0.231$ and $P = 0.106$, respectively). At low connectance, the average number of species was significantly larger in the simulation runs in which both link additions and losses ($L + A$) were observed than in those in which changes were not observed (N) (Fig. 4c; $P = 0.0304$).

The effects of link changes and the initial structure of the food web on species extinctions during the colonization stage

Species extinctions during the colonization stage may be affected not only by the likelihood of changes in the linkage pattern but also the initial food web structure. Thus, the initial food webs were classified into structures in

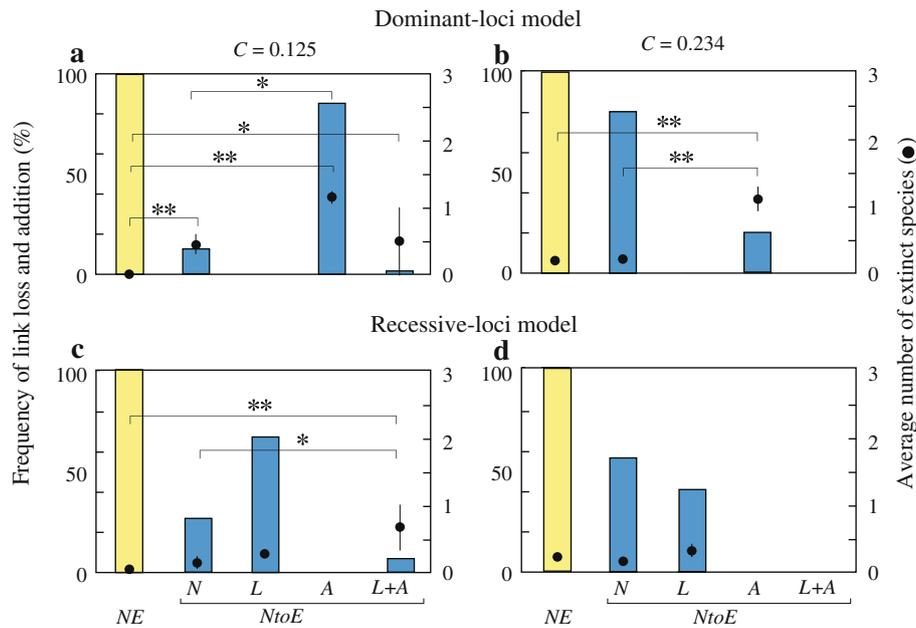


Fig. 4 The frequency (bars) and average number of extinct species (circles) for the Non-Evolution model (NE) and the Non-to-Evolution model (NtoE) during the settlement stage. For the Non-to-Evolution model, 100 simulations were conducted over 500 generations and each simulation result was classified into four cases of linkage change during the 500–2,000th generations (N no link changes, L link losses, A link additions, L + A link losses and additions); bars indicate the frequency of each case. The average numbers of extinct species (circles) were measured for each case. For the Non-Evolution model,

results for all 100 simulations showed no link changes, and thus, the average number of extinct species was calculated for the 100 replicates. **a** Dominant-loci model with initial species richness $S = 8$ and initial connectance $C = 0.125$, **b** dominant-loci model with initial species richness $S = 8$ and initial connectance $C = 0.234$, **c** recessive-loci model with $S = 8$ and $C = 0.125$, **d** recessive-loci model with $S = 8$ and $C = 0.234$. Vertical lines on the circles indicate the standard error range. $**P < 0.01$, $*P < 0.05$

which links were added or lost through evolution (Link-change-possible food web) and those in which the links did not change even in the model with evolution (Non-link-change food web), based on the results of the simulations for the Evolution model over 500 generations ($S = 8$ and $C = 0.125$ or 0.234). Link-change-possible food webs included three cases in which link losses (L), link additions (A) or both (L + A) occurred. The frequency of each case was determined among 300 simulation runs.

In the dominant-loci model, most of the evolutionary changes were link additions (A), as in the settlement stage (Fig. 5a, b). The average numbers of extinct species were compared between the Evolution model and the Non-Evolution model for the initial food webs in which link additions (A) were observed. The average number of extinct species in the Evolution model was larger than that in the Non-Evolution model in these food webs (Fig. 5a, b; GLM, family = binomial, link = logit, $P < 0.0001$ for $C = 0.125$ and $P = 0.00301$ for $C = 0.243$). However, the numbers of extinct species were similar between the Evolution model and the Non-Evolution model using the Non-link-change food webs (Fig. 5a, b; $P = 0.836$ for $C = 0.125$ and $P = 0.890$ for $C = 0.243$). For the Non-Evolution model, the number of extinct species was higher

for the Non-link-change food webs than for the Link-change-possible food webs (A) (Fig. 5a, b; $P = 0.004$ for $C = 0.125$ and $P = 0.000283$ for $C = 0.234$). These results indicate that extinction was more likely to occur in the Non-link-change food webs than in the Link-change-possible food webs (A) when evolution was not assumed. Thus, both the initial food web structure and link addition through evolution caused extinction during the colonization stage in the dominant-loci model.

In the recessive-loci model, most of the evolutionary changes were link losses (L), as in the settlement stage (Fig. 5c, d). The average number of extinct species for the Evolution model was larger than for the Non-Evolution model in the Link-change-possible food webs (L) at low connectance (Fig. 5c; $P = 0.0162$), while it was smaller for the Evolution model than for the Non-Evolution model in the Link-change-possible food webs (L) at high connectance (Fig. 5d; $P = 0.0133$). The average number of extinct species did not differ between the Evolution model and the Non-Evolution model in the Non-link-change food webs (Fig. 5c, d; $P = 0.771$ at low connectance and $P = 0.957$ at high connectance, respectively). For the Non-Evolution model, the number of extinct species was larger in the Non-link-change food webs than in the Link-change-

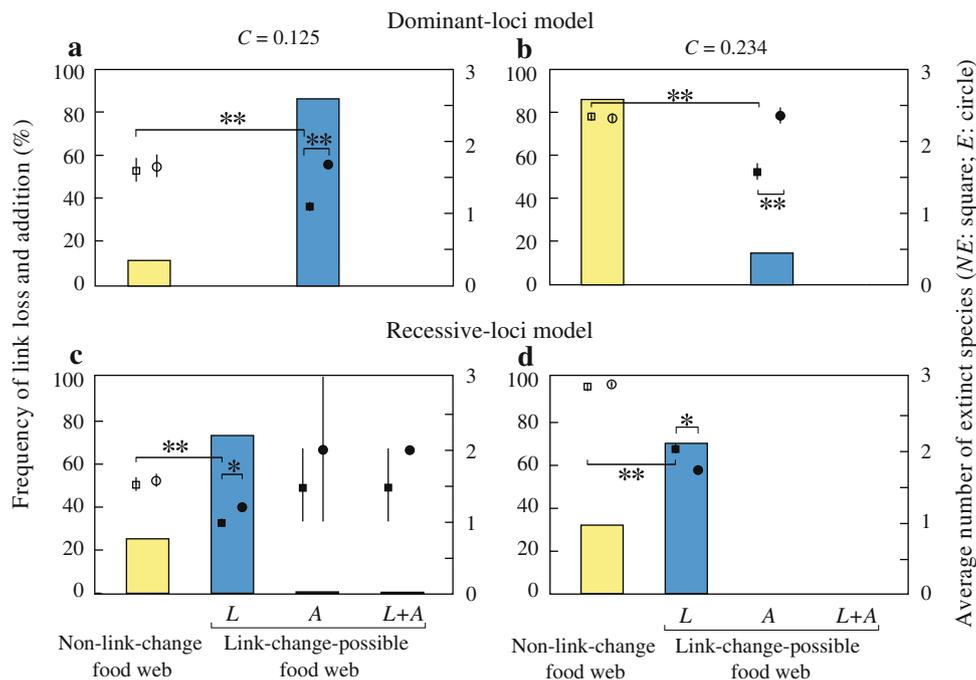


Fig. 5 The frequencies (*bars*) and average numbers of extinct species (*circles* and *squares*) of various initial food web structures during the colonization stage. For the Evolution model, 300 simulations using randomly constructed food webs were conducted over 500 generations and then the initial food webs were classified into four cases according to the results of linkage changes: Non-link-change food web; Link-change-possible food web: link losses (*L*); Link-change-possible food web: link additions (*A*); and Link-change-possible food web: link losses and additions (*L + A*). *Bars* indicate the frequency of each case. The average number of extinct species was calculated for

the simulation runs for each case (*circles*). Simulations for the Non-Evolution model were also conducted using initial food webs that were classified in the same manner, and the average number of extinct species was calculated for each case (*squares*). **a** Dominant-loci model with initial species richness $S = 8$ and initial connectance $C = 0.125$ or 0.234 , **b** dominant-loci model with initial species richness $S = 8$ and initial connectance $C = 0.234$, **c** recessive-loci model with $S = 8$ and $C = 0.125$, and **d** recessive-loci model with $S = 8$ and $C = 0.234$. *Vertical lines* on the *circles* or *squares* indicate the standard error range. ** $P < 0.01$, * $P < 0.05$

possible food webs (*L*) (Fig. 5c, d; $P < 0.0001$ at both low and high connectance). These results indicate that in the recessive-loci model, link losses through evolution reduced the extinction rate at high connectance while increasing the extinction rate at low connectance. In addition, like the dominant-loci model, extinction was more likely to occur when the initial food web was a Non-link-change. Thus, these results indicate that both the initial food web structure and link change through evolution affected extinction in the recessive-loci model.

To examine the structural characteristics of linkage patterns in the initial food web with respect to the extinction rate, the relationship between the variance in the number of links per predator species (one of the structural characteristics of food webs) and the average number of extinct species during the colonization stage was examined for the Non-Evolution model ($S = 8$, $C = 0.125$, dominant-loci model; Fig. 6a). In addition, the variance in the number of links per predator species was evaluated for both the Non-link-change food webs and the Link-change-possible food webs (Fig. 6b).

The number of extinct species during the colonization stage increased with the initial variance in links per predator species (Fig. 6a; GLM, family = binomial, link = logit, $P = 0.00434$). There were differences in the variances in the number of links per predator species between the Non-link-change food webs and the Link-change-possible food webs (Fig. 6b; $\chi^2 = 82.1696$, $df = 3$, $P < 0.0001$). The results indicated that the number of extinct species was lower in the Link-change-possible food webs for the Non-Evolution model, because these food webs had structures in which the variances in the number of links per predator species were low (i.e., variance = 0.5), while the Non-link-change food webs had structures in which the variances were high (i.e., variance = 1.5) (Fig. 6b).

Effects of evolution with a high mutation rate on the complexity–stability relationship

To examine the effects of mutation rates, simulations were conducted at varying mutation rates ($\mu = 10^{-5}$, 10^{-4} , and

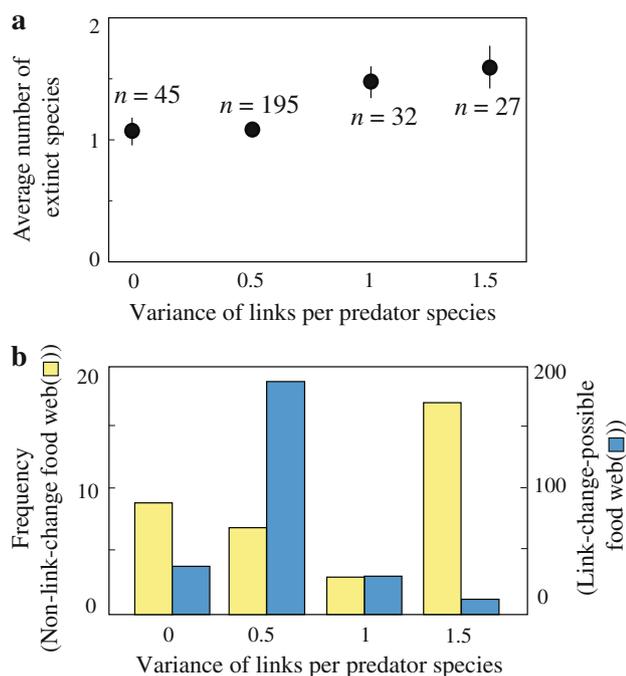


Fig. 6 The structural characteristics of linkage patterns in the initial food web with respect to the extinction rate. The initial species richness was $S = 8$ and the initial connectance was $C = 0.125$ for the dominant-loci model. **a** The relationship between the average number of extinct species during the colonization stage for the Non-Evolution model and the variance in links per predator species of the initial food webs. Vertical lines indicate the standard error range, and the number of replicates is represented by n . **b** Frequency distributions of the variance in links per predator species for the Non-link-change food webs and the Link-change-possible food webs. The number of replicates was 300

10^{-3}) with species richness $S = 4, 6,$ and 8 using the dominant-loci model. Stability increased with increasing mutation rate in the Evolution model, especially at high connectance (Fig. 7a–c). Stabilities were higher in the Evolution model than in the Non-Evolution model at high connectance (Fig. 7a–c), because link losses preventing extinctions occurred more frequently during the colonization stage at high mutation rates ($\mu = 10^{-3}$, $S = 8$, $C = 0.234$; Fig. 7d). However, the trend of stability decreasing with increasing species richness and connectance did not change even at high mutation rates (Fig. 7a–c).

Discussion

The results of this study demonstrate that the stability of food webs (i.e., the percentage of species that persist) decreases with increasing complexity (species richness and connectance) and that the effects of evolution of prey use by predators on stability depends on assumptions regarding

genetic control of prey use. In the dominant-loci model, evolution of prey use resulted in extinctions, especially at low connectance. On the other hand, in the recessive-loci model, the effect of evolution was not significant under most conditions, and at high connectance, evolution slightly increased stability, although the effect was not statistically significant. Large mutation rates ($\mu = 10^{-3}$) increased stability at high connectance through evolution, but this did not lead to a positive relationship between stability and food web complexity.

Increasing or decreasing rates of extinction of predators resulted from link addition or link loss through evolution of the predator's prey use (Table 2). In the dominant-loci model, more species became extinct when link addition occurred, both during the settlement stage and the colonization stage. However, link additions occurred more frequently at low connectance. Thus, evolution of prey use increased species extinctions with decreasing connectance in the dominant-loci model. On the other hand, in the recessive-loci model, most of the evolutionary changes were link losses during the settlement stage, which did not greatly affect species extinctions, while infrequent occurrences of link additions accompanied by link losses increased species extinctions at low connectance. During the colonization stage, link losses increased the extinction rate at low connectance, while they decreased the extinction rate at high connectance. Thus, the effect of evolution of prey use on species extinctions decreased with increasing connectance in the recessive-loci model. However, the numbers of extinct species did not differ between the Evolution and Non-Evolution models during the colonization stage, except with low connectance in the dominant-loci model, because many of the extinctions during the colonization stage were due to the initial food web structure.

Link addition suggests that species evolve to use a new food item (i.e., individuals that can use a new food item increase in frequency). This leads to competitive exclusion of other predator species that use the same food item as the evolved predator. On the other hand, link losses have variable effects on species extinctions. Link losses indicate that species have evolved in such a manner that they do not use previously utilized food items. This may reduce the number of species that use the same food items, leading to a decrease in the probability of extinction if interspecific competition is strong. In other cases, a link loss for a species might lead to increasing foraging effort for the remaining linked food items, which may cause the extinction of other species that eat those foods. In addition, if the costs of generalization are considered, the number of extinct species decreases through evolution (see Electronic Supplementary Material). These results indicate that evolution toward generalization in prey use increases

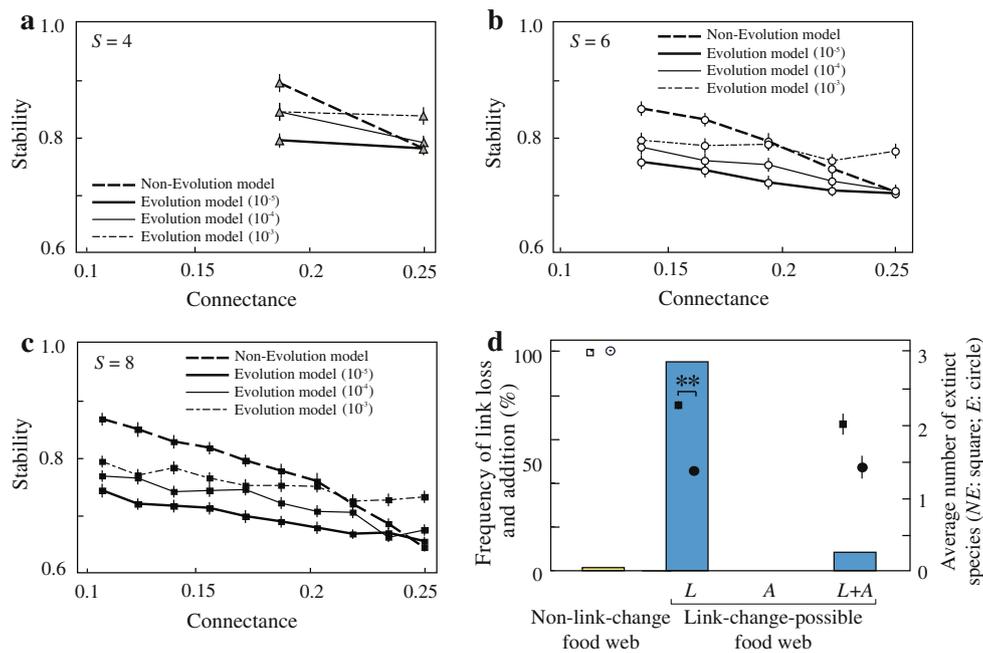


Fig. 7 The relationship between stability and species richness and connectance over 2000 generations for the Non-Evolution model and the Evolution model with varying mutation rates $\mu = 10^{-5}$ (a), 10^{-4} (b), and 10^{-3} (c) for the dominant-loci model. Seventy replicate simulations were used to measure stability. Vertical lines indicate the standard error range. **d** The frequencies (bars) and average numbers of extinct species (circles and squares) at a high mutation rate ($\mu = 10^{-3}$) for various initial food web structures with $S = 8$ and $C = 0.234$. Calculations of the frequency and the average number of

extinct species for the various initial food web structures were the same as in Fig. 5. The initial food webs were classified into four cases according to the results of linkage changes: Non-link-change food web; Link-change-possible food web: link losses (L); Link-change-possible food web: link additions (A); and Link-change-possible food web: link losses and additions (L + A). Bars indicate the frequencies for each case. Circles and squares indicate the average numbers of extinct species for each case for the Evolution model (E) and the Non-Evolution model (NE), respectively. $**P < 0.01$, $*P < 0.05$

extinction of predators, while evolution toward specialization can either increase or decrease extinction of predators.

Kondoh (2003) showed that adaptive foraging by consumers with sufficiently rapid prey changes induces rapid food web reconstruction when disturbances occur, and this stabilizes complex food webs. Thus, adaptive foraging could explain complex food webs that support large numbers of interacting species. However, in the present study, when prey use by predators was assumed to evolve through allele frequency changes, a positive relationship between food web complexity and stability was not achieved. Evolution of prey use in our model may represent slower foraging adaptation and thus, use of our model assuming more rapid evolution might support the prediction by Kondoh (2003). To consider this, we conducted simulations with larger mutation rates ($\mu = 10^{-3}$ and 10^{-4}) and the results showed that stability increased with increasing mutation rates. Larger mutation rates result in genetic variation within populations, which may facilitate more rapid evolution (link loss) to avoid extinction of the species. However, even at these larger mutation rates, a positive complexity–stability relationship was not achieved.

This may be because even with large genetic variation, it takes tens of generations for a substantial percentage of the individuals within a population to evolve to changing food items. In addition, a new mutant is likely to disappear through genetic drift even when the fitness of the mutant is high. Therefore, in field populations, several factors, such as insufficient sources of genetic variation, genetic drift, and genetic control of phenotypes, constrain optimal adaptive evolution. These results suggest that the rapid adaptive foraging shifts assumed in Kondoh (2003) could be realized through nonevolutionary processes such as plasticity within a generation for prey use by predators (Agrawal 2001; Egas and Sabelis 2001), but not through evolution of genetic traits.

Here, the stability of the prey–predator system was defined as the percentage of species that persisted for a given length of time. Using this definition, we can consider that if the large food webs can be observed, these food webs would be stable because a large portion of species can persist. In nature, ecosystems often support a large number of species (e.g., Winemiller et al. 2001; Pascual and Dunne 2006; Banasek-Richter et al. 2009), indicating that many large food webs might be stable. Thus, our results indicated

that real prey–predator food webs might be stabilized by factors other than evolution.

Mechanisms of extinction related to evolution of prey use differ with the stage of community formation (i.e., the colonization and settlement stages). During the colonization stage, the occurrence of extinctions may be affected by link addition through evolution of immigrants and the variance in links per predator species in the food web structure even when connectance is constant. In addition, rapid evolution resulting in link losses during the colonization stage after immigration can promote or prevent the extinction of predators. Several studies have shown that adaptive evolution of immigrants enabled them to colonize new habitats (Mooney and Cleland 2001; Reznick and Ghalambor 2001; Lambrinos 2004). The present results suggest that evolution of immigrant predators may increase or decrease species extinctions depending on the connectance of the food web and genetic constraints on prey use. Furthermore, a structural property of the food webs (larger variance in links per predator species) resulted in a larger probability of extinction of predators and also a low probability of link changes through evolution. Previous studies have investigated characteristics of actual food webs, such as link strengths, degree of distribution, nestedness, and compartments (Solé and Montoya 2001; Montoya and Solé 2002; Neutel et al. 2002; Krause et al. 2003; Emmerson and Raffaelli 2004; Memmott et al. 2004; Bascompte et al. 2006; Montoya et al. 2006). The results of the present study suggest that variance in the number of prey species per predator species is also an important structural property that affects the stability of food webs. In addition, during the settlement stage, further extinctions occurred due to link addition through evolution. Previous models that did not consider evolution have examined attractors that can be stable or unstable. However, evolution of prey–predator interactions can alter the stability of systems after the system reaches a stable point. Therefore, evolutionary changes should be considered when the stability of systems is examined.

The present study examining food web dynamics using explicit population genetics models indicates that evolution of food use by predators does not necessarily promote population persistence. Because a shift in food items through optimal foraging behavior can stabilize complex food webs (Kondoh 2003), our results suggest that evolution through population genetics processes often involves constraints on optimal adaptation. To evaluate more realistic evolutionary processes, our model is useful in that individuals have concrete traits relating to prey–predator interactions determined on an explicitly genetic basis, and through which evolution occurs through changes in allele frequencies driven by processes within populations. Our model can include constraints on adaptation, which are

important evolutionary factors many adaptive models have not included. Previous theoretical studies (Matsuda et al. 1996; Abrams 2000; Yamauchi and Yamamura 2005; Fussmann et al. 2007; Johnson and Stinchcombe 2007; Kinnison and Hairston 2007) have indicated that evolution of traits affecting fitness should be considered in ecological prey–predator community dynamics. However, previous studies using adaptive dynamics models or quantitative genetics models have not incorporated explicit population genetic processes. Adaptive dynamics models define evolution as the fixation of advantageous mutations (Waxman and Gavrillets 2005), and quantitative genetic models often assume fixed genetic variances. These assumptions facilitate rapid adaptive evolution and fail to consider more adequate evolutionary constraints. Some evolutionary food web models have described speciation and extinction processes (e.g., Caldarelli et al. 1998; Drossel et al. 2001, 2004; Quince et al. 2005; Rossberg et al. 2008), but did not assume evolutionary processes within the population. A number of recent studies have used individual-based models or simulations of digital organisms to examine the evolution of complex food webs (e.g., Christensen et al. 2002; Anderson and Jensen 2005; Sevim and Rikvold 2005; Bell 2007; Laird and Jensen 2007; Rikvold 2007). These models incorporated population genetics processes, but most of the models (e.g., Anderson and Jensen 2005; Sevim and Rikvold 2005; Bell 2007; Laird and Jensen 2007; Rikvold 2007) assumed asexual reproduction, and thus could not represent sexually reproducing species whose gene frequencies change via population genetics processes. Other models constructed using sexually reproducing organisms often included inadequate assumptions regarding genetic control of traits, species definitions, individual interactions, and high mutation rates. For instance, certain assumptions relating to genetic control of traits and high mutation rates result in predictions of highly evolvable systems, which in turn lead to unrealistically rapid evolution of food webs.

Although the present models incorporate explicit evolutionary processes, the resulting predictions depend on the mode of genetic control of resource use phenotypes. Indeed, evolutionary outcomes are influenced by genetic control of phenotypes (e.g., Kawata et al. 2007), although previous ecological evolutionary models have focused on modes of selection in abiotic and biotic environments. There may be no single general relationship between genomic codes and resource use phenotypes. To provide more general predictions using these models, detailed information on genetic control mechanisms of resource use phenotypes in diverse organisms is needed. The present models also include some simplifying assumptions, and future studies will be needed using models that modify these assumptions. First, we have assumed food webs with

two trophic levels. The relationship between food web complexity and stability has been discussed for various food webs, including competitive systems (Ives et al. 1999; Kokkoris et al. 2002), two trophic level systems (Thébault and Loreau 2005), and complex food web networks (May 1972; Dunne et al. 2002; Brose et al. 2003; Jansen and Kokkoris 2003; Kondoh 2003; Garcia-Domingo and Saldana 2007; Uchida and Drossel 2007). The number of trophic levels has been shown to affect ecosystem function (Duffy et al. 2005). To confirm the results of this study, we should consider not only species richness within a trophic level (horizontal diversity) but the number of trophic levels (vertical diversity) and the interactions between them (Duffy et al. 2007). Second, in the present model, all potential food items were assumed to be equally available for predators; however, consumers often choose different food items with unequal probabilities. For instance, there might be trade-offs among different food items such that consumers that use a food item incur a cost for using an alternative item (Bolnick 2001; Hawthorne and Via 2001; Rana et al. 2002). The spatial distribution of food items also involves trade-offs (Funk and Bernays 2001). In the present study, an increase in the number of food items that predators use increases the extinction rate of predators in the food web. It is important to examine whether the evolution of new prey utilization by predators increases extinction rates even when various factors affecting food availability and trade-offs among food items are considered. Third, the present model assumes evolution of food use by the predator but not evolution of prey traits such as predatory defense ability. One of the aims of this paper was to determine whether the results of Kondoh (2003) could be obtained even when explicit population genetics processes were assumed for evolution of predator foraging. Thus, our study focused on the effects of evolution of predators on the stability of food webs. However, coevolution between predators' prey use and prey defensive traits is certainly important, and several studies have shown that coevolution can affect the stability of the system (Abrams 2000). Evolution of the defensive traits of prey should be considered in future studies.

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