Theoretical investigation of the eco-evolutionary dynamics of food webs

食物網の進化生態学的動態に対する理論的研究

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Contents

Chapter 1. General introduction

The emergence and maintenance processes of a species-rich community are two of the central questions of the ecology. A lot of species coexist in a natural community and interact each other with various relationships (e.g., mutualism, competition, and predation), which results in a variety of structural properties of a community. One of the significant structures is a food web, which is a network of species linked by trophic interactions based on "who eats whom". Empirical observations have revealed that natural food webs sometimes represent huge complexity (Bascompte *et al*., 2005; Martinez, 1991; Winemiller, 1990). Because a consumer species cannot survive if the community lacks its prey species, a food web describes the dependence among members of the community.

All food webs are supported by producers, e.g., plant species. The coexistence of many plant species in a community suggests a wide range of diverse interactions among plants and between plants and consumers in the community. For example, the larger diversity of plant community will provide more diverse types of resources for herbivores allowing coexistence of diverse herbivore species. The same mechanism will be true for the higher-trophic-level species. The diversity of their food resources, i.e., other animal species, control predator diversity. Therefore, the diversity of plants has naturally been considered a key determinant of the diversity of herbivores and also the diversity of the whole community (Murdoch *et al*., 1972; Southwood *et al*., 1979; Haddad *et al*., 2001). However, unlike chemical or physical resources, organisms can evolve and change their characteristics. A heavily-attacked plant can evolve to defend itself from the foraging pressure. In turn, herbivores can evolutionarily develop their ability to keep up with the defense of host plants, or just switch their target to other resources. Therefore, the evolution of those species is essential to understand the emergence and maintenance of the diversity in the community.

Plants are key elements in a food web with potential influence on any species in the food web via ecological processes, evolution of which can affect the structure of a whole community significantly. Recently, the dynamic interactions between ecological and evolutionary processes are a growing area of research (reviewed by Facon *et al*., 2006; Fussman *et al*., 2007; Pelletier *et al*., 2009; Post & Palkovacs, 2009). Abrams (2000) theoretically indicated that coevolution between prey and predator tend to destabilize their population dynamics, suggesting that the evolution of plant–herbivore interaction can influence community stability. It is also empirically indicated that the coevolution and co-diversification of herbivores and plant's defensive traits result in the strong top-down selection pressure to increase plant diversity (Mitter *et al*., 1991; Farrell & Mitter, 1994; Leimu *et al*., 2012). Similarly, in higher trophic levels, empirical studies have revealed that a prey species coevolves with its predator species (Downes & Shine, 1998; Heiling & Herberstein, 2004; reviewed by Abrams, 2000), suggesting that the evolution of a species in a food web mutually depends on the evolution of other species. Therefore, simultaneous investigation of evolutionary and ecological processes of whole community is important to understand the dynamics of a community. To understand the emergence and maintenance mechanisms of diversity of a community, the study of the community-wide processes of eco-evolutionary dynamics including adaptation, speciation and extinction are needed.

Ecological and evolutionary dynamics had been considered as processes with different time scales so that previous studies tended to investigate those two dynamics separately. This consideration would be justified because those documented adaptive diversifications take millions of years (e.g., adaptive radiation of cichlids, Turner, 2007). However, recent studies have indicated that the selection pressure, including the trophic interaction, can dynamically induce trait displacement within a few tens of generations (Yoshida *et al*., 2003; Grant & Grant, 2002). The trait displacement dynamically alters the interaction between those evolving species, as a consequence, population dynamics

of these species also affected by the evolution. This coincidence of the evolutionary and population dynamics time scales is called as a rapid evolution, which attracts growing interests recently (Yoshida *et al*., 2003; reviewed at Jones *et al*., 2009). Theoretical models also indicated that the coincidence of time scales of evolutionary and ecological processes results in the novel dynamics controlled by the feedback among eco-evolutionary processes (Hairston *et al*., 2005; Laland *et al*., 1999; Post & Palkovacs, 2009). In the following sections, I review a brief history of theoretical studies about food webs to indicate current theoretical questions about the diverse community.

Population dynamics models of the food web and stability

Theoretical studies of the diverse communities are initiated by focusing on conditions for stable maintenance of a community that consists of species interacting with each other, which was a pioneered by May (1972). He revealed that a community consists of many species tends to be unstable. The ecological theories of food webs subsequently have indicated that the large number of species in a food web will destabilize the food web (Pimm, 1984; Pimm & Lawton, 1978). These classical studies suggest the size of food webs must be small. Kondoh (2003, 2006, 2007) introduced the behavioral adaptation of trophic interactions, i.e., an organism can optimize its resource items for each moment, to the complexity–stability debate, and indicated the appearance of positive relationships between food-web complexity and stability. These studies suggested that the dynamics of trophic interactions between species, in addition to the population dynamics, has significant effects on the community dynamics. Therefore, the dynamics of "who eats whom" interaction is crucial for understanding how natural communities emerge and persist. His studies successfully combined dynamical change of the trophic interaction between species and population dynamics of those species.

Those models contribute to understand characteristics of a community, although they mainly focus on stability of the community with ignoring the

establishment process of it. In order to understand both maintenance and emergence processes of community, evolutionary approach should be incorporated to the community dynamic model.

Evolutionary dynamics of a food web

Similar to behavioral adaptation, adaptive evolution dynamically rearranges interactions between species. However, the evolution requires some generations to take effect, while an organism can adapt its behavior in a single generation. Therefore, evolutionary effect will be delayed. Abrams (2000) reviewed both theoretical and empirical studies about effects of evolutionary determined-interspecific interactions on stability of trophic systems (i.e., prey–predator interactions) with few species. He pointed out the tendency that the evolution of a predator stabilizes the prey–predator dynamics, while the prey evolution can sometimes destabilize the dynamics. Therefore, the eco-evolutionary process, e.g., prey–predator interaction determined by evolving traits of each prey and predator pair in a community, will ultimately alter the fate of the entire community in the evolutionary time-scale. However, those models considered the coevolutionary dynamics between a few species only. To clarify community-scale dynamics, instead of extrapolating from the results of simple models, we need to investigate a model that can consider whole communities at once.

Rossberg *et al*. (2006) proposed a theoretical model that involves a speciation–extinction process and ecological dependencies between species (but did not explicitly involve population dynamic). They investigated the emergence of food web based on evolving traits that determine the trophic interactions among species. They assumed two groups of traits, foraging traits (i.e., traits that determine its foraging ability) and vulnerability traits (i.e., traits that determine its defensive strategy). The matching of foraging traits of one species (species A) and vulnerability traits of the other species (species B) represents species A is well adapted to exploit species B,

therefore, the model was named the matching model (Rossgerg *et al*., 2006). With estimated parameters, resultant food webs fit well with empirically observed food webs (Rossberg *et al*., 2006). However, it still lacks population dynamics, therefore, it is not possible to investigate the ecological processes and mechanisms that drives speciation and extinction. The eco-evolutionary processes might be common and have an important role in the natural ecosystem (Pelletier *et al*., 2009; Post & Palkovacs, 2009). Therefore, to elucidate the evolutionary dynamics, in particular the evolutionary emergence of a food web, we need to pay attention to the eco-evolutionary process behind the system.

Eco-evolutionary models but different time-scales between ecology and evolution

Adaptive evolution is in fact driven by the population dynamics of a species. To describe evolutionary dynamics, e.g., extinction and speciation, from population dynamics that may be controlled by evolutionary determined trophic interactions, theoretical models need to include details of evolution and ecological interactions. The webworld model (Caldarelli *et al*., 1998; Drossel *et al*., 2001, 2004), the niche model (Alhoff & Drossel, 2013; Guill & Drossel, 2008; Ingram *et al*., 2009; Loeuille & Loreau, 2005, 2006; Williams & Martinez, 2000), and extended version of the matching model (Rossberg *et al*., 2008) are major model frameworks that contribute both evolutionary and population dynamics. By using prey–predator equations of which coefficients were evolutionarily determined, these models connected population dynamics and evolutionary dynamics in a community.

Above models revealed the eco-evolutionary emergence of a food web with multiple trophic levels and the complex dynamics of the evolved food web. Those models also indicated the complex evolutionary dynamics of a community, e.g., intermittent large decline of species richness (Alhoff & Drossel, 2013; Guill & Drossel, 2008; Rossberg *et al*., 2008). However, the detailed eco-evolutionary processes and the

mechanism of observed dynamics are still not well investigated. Those models assumed that species is a unit of the evolution. The evolutionary dynamics is described by speciation and extinction of a species after the population dynamics reaches some stationary state. This assumption separates eco-evolutionary dynamics into two different time scales, i.e., implying that the evolution is much slower than the population dynamics. Therefore, the evolutionary and population dynamics are still not fully integrated.

Eco-evolutionary models with merged evolutionary- and ecological-time scales

On the contrary to the above species-based models, two categories of models are proposed that involve interactions among individuals. Both models treated speciation and extinction in a community as a consequence of accumulated mutations and selection pressure from inter-specific interactions. One of them is an individual-based model that is called as tangled-nature model (Christensen *et al*., 2002; Sevim & Rikvold, 2005; Rikvold, 2007, 2009; Rikvold & Sevim, 2007) and the other is Ito-Ikegami model based on the density distribution on the trait space (Ito & Ikegami, 2006; Ito *et al*., 2009).

The tangled-nature model (Christensen *et al*., 2002; Sevim & Rikvold, 2005; Rikvold, 2007, 2009; Rikvold & Sevim, 2007) adopts an individual-based approach to unify the population dynamics and the evolutionary dynamics in a community. Unlike theoretical models of which dynamics is based on species, every individual has its trait values that determine the trophic interactions among individuals. Population dynamics is based on the stochastic production of offspring at the each end of the generation, and the production of a mutated offspring is considered as a speciation. Rikvold (2009) showed that the community without the adaptive foraging flips back and forth between an evolutionary active phase with high diversity of consumers and quiet phase with very small population of consumers. The tangled-nature models successfully merged two

time scales. However, those models assumed that a mutation can alter all of the trophic interactions from its parent species, which is a relatively coarse grained approximation to represent a speciation as a consequence of evolutionary process.

Ito & Ikegami (2006) and Ito *et al*. (2009) proposed another theoretical models that intended to represent evolutionary and population dynamics simultaneously. They modeled a trait composition of a community by a density distribution on the continuous-trophic-trait space. The dynamics of the distribution represents both ecological and evolutionary dynamics of a community simultaneously, where mutations were represented by diffusion. They found the trait distribution of a community evolves to be several clusters in the trait space, which could be regarded as the evolutionary emergence of species. However, their numerical analysis is restricted to the evolutionary dynamics on one-dimensional-niche space. In a real community, a combination of many different traits may determine the trophic interactions among species. Therefore, a model that can investigate multiple-dimensional niche space is needed. Also, their model does not incorporate any stochasticity in its dynamics. Since even a small stochasticity can result in different outcomes from what are expected from deterministic models (May, 1973), the effect of stochasticity on the community dynamics should be included into the model.

Fluctuation of species richness observed in evolutionary-food-web models

In the above sections, I review a history of food web models, each of which focuses on various aspects and characteristics of a community. Despite of variation, those models indicated a similar properties, i.e., a large fluctuation of species richness and intermittent avalanches of speciation and extinction (Alhoff & Drossel 2013; Christensen *et al*., 2002; Guill & Drossel, 2008; Ito & Ikegami, 2006; Rossberg *et al*., 2008; Rikvold, 2007, 2009; Rikvold & Sevim, 2007; Sevim & Rikvold, 2005), indicating that a community can suddenly reorganize itself by the evolutionary change

of trophic interactions. The fluctuation is a common feature of multiple theoretical food-web models with different assumptions, so that it could be some universal feature of food-web evolution. These fluctuations can be interpreted as a process of the burst of speciation or the successive extinctions, which will be a key factor to understand the causality of emergence and maintenance of a food web in natural environments. Therefore, we need to understand the process and mechanism of those fluctuating dynamics from an ecological viewpoint.

Using a theoretical model, Rikvold (2009) found a sudden transition between two states: a community with multiple trophic levels and a community with only producer species. Although this study suggested that the emergence of intraguild predation could initiate successive consumer extinction in the diverged community, it did not provide an explanation of the mechanisms that would quickly remove almost all consumer species from a community. Using a niche model, Alhoff & Drossel (2013) observed sudden extinction of all consumer species when all the niche traits, i.e., body mass (niche position), width of food range, and prey–predator-body-mass difference, can evolve. They found the dominance of specialist herbivores before the extinction, and concluded that the eventual extinction of those specialists causes community collapse. However, it cannot explain the reason for sharp decline of species richness after some period of plateau.

So far, however, no mechanistic explanation of the intermittent evolutionary dynamics observed in all those models has been provided. Those fluctuations are accompanied by many speciation and extinction, therefore, mechanistic viewpoint will likely give an insight into understanding how a natural food web emerges and collapses. Therefore, we need to clarify mechanisms of how eco-evolutionary process results in the large fluctuation of species richness. To understand these mechanisms, on this thesis, I introduce a new individual-based evolutionary-food-web model, and investigate not only the structure of resultant communities but also eco-evolutionary process and

mechanisms of their dynamics.

Migration within a metacommunity

Previous studies that I introduce at above sections have mainly focused on the evolutionary and population dynamics within a single community. Recently, it has recognized that the ecological dynamics is affected by events occurring at multiple scales in space (Leibold *et al*., 2004). The simple example would be the birth–death process and dispersal. The former process is a within-population-scale event but the latter is among-population-scale event. The metacommunity is a concept to combine those multiple spatial scales, in which a regional community (metacommunity) is considered as a set of local communities that are linked by migration (Hanski & Gilpin, 1991; Hanski, 1998; Leibold *et al*., 2004; Wilson, 1992). Holt (2002) reviewed population-dynamics models that incorporated in the metacommunity. According to his review, those models show that the migrations could alter the food-chain length and population dynamics of local communities, which suggest the importance of migrations in understanding the stability of food web and community dynamics.

Even though communities are connected by migration, the sufficiently low frequency of the migration will allow local evolution to differentiate species compositions of those local communities. In such a case, each local community consists of some endemic species that may occupy different niche from any other species. When those species eventually migrate to other local communities, it will occupy an empty niche and be released from some biological interactions. If it is released from its natural enemy, the invaders will flourish due to the absence of foraging pressure, which may be possible to more easily establish than other species (enemy-release hypothesis, Keane & Crawley, 2002; Maron & Vilà, 2001; Mitchell & Power, 2003; Naeem *et al*., 2000; Ren & Zhang, 2009; Shea & Chesson, 2002). And Elton (1958) proposed that those released species potentially destabilize the invaded community. Therefore, evolution within a

local community can significantly affect the population dynamics of the migrated community, suggesting that the importance of incorporating both evolution and migration into the model in order to understand the dynamics of a community.

On the eco-evolutionary food-web models, Powell & McKane (2009) added the theory of unidirectional migration from mainland to island communities. They concluded the effect of migration on the diversity of evolved communities is essentially similar to that of the mutation. However, they assumed mainland-only evolution, ignoring the evolution within an island community. Rossberg *et al*. (2008) also introduced migrations into their matching model, and reported large fluctuations of species richness in the presence of migration. However, the detailed mechanism of the fluctuated dynamics was not investigated. For further understanding of the relationships between migration and the dynamics of a local community, in this thesis, I extend the eco-evolutionary model to incorporate migration between multiple communities. By using this model, I clarify mechanisms of the migration-induced dynamics and the eco-evolutionary processes behind the dynamics.

New eco-evolutionary model of food-web emergence and maintenance

In this thesis, I develop a new evolutionary-food-web model and investigate the dynamics of evolved community. To understand the dynamics of species richness of a community, a model should include a mechanistic base of speciation and extinction. I adopt an individual-based approach of which all of these evolutionary processes, e.g., speciation and extinction, are described as a consequence of accumulated mutations during the population-dynamics process. The trait-based fitness of each individual determines its birth and death process, and at the same time, mutations on those traits result in the difference of fitness that drives evolution. As a result, the evolutionary time-scale and the population-dynamics time-scale could be merged into a single framework, which enables one to examine the eco-evolutionary process and underlying

mechanisms that drive the dynamical change in the species composition.

To understand evolutionary dynamics of a community under ecological processes, in chapter 2, I construct and analyze a theoretical model that represents eco-evolutionary process. The analysis shows that the model indicates the intermittently cyclic transitions between two significantly different community structures, a community with more than three trophic levels or a community mostly occupied by producer species, which is driven by eco-evolutionary process. The cyclic transition consists of seven steps, which starts from a community without predators but occupied by plant species; (1) the appearance of a herbivore in a plant-rich community, (2) repeating diversification of plants and adaptations of herbivores caused by trophic interactions between them, (3) increased abundance of herbivores promotes the evolution of predators, (4) extinction of a specialist herbivore results in an abundance burst of its host plant, (5) the reduction of other plants abundance due to competition, (6) triggering of a secondary extinction of remaining herbivores that depend on those plants, and (7) repetition of step 4 to step 6 until all consumers go extinct. The analysis clarifies the scenario of diversification and successive extinction of a community from mechanistic points of view, which has been overlooked in previous model analysis. This scenario is based on the coevolutionary dynamics of ecological interactions, i.e., trophic and competitive interactions. Therefore, the present result will contribute to understand the relationships between eco-evolutionary processes and the stability of a community.

The single-community model analyzed at chapter 2 does not consider migrants come from outside of the community. If the dynamics of other communities is independent of the focal community, a migration can be a species that may not be similar with any endemic species and introduces novel interspecific interactions. Therefore, a community's evolutionary dynamics under the migration between communities can be different from what I discussed on the dynamics of isolated community. In chapter 3, I analyze the evolutionary dynamics when two communities

interact with each other. By applying the metacommunity framework (Hanski & Gilpin, 1991; Wilson, 1992; Holt, 2002; Leibold *et al*., 2004), a single-community model can naturally be extended to include migrations, by which a simple meta-community is assumed to consist of two local communities with identical environments. On this extended model, migrants connect those two local communities, while other components of the evolutionary and population dynamics, e.g., birth and death of individuals, are determined by the ecological interactions within a local community, i.e., trophic and competitive interactions. The dynamics of a metacommunity can be classified to three patterns depending on the migration rate. Without migration, two local communities are completely isolated and those dynamics are independent each other, and frequent migrations allow the metacommunity to behave as a single large community. However, when the migration rate between two communities is an intermediate level, those local communities are unlikely to have rich food webs simultaneously. The further investigations indicate the evolutionary differentiation of the species composition of two local communities, which is hindered under the frequent migration, has an important role on this dynamics. When those local communities are differentiated, migrants can be enemy-free invaders in destination, which sometimes triggers a breakdown of the destination community.

Finally, in chapter 4, I discuss the implication and validity of results obtained from two models. The observed dynamics from the present models are driven by the coevolution of plants' vulnerability traits and herbivores' foraging traits, suggesting the importance of the dynamics of plant–herbivore-interaction intensities, which often result in an emergence or extinction of a species. In one-prey-one-predator system, some empirical studies proposed the scenario of the genetic diversification of prey and predator, and the predator extinction after the evolution of a resistant prey (e.g., bacteria–bacteriophage system, Bohannan & Lenski, 2000; Weitz *et al*., 2005). The present analysis extends this scenario of diversification–extinction cycle to a

community that consists of many species and multiple trophic levels. Although the model includes trophic interactions and competitions only in the absence of mutualism and commensalism, it will give some insights to understand the complex dynamics of evolving community.

Chapter 2. Abrupt community transitions and cyclic evolutionary dynamics in complex food webs

2.1 Introduction

Biodiversity emerges over time through speciation and extinction, which involves both ecological processes that stem from species/individual interactions and evolutionary processes with natural selection. For example, plant species undergo many interactions such as competition among other plants and attack by a wide range of herbivores. These ecological processes influence their fitness, which determine their evolutionary changes. Such evolutionary changes, in turn, can propagate the rearrangement of interactions, which may result in significant effects on entire dynamics of a community. A recent study of environmental changes and species extinction suggests that the dynamical change in species interactions is an important proximate cause of species extinction (Cahill *et al*., 2012). Accordingly, understanding the eco-evolutionary processes is important to reveal mechanisms of emergence and maintenance of biodiversity.

The last few decades have seen impressive advances in our theoretical understanding of eco-evolutionary dynamics. In community evolution, the main focus is on understanding the dynamics and complexity of food webs (e.g., Verhoef & Morin, 2010), and much research has been devoted to analyzing models that describe food-web formation and maintenance (see the recent review by Brännström *et al*., 2012). Such models are typically extended predator–prey models with interactions depending on assigned traits, so that food webs can ultimately emerge through evolution of these traits. The previous theoretical models successfully show the evolutionary emergence of food webs with many coexisting species; however, the ecological and evolutionary mechanisms that describe the dynamics of a community are still unclear. A surprising finding in many studies is that communities sometimes exhibit a sudden transition from one evolutionary state to another and the large fluctuation of species richness

(Christensen *et al*., 2002; Ito & Ikegami, 2006; Rikvold 2007, 2009; Guill & Drossel, 2008; Rossberg *et al*., 2008; Murase *et al*., 2010), suggesting the evolutionary emergence of an unstable community. To understand the ecological meanings of the instability, we need to clarify the processes and mechanisms that drive the evolving community's dynamics.

Most models of community evolution mentioned above focus on speciation–extinction dynamics by regarding species as the unit of the modeled community and by considering mutation as being equivalent to speciation (Bell, 2007; Christensen *et al*., 2002; Drossel *et al*., 2001, 2004; Guill & Drossel, 2008; Guttenberg & Goldenfield, 2008; He & Yu, 2006; Ingram *et al*., 2009; Murase *et al*., 2010; Pękalski *et al*., 2008; Powell & Boland, 2009; Rossberg *et al*., 2005, 2006, 2008; Stauffer *et al*., 2005; Yoshida, 2002, 2006). Recently, accumulating empirical evidence suggests the reciprocal interactions between evolution and community's population dynamics (Facon *et al*., 2006; Fussman *et al*., 2007; Pelletier *et al*., 2009; Post & Palkovacs, 2009), indicating the importance of understanding the underlying ecological mechanisms of evolutionary dynamics of a community. However, this approach to modeling speciation, which forgoes a detailed accounting of the mechanisms of mutation accumulation and trait divergence, precludes an understanding of species emergence as an adaptive process. Instead of species, on this thesis, I selected individuals as the unit of the modeled community, which called as an individual-base model. In this model approach, evolution is represented by the accumulation of mutations.

In this chapter, I investigate trophic interactions in a continuous niche space through an individual-based stochastic model with the aim of elucidating the evolutionary processes that lead to the emergence and collapse of multi-layered communities.

2.2 Methods

I consider an individual-based stochastic model in continuous time, in which birth and death events are realized with probabilistic rates that depend on foraging success, predation pressure, and interference competition. Selection on foraging and vulnerability traits, which are inherited nearly faithfully by the asexually produced offspring, over time lead to the emergence of clusters of related individuals in trait space, which I identify as species. These species, together with the trophic interactions among them, define the food web, of which I analyze the structure, stability, and certain network properties. The details of the present model are described below.

2.1.1 Evolving traits

Each individual is assumed to be haploid with nearly faithful asexual reproduction. All individuals are thus considered to reproduce clonally and to produce mutated offspring with a small probability. Each individual has two sets of quantitative trophic traits: foraging traits and vulnerability traits. Both sets of traits are represented by two-dimensional vectors. Following previous work by Ito & Ikegami (2006) and Rossberg *et al.* (2006), the foraging trait vector of the i-th individual, f_i, represents its niche as a consumer, while the vulnerability trait vector v_i represents its vulnerability to foraging, that is, the niche it provides as a resource. Like these authors, I do not assign specific biological interpretations (with reference to features such as color or toxicity) to any axes or points in the trait space; instead, I consider this space as an abstract representation of all relevant biological traits.

2.1.2 Demographic dynamics

I consider two types of events, birth and death events. A birth event increments the community's total abundance by 1, and a death event decrements it by 1. Events are realized sequentially one after the other, and average waiting times are exponentially

distributed, following a Poisson process.

I implement the resulting stochastic demographic dynamics using the Gillespie algorithm (Gillespie, 1976, 1977). Event rates depend on the intensities $F(f_i, v_j)$ and $I(f_i, f_j)$ of foraging and interference competition between i-th and j-th individuals, respectively. I assume that those interaction intensities between two individuals are given by their traits, in conjunction with a foraging kernel and an interference competition kernel, which are both assumed to be Gaussian functions,

$$F(f_i, v_j) = \exp(-\| f_i - v_j \|^2 / 2\sigma_{\mathrm{F}}^2) / \sqrt{2\pi}\sigma_{\mathrm{F}}$$
$$I(f_i, f_j) = \exp(-\| f_i - f_j \|^2 / 2\sigma_{\mathrm{I}}^2) / \sqrt{2\pi}\sigma_{\mathrm{I}},$$

with σ_{F} and σ_{I} being the standard deviations, or widths, of those kernels. Interactions become more specific for small widths, and less specific for large widths. The foraging intensity is higher when a consumer's foraging traits and a resource's vulnerability traits are more similar, corresponding to an overlap of the utilizable niche of the consumer and the providing niche of the resource. Moreover, the intensity of interference competition is maximal between individuals with the same foraging traits, as consumers can be expected to interfere with one another most strongly when utilizing the same resource.

Without any restrictions on trait values, vulnerability traits of a prey and foraging traits of a predator can coevolve to be infinitely large values, which make the numerical computation to be impossible, as a result of the arms race. To prevent this runaway selection, I furthermore assume a cost for vulnerability traits that increases quadratically with their distance from the origin, $D(v_i) = \| v_i \|^2$. I assume the availability of an external resource, with vulnerability trait vector v_{R} and abundance N_{R} that are constant during a realization. For simplicity, I set the vulnerability trait vector of the external resource equal to the origin, $v_{\mathrm{R}} = (0,0)$.

Based on the assumptions above, the instantaneous rates of birth events, $r_{\mathrm{b}i}$,

and of death events, $r_{\mathrm{d}i}$, of the i-th individual are given by

$$r_{\mathrm{b}i} = aC_{\mathrm{F}} \sum_j F(f_i, v_j) + aC_{\mathrm{F}} F(f_i, v_{\mathrm{R}}) N_{\mathrm{R}},$$
$$r_{\mathrm{d}i} = C_{\mathrm{F}} \sum_j F(f_j, v_i) + C_{\mathrm{I}} \sum_j I(f_i, f_j) + C_{\mathrm{D}} D(v_i) + d.$$

Here, the summations extend over all individuals in the community, and the coefficients C_{F}, C_{I}, and C_{D} scale the intensity of foraging, the intensity of interference competition, and the cost of the vulnerability traits, respectively. The remaining parameters a and d quantify the trophic efficiency and the natural death rate, respectively. As event rates are determined by summing over terms that do not depend on total population size, the corresponding averaged deterministic dynamics are described by multispecies Lotka–Volterra dynamics.

2.1.3 Evolutionary dynamics

As I assume haploid individuals with asexual reproduction, mutation is the only source of phenotypic variation. I assume the constant probability of mutation occurrence for all reproductions of individuals (Stauffer *et al*., 2005; He & Yu, 2006; Bell, 2007; Rikvold & Sevim, 2007; Rikvold, 2007, 2009; Powell & Boland, 2009; Murase *et al*., 2010), with the probability being called as a mutation probability. Based on their analysis of empirical data, Rossberg *et al.* (2006) argued that the mutation rate of foraging traits tends to be much higher than that of vulnerability traits. I therefore consider different mutation probabilities for the foraging and vulnerability trait vectors, μ_{f} and μ_{v}, respectively, with $\mu_{\mathrm{f}} > \mu_{\mathrm{v}}$. I assume that the occurrences of mutations in foraging and vulnerability traits are independent of each other. A mutation alters an offspring's trait vector from that of its parent by adding a random vector whose components are drawn independently from a normal distribution with expectation 0 and variance σ_{m}^2.

2.1.4 Parameter values and initial conditions

Table 1 lists the parameters and their values in my investigations. These are chosen in agreement with previous theoretical studies, in particular Loeuille & Loreau (2005) and Rossberg *et al*. (2008). To induce predator–prey diversification, the differentiation between branched prey species needs to be sufficiently large (Doebeli & Dieckmann, 2000): as the distances among the vulnerability clusters of species are controlled by the width of the foraging kernel, I assume that the foraging kernel is considerably wider than the competition kernel.

I start the evolutionary investigations with a small population of 100 individuals with foraging and vulnerability traits equal to those of the external resource. This choice of initial conditions only affects the initial transient dynamics and has no impact on the long-term outcomes of the investigations.

2.1.5 Species determination

Determining what constitutes a species is not trivial when mutational steps are small and reproduction is asexual. However, in the present model, distinct clusters tend to form in trait space, and the strains in a cluster are mostly close relatives of each other. I can thus define a species as a cluster of strains in trait space, in accordance with the genotypic-cluster species concept introduced by Mallet (1995). To identify these clusters, I apply the QT-clustering algorithm (Heyer *et al.,* 1999) to the distribution of strains. Due to the small mutation rate, mutation–selection balance can remove all the relatives of a strain, which results in an isolated strain being detected as outliers. An outlier strain is treated as a species consisting of a single trait type.

2.1.6 Trophic-level determination

For every species $i > 0$, its real-valued fractional trophic level t_i is calculated following Odum & Heald (1972) as the weighted average of the trophic level of its prey

species plus 1,

$$t_i = 1 + \sum_j w_{ij} t_j . \qquad (2.1)$$

Here, the trophic level of the external resource, which can be thought of as the 0th species, is defined as $t_0 = 0$. The weights w_{ij} are defined by $w_{ij} = \bar{F}_{ij} / \sum_k \bar{F}_{ik}$ with $\bar{F}_{ij} = \sum_{x \in S_i} \sum_{y \in S_j} F(f_x, v_y) / n_i$. Here, S_i and S_j are the sets of individuals that belong to species i and j, respectively, and n_i is the abundance of species i. The weight w_{ij} thus measures the fraction of the average energy input an individual of species i receives from all individuals of species j. Eq. 2.1 define a linear system in which the trophic levels $t_1, t_2, \ldots$ appear as unknowns; this system is solved by elementary matrix algebra.

For $i > 0$, the trophic levels thus determined are always larger than or equal to 1. Species in the present model community tend to cluster around integer trophic levels; I can thus classify species by their trophic level as plants ($1 \le t_i < 1.5$, utilize the external resource), herbivores ($1.5 \le t_i < 2.5$, utilize plant species), and predators ($2.5 \le t_i$, utilize other consumers) based on the calculated trophic levels of those species. Both herbivores and predators belong to consumers.

2.3 Results

The individual-based stochastic model described above allows for the emergence of diverse communities with several trophic levels.

After an initial transient phase, the abundance of individuals fluctuates over time, but mostly takes values in two markedly different ranges (Fig. 2.1), similar to the flip-flop dynamics reported by Rikvold (2009). These ranges correspond to two characteristic community states. I refer to these community states as the low-trophic-level (LTL) state and the high-trophic-level (HTL) state. An LTL community mainly consists of highly abundant plants, while herbivores are rare and

ephemeral (Fig. 2.1a). In contrast, an HTL community comprises also predator species (Fig. 2.1b).

Evolution is characterized by long periods of HTL and LTL states punctuated by fast transitions. Below I offer a process-based explanation for the observed evolutionary dynamics, and also demonstrate that the results remain robust to changes in parameter values and model assumptions.

I now describe these findings in turn. All model parameters used for this investigation are specified in Table 2.1 (for the parameters used for the robustness checks, see Section 2.3.4).

2.1.7 Emergence of complex food webs with multiple trophic levels

Over time, demographic changes and small mutational steps lead to the emergence of a large number of species organized in several trophic levels. Figure 2.1 shows the typical structures of the emerging communities. In the HTL state, communities include plants and predators, exhibiting three distinct trophic levels (Fig. 2.1b).

2.1.8 Community-level evolutionary cycles

Figure 2.2a shows that the total abundance of individuals belongs to the different trophic levels in the community on a long time scale. Transitions between these states are relatively fast (Fig. 2.2a), and I consistently observe cyclic evolutionary dynamics (Fig. 2.2b). The distributions of durations of both LTL and HTL states match exponential distributions (Fig. 2.2c, d), suggesting that transitions between the two states are triggered by rare random events that occur with constant probabilities per unit time. The dynamics of abundances (Fig. 2.2a) tends to remain around either of two levels for long periods, each corresponding to one of the characteristic community states shown in Fig. 2.1. As the presence of herbivores effectively regulates the abundance of the plants, the total abundance of plants in an HTL-state community (Fig. 2.2a, shaded

periods) tends to have lower total abundance than that in LTL-state communities (Fig.2.2a, non-shaded periods). Occasional mutations from plants to herbivores do occur in the LTL state, but they typically fail to establish.

2.1.9 Understanding the evolutionary cycles

I will now present a detailed implication of the observed evolutionary cycles (Fig. 2.2b). Starting from the LTL state, figure 2.3 shows the key steps in a schematic diagram. In practice, the steps constituting the fast transitions may occur nearly simultaneously.

In the LTL state (Fig. 2.3, middle left to top left), plants initially mainly diversify in their foraging traits, so as to avoid interference competition. At the same time, they form relatively large clouds in terms of their vulnerability traits, because there is little selection pressure on those. Initially, the number of such clouds almost equals the number of plants during the preceding HTL state. Gradually, however, the number of those clouds decreases through random extinction. Also, the occasional and temporary emergence of an herbivore impose strong foraging pressure on one of those clouds, and thereby increases its risk of random extinction of the foraged cloud that followed by the extinction of the herbivore. Because of those processes, the number of those clouds decreases during the LTL period, and finally, only a few vulnerability clouds survive. While all vulnerability trait vectors evolve toward the cost minimum at the origin, directional selection ceases at some distance from the origin, since this allows plants to avoid trophic interaction with other individuals.

After the extinction of the most of vulnerability clouds, transition from the LTL state to the HTL state is initiated by the appearance of a mutant individual with foraging traits that allow it to forage on the extant plant species (Fig. 2.3, top left to top right). This mutant tends to be the offspring of a plant with a foraging trait vector that is already relatively far away from the vulnerability trait vector of the external resource (i.e., the origin). As only a few vulnerability clouds exist at the end of the LTL period,

the newly emerged consumer species can typically forage on a large number of plant species. Consumer control now regulates plant abundance, leading to increasing plant evenness (Fig. 2.4a). The proportion of foraged-plant-species richness very quickly increases from 0 to 1 (Fig. 2.4b). Because of the foraging pressure, the abundances of the plants quickly decrease, leading to the eventual (stochastic) extinction of a number of plants due to overexploitation, in what can be viewed as a top-down process.

The extinction of some plants leads to mounting foraging pressure by the consumer on the remaining plants, generating a strong selection pressure towards a diversification of their vulnerability traits (Fig. 2.3, top right to bottom right). This promotes differentiation of the vulnerability trait vectors within the plant community, which makes consumers with intermediate foraging trait vectors to be unprofitable. The coevolution of foraging traits of the herbivores undergo a corresponding specialization on a plant species, resulting in the emergence of herbivores each specialized on one plant species. Because I assume that the costs associated with vulnerability trait vectors increase with their distance from the origin, the process of diversification ceases once the viable vulnerability trait space is mostly occupied by plants. A predator foraging on herbivores can also emerge (Fig. 2.3, middle right). Because vulnerability trait vectors have not been differentiated before the evolution of predators, the species can utilize many herbivores. This is the HTL community state (Fig. 2.3, bottom right). The HTL plants are diversified in their foraging trait vectors (because of interference competition) as well as in their vulnerability trait vectors (because of foraging pressure). The herbivores of the HTL state are diversified in their foraging trait vectors, but not so much in their vulnerability trait vectors (for the same reason that LTL plants are not, i.e., because of the absence of predation). The high evenness among plants suggests that plant abundances are strongly controlled by consumers (Fig. 2.4a,c). More complex communities rarely evolve in our model, except for extreme parameter settings ($a = 0.9$, Fig. A.2 in Appendix), because the strongly decreasing abundance of the

higher-trophic-level species makes their persistence less likely.

The random extinction of an herbivore initiates the transition from the HTL state to the LTL state (Fig. 2.3, bottom right to bottom left). Since plants are mostly foraged on by specialists, the extinction of such a specialist consumer, which can be caused by the counter evolution of its host plants' vulnerability trait or demographic stochasticity due to its small abundance, removes the foraging pressure from the corresponding plant. As a consequence, the abundance of this plant quickly increases, which, in turn, increases the level of interference competition exerted by it. Strong interference competition effectively decreases the abundance of the other plants, and consequently, the abundance of the corresponding herbivores, threatening their survival (and the survival of all higher-trophic-level consumers). This destabilization of the plant level manifests itself in terms of decreasing plant evenness, which slightly precedes the decrease in consumer richness (Fig. 2.4c). As more and more higher-trophic-level species become extinct, the proportion of plants that are free from foraging pressure increases (Fig. 2.4d), and so does the competitive pressure on the remaining pairs of plants and herbivores (Fig. 2.3, middle left). Ultimately, only a few plant species survive, which means that the community has reverted to its initial state (Fig. 2.3, top left). This extinction of the higher-trophic-level species can be seen as a bottom-up extinction process, as it is driven by the competitive dynamics of plant species.

2.1.10 Robustness of the evolutionary cycles

To explore the robustness of the results, I consider alternative minima of the vulnerability costs, different dimensionalities of the trophic trait space, variation in four salient model parameters, and nonlinear functional responses (see Appendix).

First, I relax the assumption that the cost minimum for vulnerability traits coincides with the vulnerability trait of the external resource (Fig. A.1, in Appendix). If there are no other constraints, e.g., foraging pressure, vulnerability traits will evolve to

the cost minimum. As a consequence, the coincidence of those two positions induces the selection pressure to have the similar vulnerability to the external resource, which can promote the resource switch of the plant species. As expected, I find that the reemergence of the trophic structure becomes difficult when this distance between cost-minimum of vulnerability traits and vulnerability traits of the external resource is made large, but at the same time I can confirm that the results presented here remain valid for small to moderate distance.

Second, I investigate the effect of altering the trait-space dimensionality on the cyclic evolutionary dynamics (Fig. A.2 in Appendix). I relax the assumption that vulnerability trait vectors and foraging trait vectors are two-dimensional and investigate also one-, three-, and four-dimensional trait vectors. In a few selected trials (limited by the rapidly increasing computational time), I find qualitatively similar outcomes – cyclic transitions between HTL states and LTL states – with the relative duration of the LTL state increasing with the dimensionality.

Third, I increase the trophic efficiency a from 0.2 to 0.9, which results in qualitatively similar intermittent dynamics, except that for higher trophic efficiencies food webs with higher abundances, greater species richness, and higher trophic levels evolve (Fig. A.3 in Appendix). Higher trophic efficiencies directly increase the energy flow from the external resource to consumers, and therefore can maintain a larger number of consumers, enabling the evolution of higher-trophic-level species. In turn, larger consumer abundances decrease demographic stochasticity, and thus increase the relative duration of the HTL state. Nevertheless, the HTL-to-LTL transition is eventually still triggered by the extinction of an herbivore.

Fourth, I increase the abundance N_{R} of the external resource by a factor of 2 (from $N_{\mathrm{R}} = 4{,}500$ to $9{,}000$), which raises the observed total abundance as well as the abundance within all species by roughly the same factor (Fig. A.4 in Appendix). I find that the community's overall behavior remains very similar, except for a prolonged

duration of the HTL state due to diminished demographic stochasticity.

Fifth, varying the scales of foraging intensity and interference-competition intensity ($C_{\mathrm{F}} = 0.45$, 0.9, or 1.8; $C_{\mathrm{I}} = 0.05$, 0.1, or 0.2) results in one of three patterns: (1) a stable LTL community, (2) evolutionary cycling, or (3) complete extinction (Figs. A.5 in Appendix). A larger foraging intensity improves the effectiveness of resource consumption, which enables a consumer to survive with fewer resources. It thus facilitates the establishment of consumers, which marks the beginning of the evolutionary cycle. Overexploitation, in contrast, leads to complete extinction. Although there are three patterns, once a community evolves to the HTL state, it starts cyclic dynamics that is analyzed in this chapter.

Sixth, I relax the assumption that the offspring trait distributions have the same variances for foraging and vulnerability traits (Fig. A.6 in Appendix). Newly introduced two variables, $\sigma_{\mathrm{m,f}}^2$ and $\sigma_{\mathrm{m,v}}^2$, which represents variances of foraging and vulnerability traits mutations, respectively, control the evolutionary speed of these two trophic traits. By fixing $\sigma_{\mathrm{m,v}} = 0.03$ and varying $\sigma_{\mathrm{m,f}}$ to equal 0.01 or 0.09, I find that a smaller $\sigma_{\mathrm{m,f}}^2$ causes the abundance in the LTL state to become higher and consumers to die out. With a larger $\sigma_{\mathrm{m,f}}^2$, on the other hand, the HTL state is stabilized, and the recovery time from the LTL state to the HTL state is shortened. This is as expected: in the former case, plants can more easily evolve away from their consumers, freeing them from consumer control and thus triggering the community's collapse, while in the latter case, consumers can switch their resource more easily, keeping the plants under consumer control and thus preventing the community's collapse. While the waiting time until community collapse is thus changing, the overall community dynamics remain largely the same a when community evolves to be the HTL state.

Finally, I introduce handling times, by considering a Holling's type-II functional response instead of a linear functional response (Fig. A.7 in Appendix). If the handling times are sufficiently short, I observe the same evolutionary cycles as with the

linear response. On the other hand, the large handling time results in the lower efficiency of foraging, in particular when the abundance of its prey is high. As a consequence, the evolutionary emergence of consumers will be difficult. As expected, the evolved consumer species tend to go extinct quickly, and the HTL state is not established when the handling time is sufficiently large.

2.4 Discussion

In this chapter, I introduced and investigated a stochastic individual-based model of coevolutionary dynamics driven by predation and interference competition. Individuals are fully described by vulnerability and foraging trait vectors, characterizing their ecological niche. Over time, demographic dynamics with small mutations in these traits leads to the establishment of large interconnected ecological communities with three to four trophic levels. The subsequent evolutionary dynamics is characterized by relatively long periods that the community spends around either of two characteristic states, occasionally punctuated by fast transitions. During these transitions, the composition of the community is altered by mass extinctions and rapid diversification.

To the extent that similar transitions happen in natural communities, they might be triggered more or less easily than in the present model. Because of constraints on computational time, the model community comprises a relatively small number of individuals as compared with most real ecological communities. This small community size potentially increases the importance of demographic stochasticity, which can cause stochastic extinction, in particular for species at higher trophic levels that have less per-species abundances than plants. This demographic stochasticity might facilitate the triggering of community-level transitions that I demonstrated in this chapter. On the other hand, in natural communities these transitions might alternatively be triggered by environmental stochasticity or random external impacts, such as occasional release from natural enemies (Keane & Crawley, 2002), which are not included in the present model.

At any rate, once events have been set in motion towards a transition, the resultant cascade of coevolutionary changes might be a principal cause of extinctions in a community.

Using a ratio-dependent functional response, the Tangled-Nature model may also exhibit flip-flop dynamics between species-rich communities and producer-dominated communities (Rikvold, 2009). Based on the analysis of a simplified two-species model, Rikvold (2009) proposed that the emergence of intra-guild predation (IGP, i.e., the ability of species to forage on competitors on their own trophic level) destabilizes a diverse community. The single emergence of IGP can alter the stability of some species, so that it may trigger the community collapse. However, after it is triggered, the mechanism that drives the community collapse had not been mentioned. By focusing on the transition process, I clarify that the strong inter-plant competitions can be a driver of the community collapse. Although Rikvold (2009) did not explicitly include interspecific competition, a ratio-dependent functional response implicitly introduces competition between species that share the same resource (Getz, 1984). The consumer extinction that is induced by competition among plants in the present model, therefore, could potentially be a cause of the breakdowns of species-rich communities of Rikvold (2009).

It is informative to compare the cyclic community dynamics reported here with the cyclic arms-race dynamics observed in gene-for-gene models, which is a widely applied theoretical model of the evolution of resistance of a host plant species against virulence of a pathogen species (reviewed by Brown & Tellier, 2011, Thompson & Burdon, 1992). In this viewpoint, the evolution and extinction of consumers reported here is analogous to the evolution and removal of virulent gene from pathogen population. The arms race starts from the increase of both virulence and resistance due to the attack from pathogens. When all of the pathogens become virulent, the resistance does not affect fitness and removed from the population due to its cost, then the virulent

gene is removed from the population. These two processes may correspond to the emergence of a high-trophic-level (HTL) community and collapse of it, respectively. While this comparison will help our intuitive understanding of the cyclic dynamics of a community presented here, however, the limitation of this comparison is the difference in the time-scale of those processes. The gene-for-gene models predict the collapse of virulence and resistance is relatively slow process, while the present result show the rapid transition from HTL state to LTL state. This difference mainly comes from extinction that is included in the present model. The gene-for-gene models assume abundant pathogens (e.g., fungal pathogen) to eliminate the potential extinction of pathogens. On the other hand, the transition from HTL state to LTL state is driven by successive extinction of consumers, which explains more rapid transition than the evolutionary transition of gene frequency.

It is helpful to compare the cyclic community dynamics reported here to the classical phenomenon of predator–prey cycling for intuitive understanding. From this perspective, a community that mainly consists of plants, being in the LTL community state, is analogous to a prey-abundant community. When a predator–prey system is in this state, the predator can establish itself and easily increase its abundance, resulting in the build-up of predation pressure. This leads to a community in which predator and prey temporarily coexist at relatively high abundance, analogous to the high-trophic-level (HTL) state of the present model, which also comprises higher-trophic-level consumers. In a predator–prey system, this gradually engenders a shortage of prey, causing in turn a reduction of the predator population. Similarly, in the present model consumer species start to go extinct once they have reached a high diversity, owing to abundance reduction of their resource species that are induced by the strong foraging pressure and interspecific competition. While these considerations help to appreciate some key similarities between the predator–prey cycling of population-level demographic states and the cycling of community-level evolutionary

states reported here, an obvious limitation of this analogy is the relatively short duration of the plant- and consumer-abundant communities in predator–prey cycling, which contrast with the relatively long durations of the LTL and HTL states I have observed. The main reason for this difference is that the present model describes not only the demography of trophic interactions but also their evolution and diversification. The latter being slow processes results in the long durations of the LTL and HTL states.

A key finding of the present chapter is that the HTL state can be unstable: a small perturbation is eventually responsible for inducing its collapse. This kind of instability is by no means coincidental – instead, natural selection at the species level systematically favors the evolution of such an unstable condition at the community level. A similarly counterintuitive outcome of evolution, evolution toward extinction, is known as evolutionary suicide, and has been observed in several model systems (Dieckmann *et al.*, 1995; Ferrière, 2000; reviewed by Parvinen 2005). Likewise, Rand *et al*. (1995) demonstrated that unstable interspecific interactions can emerge through the coevolution of host–pathogen interactions. Specifically, they found that, under certain conditions, the pathogen's transmissibility evolves to a critical level at which the host–pathogen system could go extinct. By analyzing the mechanisms of crash and reemergence of a evolving community, the present result extends these concepts of the evolution–toward–extinction to the community scale. It highlights the potential for community crashes to occur as the outcome of the evolutionary dynamics of interspecific interactions.

Altering several parameters in the present model results in communities that differ in terms of their species richness, total abundance, and maximum trophic level. Within those parameters, relative evolutionary speeds of two trophic traits in particular have notable effects on the community dynamics (see Fig. A.6 in Appendix). When the evolution of foraging traits is relatively slow, a community cannot evolve to be the HTL state. On the other hand, the LTL state almost disappears under the rapid evolution of

the foraging traits. It is also known that the strong persistence of a complex food web under the assumption of behavioral adaptation (Kondoh, 2003, 2006, 2007), which suggests the possible disappearance of the cycle under the very rapid evolution of the foraging traits. It implies that the cyclic dynamics may be a consequence of the balance between foraging and vulnerability traits evolution, though, the present result indicates the cyclic dynamics whenever the HTL state evolves. As I have shown, intermittent and cyclic transitions between HTL and LTL states are observed for a wide range of model parameters. While this inspires confidence in the results, an important challenge for future research is to infer reasonable parameter ranges from empirical observations. The most immediate concern might be to improve empirical estimates of the intensities of foraging and interference competition and the speed of foraging and vulnerability traits evolutions, as these parameters have a particularly strong effect on the presence or absence of cyclic transitions (see Fig. A.5, A.6 in Appendix).

As I increase the number of trait-space dimensions, I observe decreasing durations of the HTL period. This can be explained by the fact that, in higher-dimensional trait spaces, specialist consumers increasingly tend to "lose" the plants on which they forage, which results in the emergence of consumer-free plants and triggers the transition to the LTL state with increasing frequency. Gilman *et al*. (2012) theoretically analyzed such evasive evolution for host–parasite systems, .

In this chapter, I demonstrated the evolutionary emergence and breakdown of complex food webs through the coevolution of generic foraging and vulnerability traits. I hope that the work presented here will contribute to a better understanding of our rich evolutionary past, and thereby enable an enhanced appreciation for the eco-evolutionary dynamics that shape our future.

Table

Description	Symbol	Value
Abundance of external resource	N_{R}	4500
Scale of the intensity of foraging	C_{F}	0.9
Scale of the intensity of interference competition	C_{I}	0.1
Scale of the vulnerability costs	C_{D}	20
Trophic efficiency	a	0.2
Intrinsic death rate	d	0.1
Width of foraging kernel	σ_{F}	0.3
Width of competition kernel	σ_{I}	0.1
Vulnerability traits of external resource	v_{R}	$(0,0)$
Mutation probability of foraging traits	μ_{f}	0.001
Mutation probability of vulnerability traits	μ_{v}	0.0001
Width of mutation kernel	σ_{m}	0.03

Table 2.1: Model parameters. The abundance of external resource, N_{R}, the scale of the vulnerability costs, C_{D}, and the intrinsic death rate d can be considered as scaling the units of population abundance, trait-space distances, and time, respectively.

Figures

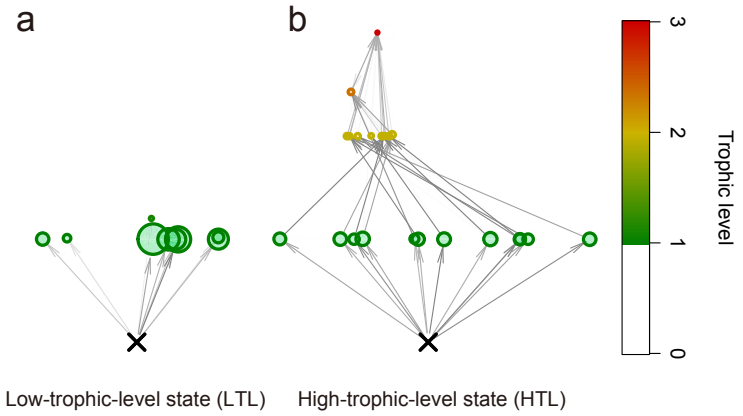

Figure 2.1: Examples of the two distinct community states observed in the present model. Each circle represents a species, with their areas being proportional to the species' abundance, vertical positions indicating the species' trophic level, and their horizontal positions indicating the species' first vulnerability trait. The cross at trophic level 0 represents the external resource. Arrows indicate trophic links, with darker shades indicating stronger interactions.

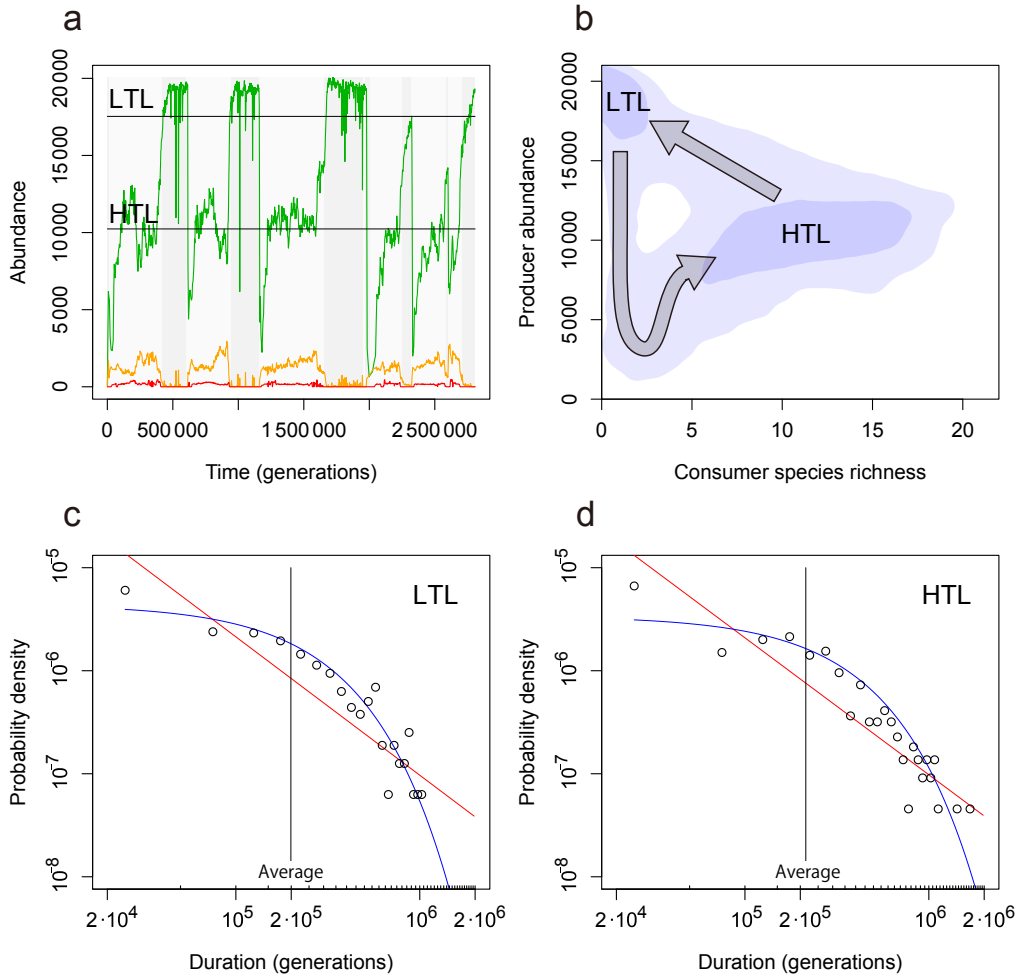

Figure 2.2: Cyclic evolutionary transitions between the two community states. (a) Continuous curves represent the total abundance of plants (green), herbivores (orange), and predators (red). (b) Frequency distribution of community states: 99% of community states are observed in the shaded areas, and 75% of community states are observed in the dark-shaded areas. (c, d) Probability distributions of community-state durations (c: low-trophic-level communities, LTL; d: high-trophic-level communities, HTL). Minor tics indicate the bins used for constructing the histogram. A red line and a blue curve indicate the best-fit power-law distributions and the best-fit exponential distributions, respectively. The frequency distributions shown in (b–d) are obtained by convolving a Gaussian distribution with 72,060 sampled community states from 60 independent model runs.

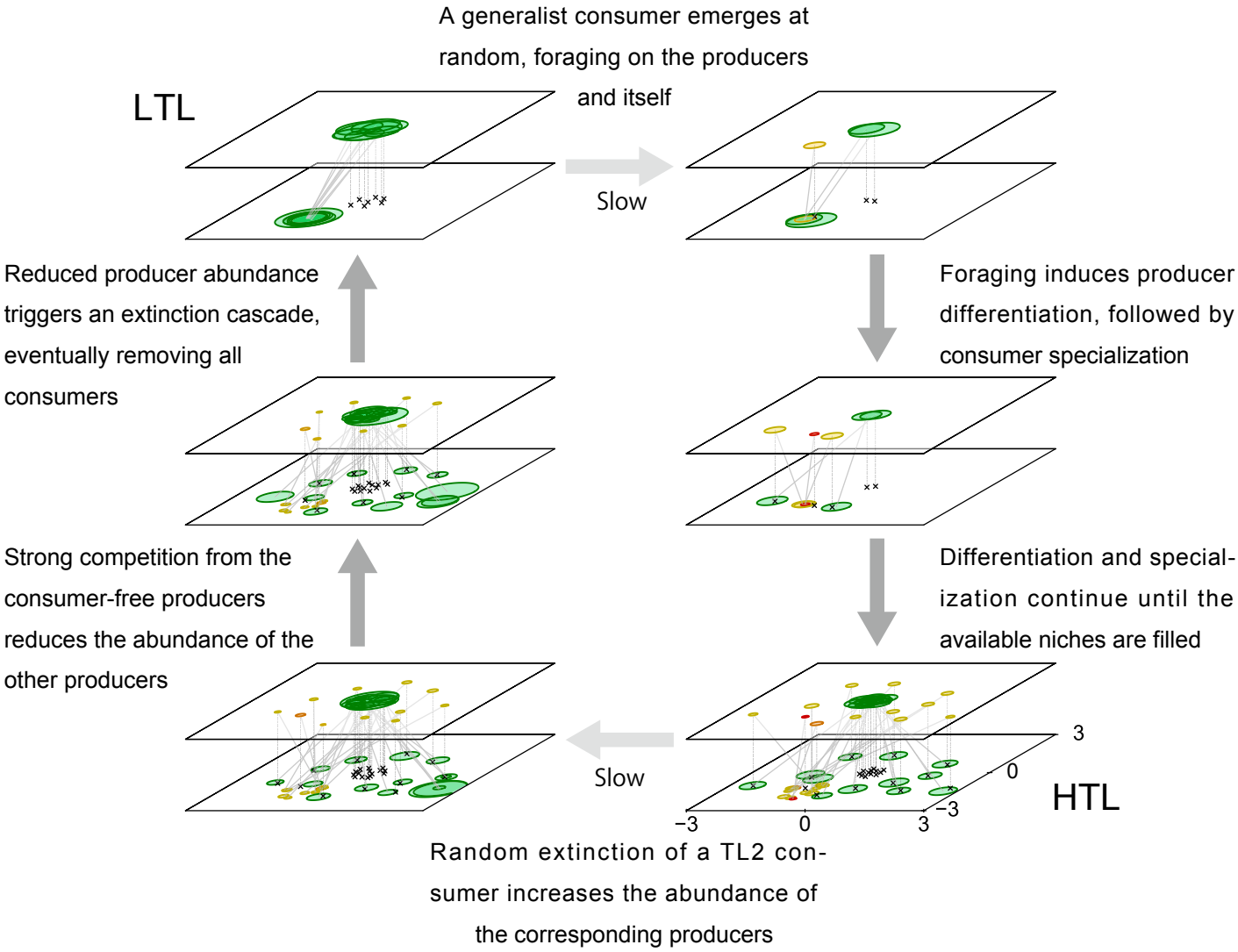

Figure 2.3: Mechanistic explanation of the cyclic evolutionary transitions between an LTL state and an HTL state. In each panel, the top and bottom layers represent the trait spaces of foraging traits and vulnerability traits, respectively. The foraging traits and vulnerability traits of a species are indicated by two circles, one on the top layer and one on the bottom layer, connected by a gray line. The area and color of each such circle indicate a species' abundance and trophic level, respectively, as in Fig. 1. For ease of readability, vertical line segments with crosses at their lower ends indicate the mean foraging traits of each species, describing where the consodered species forages most effectively. Dark arrows between the panels indicate fast transitions, while light arrows indicate slow transitions triggered by rare random events.

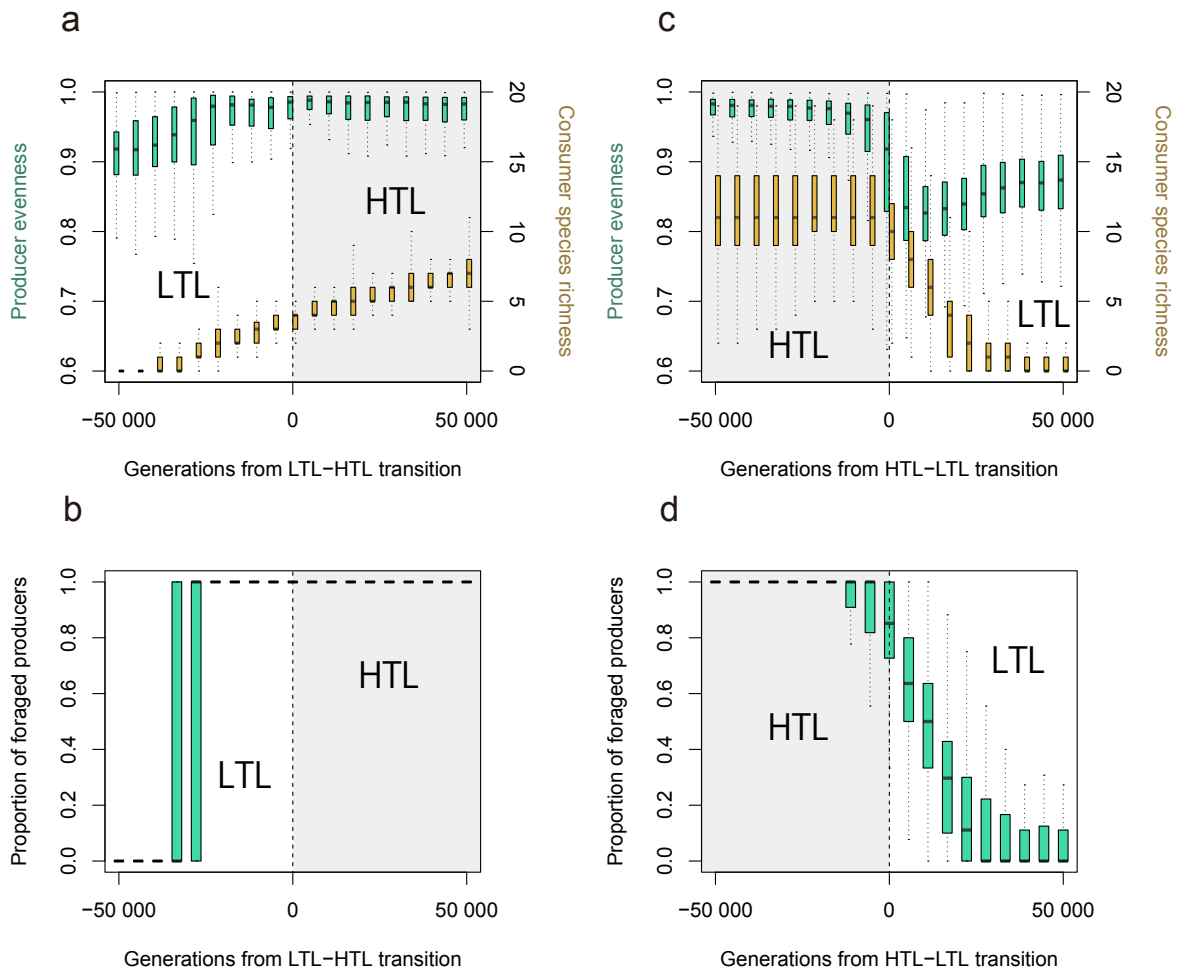

Figure 2.4: Transient dynamics associated with the cyclic evolutionary transitions between the two community states. Panels (a, b) show that the time course during the consumer emergence, while panels (c, d) show that the time course during the consumer collapse. Shaded areas highlight the HTL state. (a, c) Green and orange boxes indicate plant evenness (Pielou, 1966) and consumer species richness, respectively. (b, d) Boxes indicate the proportion of plant-species richness foraged by herbivroes. An interaction is counted as foraging only if the corresponding trophic link satisfies $F(f_i, v_j) > 0.5$. The HTL state is defined as a continuous time interval during which a community comprises predators. To reduce stochastic fluctuations, time courses from 60 independent model runs, each comprising more than $2{,}000{,}000$ generations, are smoothed by convolution with a Gaussian kernel prior to the detection of the HTL intervals.

Chapter 3. Suppression of simultaneous development of complex food webs by intermediate migration in an evolving metacommunity

3.1 Introduction

The previous chapter focuses on the dynamics of a well-mixed community. However, it has been recognized that ecological dynamics are affected by events occurring at multiple scales in space (Leibold *et al*., 2004). For example, population dynamics is a within-population-scale event, whereas dispersal among populations is an among-populations-scale event. The concept of metacommunity is a way to combine those multiple spatial scales, in which a regional community (metacommunity) is considered as a set of local communities that are linked by migration (Hanski, 1998; Hanski & Gilpin, 1991; Leibold *et al*., 2004; Wilson, 1992). Also for trophic interactions, the metacommunity concept suggested the significant effects of migration on both the food-chain length and population dynamics (Holt, 2002). From an evolutionary viewpoint, immigrations can be considered as an introduction process of novel genotypes into the local population, which is a similar process to a mutation. However, migrants may not be relatives of any species in the local community and can introduce novel trophic interactions or escape from existing foraging pressure. The emergence and disappearance of foraging behavior from herbivores to plants are the key factors that trigger the community-state transition (see chapter 2). Therefore, migrants will also be important parts to understand the emergence and maintenance of food webs.

Recently, the coupled effect of evolution and migration on community dynamics has attracted mounting interest (Urban *et al*., 2008). Empirical studies indicate the simultaneous occurrence of the evolution and migration can result in different dynamics from predictions based on a separate understanding about them, in particular when those occur at similar timescales (Urban *et al*., 2008). For example, a microbial community indicates that the frequency of migration can control the evolved

genetic diversity (Fukami *et al*., 2007). Such coincidence of timescales may be possible if migrations are sufficiently rare, e.g., an occasional invasion from a geologically distant community.

The sufficiently rare migration results in parapatric evolution of different species composition among communities. However, because of the differentiated species compositions, migrants can occupy empty niche space and be released from existing biological interactions after migration (e.g., predation and competition). The invading species that is released from those natural enemies will establish easier than the other species (enemy-release hypothesis, Keane & Crawley, 2002; Maron & Vilà, 2001; Mitchell & Power, 2003; Naeem *et al*., 2000; Ren & Zhang, 2009; Shea & Chesson, 2002), and Elton (1958) suggested the potentially large impact of those enemy-released invaders on the community. Species invasion is considered as one of the major threats on the ecosystems (Shea & Chesson, 2002; Vitousek *et al*., 1997; Wilcove *et al*., 1998). For example, plant invaders can significantly reduce the plant richness of the endemic community (Gaertner *et al*., 2009; Hejda *et al*., 2009; Ren & Zhang, 2009). The impact of those plant invaders is especially large when the invader is dissimilar from any plant species in the endemic community (Hejda *et al*., 2009). The evolution in a local community would be a source of those species' difference. Therefore, the investigation of coupled dynamics of evolution and migration contributes to understand how and why an invasive species impacts on a community.

Although there is the potential importance of migrations on a community, most of the evolutionary-food-web models assume a single community, i.e., new species arise by mutation only (Caldarelli *et al*., 1998; Christensen *et al*., 2002; Drossel *et al*., 2001, 2004; Guill & Drossel, 2008; Loeuille & Loreau, 2005, 2006; Ito *et al*., 2009; Ito & Ikegami, 2006; Rikvold, 2007, 2009; Rikvold & Sevim, 2007; Rossberg *et al*., 2006). On the other hand, Powell & McKane (2009) added the unidirectional migration process to the webworld model. By comparing mainland and island

communities, they concluded that effects of migration on island communities are essentially similar to that of mutation. However, they considered only unidirectional migration from evolving-mainland community to non-evolving-island community. Rossberg *et al*. (2008) proposed a model with both speciation and invasion in metacommunity to investigate body-mass–abundance relationships. They reported the large fluctuation of species richness in the presence of migration, but not explain the mechanisms of the observed fluctuation. The large fluctuation of species richness suggests the potential effect of migrations on the entire community and/or evolutionary processes in local communities. Therefore, now we need to investigate the relationships between mutation and migration on the metacommunity level of dynamics.

In chapter 2, I described the dynamics of a new individual-based model with eco-evolutionary process of food webs, which showed the switching dynamics between communities with more than three trophic levels (HTL: high-trophic-level state) and plant-abundant communities (LTL: low-trophic-level state). In this chapter, I extend the model by including migration between two local communities, and analyze the effects of migration on dynamics of evolving local communities and metacommunity from an eco-evolutionary viewpoint.

3.2 Model

To introduce the metacommunity structure into the model that was developed in chapter 2, I adopt the mass-effect paradigm (Leibold *et al*., 2004) on two local communities with the identical environmental condition.

3.2.1 Local community

The individual-based-evolutionary model of a food web that was proposed in chapter 2 is employed to describe local dynamics of a community. Each individual in the local community is characterized by two sets of two-dimensional quantitative trophic traits:

foraging traits and vulnerability traits (Ito & Ikegami, 2006; Rossberg *et al*., 2006). Any trait combinations are possible, although the vulnerability is accompanied by costs. Individuals are assumed to be haploid and to reproduce asexually. The reproduction induces a small mutation rate, which is a source of phenotypic variation in the local community.

The model includes two types of interactions that are determined by combination of traits of two individuals, (1) foraging interaction, and (2) interference competition. The foraging intensity between two individuals, i.e., a consumer and a resource, is higher when the consumer's foraging traits are similar to the resource's vulnerability traits. On the other hand, interference competition is stronger when two individuals' foraging traits are more similar, because individuals can be expected to interfere with one another due to the similarity of their resource. These parameter values are the same as those in chapter 2 but only the width of the foraging-trait-mutation kernel is increased to 0.09 (the width of the vulnerability-trait-mutation kernel is kept to be 0.03, see Appendix for results of a single-community model) to increase the persistence of high-trophic-level species.

3.2.2 Metacommunity

I assumed that a metacommunity consists of two local communities with an identical set of environmental parameters. Migrations between local communities are treated as a type of event in addition to the birth and death events in calculations. A relative probability of occurrence of those events on i-th individual is characterized by birth rate ($r_{\mathrm{b}i}$) death rate ($r_{\mathrm{d}i}$) and migration rate ($r_{\mathrm{m}i}$). An event x ($x \in \{\mathrm{b},\mathrm{d},\mathrm{m}\}$, representing birth, death, and migration event, respectively) on the i-th individual is selected with probability $r_{xi} / \sum_j r_{\mathrm{b}j} + r_{\mathrm{d}j} + r_{\mathrm{m}j}$ in each step. The denominator of the event probability is summed over all individuals, therefore, the large abundance results in the small per-individual-event probability. This bias on the event probability can be

removed by normalizing the time duration to a certain event by the average waiting time to the event, $\sum_i r_{\mathrm{b}i} + r_{\mathrm{d}i} + r_{\mathrm{m}i}$. The definition of birth and death rates are the same as that defined in chapter 2. The migration rate is constant for all individuals, a value of which is a given property of the metacommunity. An individual is selected to migrate randomly, to be transported into other local community without any risk of death during migration.

Species are defined by the same way as described in the previous chapter, in which a cluster of individuals in a trait space is defined as a species. An individual with certain foraging and vulnerability traits can belong to the different trophic position between two local communities, due to the difference of trait compositions of the two communities. Therefore, the trophic levels of species are defined for each local community separately.

3.3 Result

3.3.1 Metacommunity dynamics

In the absence of migration, the model indicates the switching dynamics between HTL and LTL, as shown in the previous chapter. Following chapter 2, I regard trophic-level-1 species, trophic-level-2 species, and higher-trophic-level species as plants, herbivores, and predators, respectively. Figure 3.1 shows the typical dynamics (abundance and species richness in top and bottom row, respectively) under the three different migration frequencies, i.e., no migration (Fig 3.1a,d, $m = 0$), intermediate migration (Fig. 3.1b,e, $m = 10^{-4}$), and frequent migration (Fig. 3.1c,f, $m = 10^{-2}$). In all cases, two local communities repeat collapse–rebuild cycle of trophic levels, i.e., transitions between HTL and LTL states. However, the observed time courses are qualitatively different among these three cases. When two local communities are isolated (Fig 3.1a,d, $m = 0$), both local communities tend to have predator species (species of which trophic level is higher than 3.5, HTL state), but transit to LTL state

independently. On the other hand, at the intermediate migration rate (Fig. 3.1b,e, $m = 10^{-4}$), either of the two local communities is likely to include predators. Under the frequent migration (Fig. 3.1c,f, $m = 10^{-2}$), two local communities tend to have the same maximum trophic levels and species richness simultaneously.

Based on the state of two local communities, a metacommunity can be classified to three types; (1) both local communities are HTL state (HH state), (2) both local communities are LTL state (LL state), and (3) one of the local communities is HTL and the other is LTL (HL state). By denoting the observed durations of HH, HL, and LL states as τ_{HH}, τ_{HL}, and τ_{LL}, respectively, the proportion of the HTL-local community in the metacommunity, can be determined as $p_{\mathrm{H}} = (2\tau_{\mathrm{HH}} + \tau_{\mathrm{HL}}) / T$, where $T = \tau_{\mathrm{HH}} + \tau_{\mathrm{HL}} + \tau_{\mathrm{LL}}$ is a total time length of the observations. In order to examine the correlation between states of two communities, I define $\tilde{p}_{\mathrm{H}} = 2\tau_{\mathrm{HH}} / (2\tau_{\mathrm{HH}} + \tau_{\mathrm{HL}})$, which represents the proportion of the HTL-local community if the other local community is HTL state. When the dynamics of two local communities are independent, p_{H} and $\tilde{p}_{\mathrm{H}}$ should be equal each other. If p_{H} is larger than $\tilde{p}_{\mathrm{H}}$, two local communities tend to be HTL state simultaneously. If p_{H} is smaller than $\tilde{p}_{\mathrm{H}}$, a local community tends not to be HTL state when the other is HTL state. Therefore, $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$ indicates correlation of local-communities' dynamics; the larger (or smaller) ratio than one can be interpreted as positive (or negative) bias on the occurrence of a HH metacommunity than the expected frequency under independent dynamics of two local-communities.

Figure 3.2a shows this ratio for different migration rates. With $m = 10^{-4}$ and 10^{-3}, the $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$ is significantly smaller than one, indicating that the HH state tends to occur less frequently that at random (Fig. 3.2a). The total number of species that are observed simultaneously in both local communities (referred by shared species) increases with the migration rate (dashed line in Fig. 3.2b). However, the time-averaged mean species richness of two local communities (time-averaged-α-species richness)

can be concave relationships to the migration rate (solid line in Fig. 3.2b), i.e., less diverse communities at the intermediate migration rate. The mean species richness of a local community is similar at the both ends of the migration rates suggests the similarity of local dynamics between those two parameter combinations (Fig. 3.2b, at $m = 0$, 10^{-2}). The number of shared species is greater at the frequent migrations, which indicates that two local communities could be understood as a single large community (Fig. 3.2b, at $m = 10^{-2}$). On the other hand, at intermediate migration rates, those local communities are still differentiated. However, the smaller average richness of a local community than other two cases (Fig. 3.2b, at $m = 10^{-4}$) suggests that the evolutionary dynamics of a local community is qualitatively different from that of the isolated community.

3.3.2 State dynamics

To understand the process that drives the correlation between two local communities, I investigate transition dynamics among three metacommunity states, HH, HL, and LL. The importance of those metacommunity-state transitions, e.g., a transition from an HH-state metacommunity to an HL-state metacommunity, can be quantified by the transition rate among those metacommunity states. For this quantification, I examine fates of migration events from one local community to the other. I prepare communities for the examination by following process. First, I sample HTL- and LTL-local communities from the results of realizations with bidirectional migration and create HTL-community pool and LTL-community pool. Second, I randomly choose two local communities from corresponding community pools, and make a metacommunity that consists of those chosen communities. Since those local communities are randomly chosen from community pools, they share almost no species, by which the effect of novel species' migrations will be indicated clearly. The migration is restricted to be unidirectional from one community (source community) to the other (sink community)

to separate the effect of reverse migration. Waiting time until the initial transition in the sink community is collected.

By assuming the probabilities of metacommunity-state transitions are constant during the observation period, I estimate the transition rate λ_Y^X, which represents the average frequency of transitions from a metacommunity state X to the other state Y ($X, Y \in \{\mathrm{HH}, \mathrm{HL}, \mathrm{LH}, \mathrm{LL}\}$, where $X = \mathrm{HL}$, for example, indicates the source community is H state and the sink community is L state), by dividing the total number of transitions by the sum of observation periods. Under the assumption of the constant transition probability, those estimated rates could be understood as maximum-likelihood estimations of transition rate. Both communities also have their own intrinsic evolutionary and population dynamics. Observations are stopped after the source-community's intrinsic state transition in order to avoid contaminations of sink's transitions caused by the source community with undesired state. Thus, the first letter in the metacommunity-state X always coincides to that in Y. According to the exclusion of state change of a source community, calculated transition rate consists of (1) immigration-induced state transitions of the sink community and (2) intrinsic state transition of the sink community (see also chapter 2).

Figure 3.3a illustrates estimated transition rates for various source–sink combinations among HTL and LTL communities. It shows that the frequent migration tends to promote all types of transitions. The values at $m = 0$ are the estimated transition rates without the effect of migration, which indicates the intrinsic dynamics of the local-sink community. The estimated transition rate from HH metacommunity to HL metacommunity ($\lambda_{\mathrm{HL}}^{\mathrm{HH}}$) is much larger than other transition rates (as the definition, in this case, the source community is in HTL state). It suggests that the collapse of HTL-local communitie is highly induced by migrants from other HTL-local community, which is a dominant event in the metacommunity dynamics.

To compare the dynamics of the source–sink model and the

bidirectional-migration model, I reconstruct the state dynamics under the bidirectional migrations using the transition rates that are estimated with the source–sink model. The estimated transition rates can be interpreted as conditional-transition rates of one local community given the state of the other local community (e.g., $\lambda_{\mathrm{HL}}^{\mathrm{HH}}$ can be interpreted as a collapse rate of an HTL-state-local community when the other community is also HTL). By letting a time-dependent frequency of a metacommunity to be state X as q_X ($X \in \{\mathrm{HH}, \mathrm{HL}, \mathrm{LL}\}$), a stationary point of a continuous-time-Markov chain (Eq. 3.1) gives the expected frequency distribution of those metacommunity states.

$$\begin{aligned}
&\frac{\mathrm{d}q_{\mathrm{HH}}}{\mathrm{d}t} = \lambda_{\mathrm{HH}}^{\mathrm{HL}} q_{\mathrm{HL}} - 2\lambda_{\mathrm{HL}}^{\mathrm{HH}} q_{\mathrm{HH}}, \\
&\frac{\mathrm{d}q_{\mathrm{HL}}}{\mathrm{d}t} = 2\lambda_{\mathrm{LH}}^{\mathrm{LL}} q_{\mathrm{LL}} + 2\lambda_{\mathrm{HL}}^{\mathrm{HH}} q_{\mathrm{HH}} - \lambda_{\mathrm{HH}}^{\mathrm{HL}} q_{\mathrm{HL}} - \lambda_{\mathrm{LL}}^{\mathrm{LH}} q_{\mathrm{HL}}, \\
&\frac{\mathrm{d}q_{\mathrm{LL}}}{\mathrm{dt}} = \lambda_{\mathrm{LL}}^{\mathrm{LH}} q_{\mathrm{HL}} - 2\lambda_{\mathrm{LH}}^{\mathrm{LL}} q_{\mathrm{LL}}, \\
&\text{where } q_{\mathrm{HH}} + q_{\mathrm{HL}} + q_{\mathrm{LL}} = 1.
\end{aligned} \tag{3.1}$$

Therefore, the expected frequency distribution of those metacommunity states $(p_{\mathrm{HH}}, p_{\mathrm{HL}}, p_{\mathrm{LL}})$ can be derived as $(p_{\mathrm{HH}}, p_{\mathrm{HL}}, p_{\mathrm{LL}}) = (c\lambda_{\mathrm{HH}}^{\mathrm{HL}}\lambda_{\mathrm{LH}}^{\mathrm{LL}}, 2c\lambda_{\mathrm{HL}}^{\mathrm{HH}}\lambda_{\mathrm{LH}}^{\mathrm{LL}}, c\lambda_{\mathrm{HL}}^{\mathrm{HH}}\lambda_{\mathrm{LL}}^{\mathrm{LH}})$, where $c = 1/(\lambda_{\mathrm{HH}}^{\mathrm{HL}}\lambda_{\mathrm{LH}}^{\mathrm{LL}} + 2\lambda_{\mathrm{HL}}^{\mathrm{HH}}\lambda_{\mathrm{LH}}^{\mathrm{LL}} + \lambda_{\mathrm{HL}}^{\mathrm{HH}}\lambda_{\mathrm{LL}}^{\mathrm{LH}})$ is a scaling term to keep the sum of those fractions to be one. The ratio $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$, which is argued at the last subsection, can be estimated from those expected frequencies.

A solid line in Fig. 3.3b illustrates this ratio $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$ estimated from the results of the source–sink model, which are shown at Fig. 3.3a (see also Fig. 3.2a for the corresponding result in the bidirectional-migration model). The estimations from a source–sink model indicate the decrease of the $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$ ratio when the migration rates are small to intermediate range (solid line in Fig. 3.3b). This decreasing tendency is qualitatively similar to the behavior of the $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$ ratio observed at the original bidirectional-migration model (Fig. 3.2a). In the source–sink model, the initial species compositions of two local communities are randomly chosen from community pools. Therefore, the source and sink communities do not share any species and a migrant

from the source community always introduces a novel species to the sink community. Although it is a rough approximation of differentiated local-species compositions observed in the bidirectional-migration model, it reproduces the decreasing tendency of $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$. Suggesting the importance of the migration of a novel species to destabilize HH-state metacommunity in the bidirectional-migration model. On the other hand, this source–sink model does not represent an increment of $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$ ratio at the frequent migration rates, which differs from that is observed at Fig. 3.2a. On this range of migration rates, species compositions of two local communities are similar and finally those two species compositions become almost identical under the bidirectional migration (see also a dashed line on Fig. 3.2b). Therefore, in the bidirectional-migration model, the introduction of a novel species is uncommon under the frequent migrations. However, the source–sink model still start from communities with fully differentiated species compositions, implying the frequent introduction of novel species to the sink community. Therefore, the inconsistent trend of $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$ ratio at the frequent migration rates could be understood as a consequence of different introduction frequencies of novel species between those two models.

If transitions from an HH-state metacommunity to an HL-state metacommunity (i.e., collapse of either one of local communities) have a dominant effect on the metacommunity dynamics, the trend of $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$ may be explained by such a transition only. In order to extract the effect of the collapse rate of an HH-state metacommunity on $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$, the expected frequency of HTL local community p_{H} is also derived from transition rates of which $\lambda_{\mathrm{HH}}^{\mathrm{HL}}$, $\lambda_{\mathrm{LH}}^{\mathrm{LL}}$, and $\lambda_{\mathrm{LL}}^{\mathrm{LH}}$ are replaced by values that are calculated in the absence of migration. Excluding the effect of migration except for $r_{\mathrm{HL}}^{\mathrm{HH}}$, this estimated $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$ monotonically decreases with the migration rate (dashed line in Fig 3.3b). It suggests that the transition rate from an HH-state metacommunity to an HL-state metacommunity can explain the decrease of $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$ ratio between no-migration and intermediate-migration rate observed in the

bidirectional-migration model. However, with increasing migration rate, frequencies of other transition rates, e.g., recovery rate from HL to HH state λ_{HH}^{HL}, also increase and become more significant (Fig. 3.3a). As a result, the estimated $\tilde{p}_H / p_H$ from λ_{HL}^{HH} alone indicates larger difference from the bidirectional-migration model than the estimations from all transition rates (Fig. 3.2a and Fig 3.3b).

3.3.3 Release from enemy and collapse of local community

Here, I investigate the characteristics of migrants that can trigger a collapse in order to understand the migration-driven collapse of an HTL-local community. Since I assume that all individuals have a restricted range of utilizable food items (i.e., foraging traits of a consumer must be similar to vulnerability traits of at least one resource species), any species tend to evolve to be specialist. In such a case, a consumer invader highly tends to go extinct quickly due to the absence of its target resource species. On the other hand, a plant invader can always find its depending resource because of the assumption of the same environmental parameters (e.g., identical vulnerability traits of the external resource). Therefore, I analyze the effects of migrant species by focusing on the invasion of a plant species.

According to chapter 2, the appearance of an enemy-released plant (e.g., after the extinction of its herbivore in the case of chapter 2) can trigger a transition from HTL state to LTL state. An invader plant can be released from its natural enemy in the invaded community. Therefore, by focusing on the plant invasion, the metacommunity dynamics of present model would be described. Here, I investigate the effect of a plant invader on a fate of a HTL community. Foraging traits of an invader plant are equal to the hypothetical vulnerability traits of the external resource $(0,0)$, although its vulnerability traits can be any combinations on the two-dimensional trait space. In order to demonstrate the impact of an invasion on the community with different richness, I randomly choose two typical HTL-state communities from the community pool that

described at the previous subsection, as examples of sink communities. One of them consists of 33 species (16 plants 15 herbivores, and two predators), and the other community consists of 15 species (eight plants, six herbivores, and a predator), namely, a rich-HTL community and a poor-HTL community, respectively.

Figures 3.4 and 3.5 illustrate the effect of invaders, which immigrate into the rich-HTL community and the poor-HTL community, respectively, on the fate of sink communities. Figures 3.4a and 3.5a indicate the invader's vulnerability trait that can trigger the collapse of the local community. The vulnerability traits triggering the collapse are indicated by dark color on the corresponding trait position. Circles indicate the foraging traits of resident species in the sink community to show the relationships between the existing foraging traits and the invader's vulnerability trait that can trigger the collapse. After the invasion, a collapse process of the sink community takes place the same process as described in chapter 2; it starts from the burst of non-palatable plants, then other plants decrease in abundance, and finally consumers supported by those plants go extinct from the sink community. In the well developed community, Fig 3.4a illustrates that the vulnerability-trait space is almost completely covered by resident consumers, in which only invaders with limited range of vulnerability traits can trigger the collapse. On the other hand, in the poor-HTL community illustrated at Fig. 3.5a, lots of vulnerability traits are not covered by resident consumers, allowing wide range of vulnerability traits of invaders to trigger the collapse.

Basically, only invaders that escape from foraging pressure, i.e., enemy released invaders, can trigger the collapse of the resident community (Figs. 3.4b, 3.5b). In addition to this, I also find another process that the trigger collapse, which is represented a foraging pressure from a predator species around a position (1.5,0) of Fig. 3.5a. In this case, an introduced-plant species provides additional resource for the endemic predator. Therefore, the abundance of the predator increases, then, the increased predation pressure decreases the abundance of resident herbivores. As a

consequence, predators overexploit herbivores and promote stochastic extinction of the resident herbivore species, which can trigger the transition to the LTL state.

3.4 Discussion

In this chapter, I investigated effects of migrations within a metacommunity on the dynamics of local communities using an individual-based model. Under the frequent migration, local communities synchronize each other, so that the two communities tend to be in the same state with an identical species composition. On the other hand, when the migration rate is very low, the waiting time before migration can be very large, which allows both local communities maintaining complex-food webs for long period even though these local communities consists of many endemic species (Fig. 3.2a). However, with an intermediate migration rate, two local communities do not only realize differentiated species compositions, but also exchange species at some level of migration. In such a case, the migrants are potentially released from their enemy, which can trigger the state transition of the invaded community. Accordingly, under the intermediate migrations, HH-state metacommunities are tended to be unstable and either local community quickly transits to LTL state, resulting in differentiation of the community state between the two local communities.

The previous theoretical studies predicted that the species diversity of a local community is maximized by an intermediate migration rate (Gonzalez *et al*., 2009; Loreau *et al*., 2003). Using a species-based model of the evolution of competing species, they reported that the average species richness of a local community has a maximum when the migration rate is frequent enough to prevents competitive exclusion but rare enough to prevent homogenization. In other words, the intermediate migration rates allow local communities to evolve different composition of species traits, by which each community will have many endemic species. The migration of those species potentially contributes to increase the species diversity of a local community. However, empirical

studies have indicated invasions of a novel plant species can significantly disturb a community by disturbing the existing trophic interactions or altering ecosystem's properties, e.g., nutrient cycling and energy budget (Mack *et al*., 2000, 2007; McCann 2000). It suggests that the invasion of an evolutionary differentiated species does not always result in an increase in species diversity, in particular when the foraging interactions are considered. The present study theoretically indicates that the migration among communities with different species compositions does not always result in the high species richness. Therefore, the emergence of spatial insurance at intermediate migration rates is not as simple consequence as it has been thought.

In the present analysis, I examined the effect of the invasion of a plant species on the HTL-state-sink communities. However, invasions of herbivores and predators, i.e., higher-trophic-level species, can occur in general. The invasion of consumers species also occurs in the present model, however, several properties of the present model weaken the influence of those invaders. First, an individual can utilize only resources with vulnerability traits that correspond to its foraging traits. Second, an individual cannot adapt its foraging trait quickly. Because of those properties, most of consumer invaders may not utilize resident species in the sink community, which will have different vulnerability traits from the resource species in the source community of invaders. Also the analysis in chapter 2 indicated the importance of unpalatable plants for the collapse of a community, so that I focused on the outcome of the plant invasions that may directly introduce enemy-released species into the sink community. The observed pattern from the present result is basically described by focusing on the plant invasion, however, it does not undermine the secondary extinction triggered by consumer invasions (e.g., Mack *et al*., 2000). For example, the generalist consumers have been considered to be more invasive than specialists (Dukes & Mooney, 1999). However, simple coevolutionary dynamics, which I used in the present model, tends to result in species specialized to a single type of resource (see also chapter 2). Therefore,

in the future work, the mechanisms of emergence and maintenance of specialist and generalist species should be clarified for further understanding of the effect of invaders on the eco-evolutionary dynamics of a metacommunity.

The release from enemies in the invading habitat has been considered as a potential reason of the invader's success, which is so-called enemy-release hypothesis (Elton, 1958; Keane & Crawley, 2002; Maron & Vilà, 2001; Mitchell & Power, 2003; Naeem *et al*., 2000; Ren & Zhang, 2009; Shea & Chesson, 2002). The present result indicates clear linkage between the release from the foraging pressure and the collapse probability of the invaded community, supporting the enemy-release hypothesis. The present analysis also indicates that an invasion of species with extreme vulnerability traits, which are assumed to be costly, tend to cause the collapse of community (see Fig. 3.4). Since the costly vulnerability traits can be regarded as costly defensive traits against attacks of its natural enemy in some cases, the present analysis predicts a positive correlation between defensive ability and invasive ability in herbivores. It corresponds with a statistical suggestion of meta-analysis of observations (Ren & Zhang, 2009).

The present result indicates that a species-rich community due to the diversity of foraging traits, which prevents invaders to be enemy released (see Figs. 3.4, 3.5). From empirical observations, Elton (1958) proposed a hypothesis that the diversity of a community correlates negatively to the invasion success. Although the opposite correlation is sometimes observed in particular when there are spatial variances in environment condition and population dynamics (Fridley *et al*., 2007), the negative correlation between invasion success and species richness is supported by various empirical studies (Fargione & Tilman, 2005; Levine *et al*., 2004; Naeem *et al*., 2000; Prieur-Richard & Lavorel, 2000; Stachowicz *et al*., 1999), also some empirical observations suggested, in some cases, the negative correlation between the impact of invader and species richness (Dukes 2001, 2002). If the enemy-released invaders are the

major cause of triggering the collapse as observed in the present result, the diversity of foraging traits may restrict the types of invaders that potentially have impact. It could be considered as a possible mechanism that the trophic interactions introduce the negative correlation between species richness and the impact of invaders.

By extending the previous model to the metacommunity scale, I investigated the relationships between the eco-evolutionary dynamics of a community and migrations between two local communities. The resultant dynamics suggests the importance of an enemy-released invader on the large transition of the community-state. The analysis also suggests the species richness can be minimized at the intermediate frequency of invasions, when trophic interactions are included. The evolutionary dynamics clarified in this chapter will contribute to understanding the evolutionary-timescale effect of the invaders on the meta- and local community dynamics.

Figures

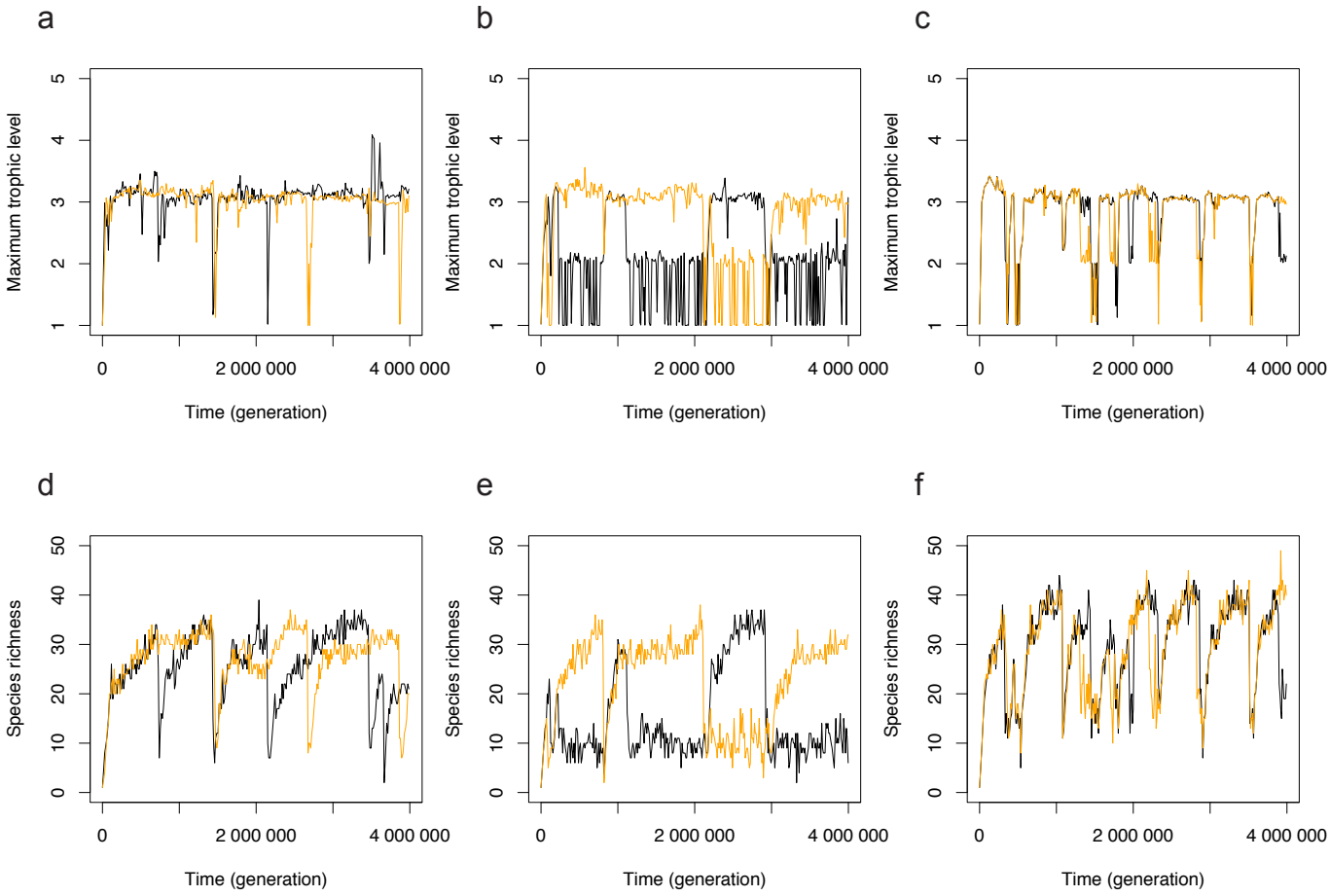

Figure 3.1: The time courses of the state dynamics of a metacommunity. Orange and black curves indicate observed results in two local communities. Each column corresponds to the different levels of migration rates, (a,d) without migration ($m = 0$), (b,e) intermediate migration ($m = 10^{-4}$) and (c,f) frequent migration ($m = 10^{-2}$). Panels (a-c) indicate the time courses of the maximum-trophic level observed in each local community, and panels (d-f) show the species richness.

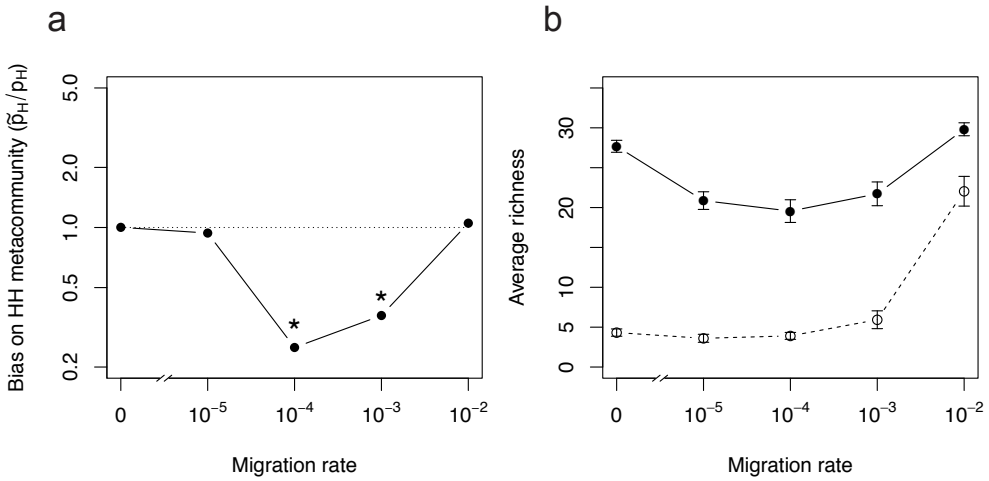

Figure 3.2: Properties of evolved communities. (a) The bias on the HH-metacommunity occurrence ($\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$) is plotted to the migration rate. Stars indicate statistically significant difference between p_{H} and $\tilde{p}_{\mathrm{H}}$ (Welch's t-test, $p < 0.05$). (b) Two types of species richness are indicated to the migration rates. Solid line indicate the time-average of mean species richness of two local communities, whereas dashed line is the time-average of the number of species that observed simultaneously in both local communities. Each plot is on average of five trials with an error bar (standard deviation),

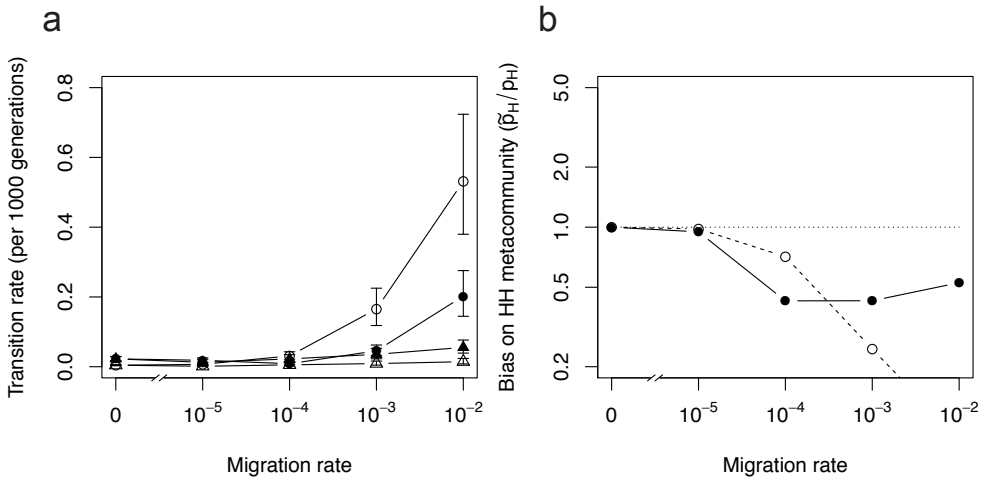

Figure 3.3: Transition dynamics on the source–sink model. (a) Lines indicate the mean estimated transition rate, which is an average of estimations of 40 trials. Error bars represent 95% confidence intervals under the assumption of exponentially distributed waiting time to the transition. Open circles, closed circles, open triangles, and closed triangles indicate transition rates from HH metacommunity to HL metacommunity ($\lambda_{\mathrm{HL}}^{\mathrm{HH}}$), from HL to HH ($\lambda_{\mathrm{HH}}^{\mathrm{HL}}$), from LH to LL ($\lambda_{\mathrm{LL}}^{\mathrm{LH}}$), and from LL to LH ($\lambda_{\mathrm{LH}}^{\mathrm{LL}}$), respectively. (b) Lines indicate the bias on the HH-metacommunity occurrence ($\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$) in reconstructed bidirectional-migration dynamics based on estimation from the source–sink model (panel (a)). Solid line indicates $\tilde{p}_{\mathrm{H}} / p_{\mathrm{H}}$ of state dynamics estimated using all transition rates. Dashed line indicates the ratio, in which a rate of transition from HH to HL ($\lambda_{\mathrm{HL}}^{\mathrm{HH}}$) is estimated from the source–sink model (as each plot in panes (a)) but those of other types of transitions are estimated in the absence of migration (was a plot at migration rate = 0 in panel (a)).

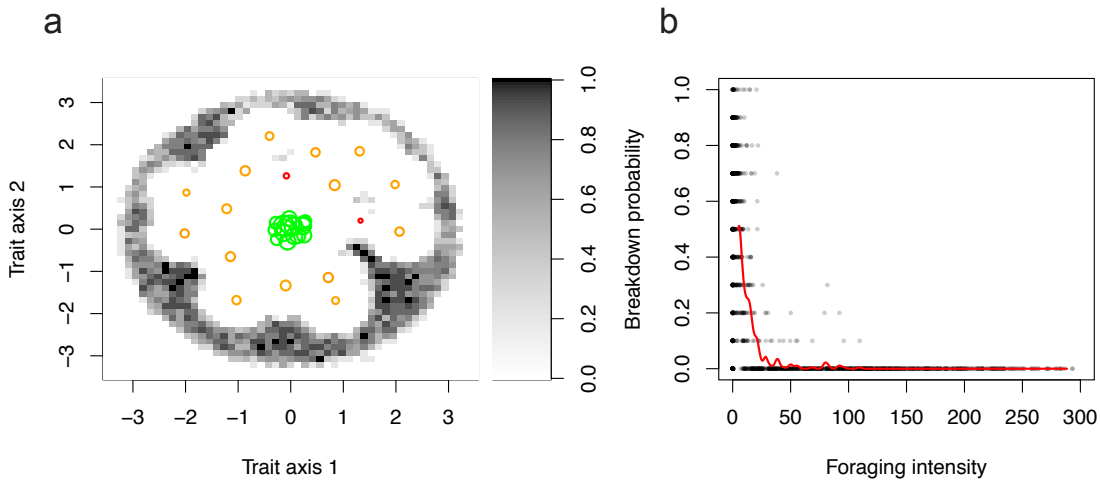

Figure 3.4: Relationships between the invader's vulnerability and the possibility of collapse of rich-HTL community. (a) Darker area indicates the higher probability of the collapse caused by an invading species with corresponding vulnerability traits. Green, orange, and red circles indicate the foraging traits of plants, herbivores, and predators, respectively. (b) Relationships between foraging pressure on invaders and probability of collapse. A red curve indicates the moving average convolved by Gaussian distribution of collapse probability as a function of the intensity of foraging pressure. Ten trials are conducted for each combination of vulnerability traits.

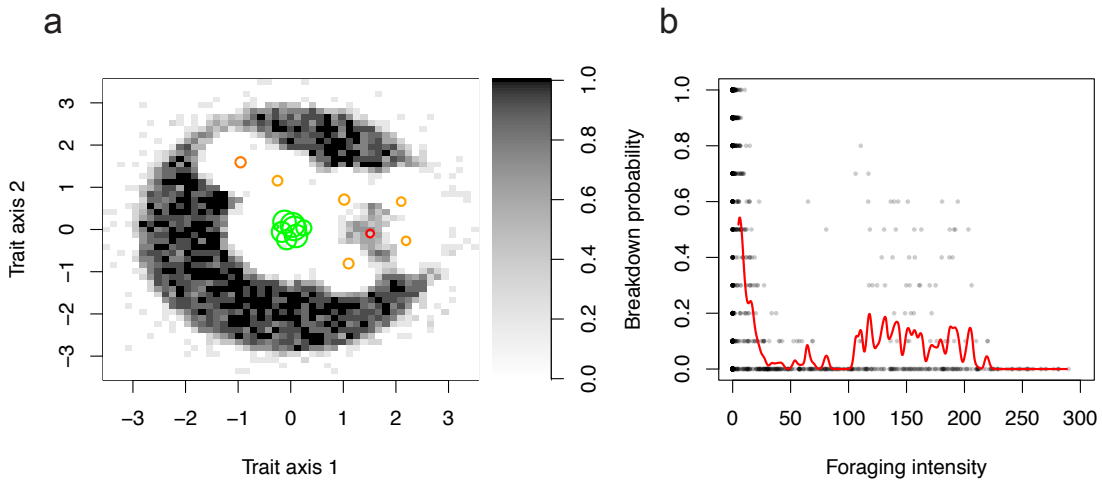

Figure 3.5: Relationships between the invader's vulnerability and the possibility of collapse of poor-HTL community. All conditions but an initial sink community are the same as Fig. 3.4. (a) Probability of the collapse on the trait space. (b) Relationships between foraging pressure on invaders and probability of collapse. A peak around the intermediate foraging intensity corresponds to the invaders that predated by trophic-level-3 consumers, i.e., predators (large collapse probability around (1.5,0) of the left panel).

Chapter 4. General discussion

Importance of eco-evolutionary processes in community dynamics

The emergence and maintenance processes of a diverse community are the central questions to understand in the complex-food webs that are empirically observed. Ecological interactions, e.g., trophic interactions, will directly affect the stability of those food webs, however, those ecological interactions among organisms would be modified by evolutionary dynamics. Therefore, we need to reveal both ecological and evolutionary processes that control the emergence and maintenance of complex-food webs. Theoretical models suggest that the evolution promotes the emergence of repeating collapse and reemergence of complex-food webs (Alhoff & Drossel 2013; Christensen *et al*., 2002; Guill & Drossel, 2008; Ito & Ikegami, 2006; Rossberg *et al*., 2008; Rikvold, 2007, 2009; Rikvold & Sevim, 2007; Sevim & Rikvold, 2005). However, the detailed processes and mechanisms have not been investigated.

Using an individual-based model, the model that is developed here successfully couples ecological processes and evolutionary processes into a single time scale. With this coupling, the evolutionary process, e.g., the process during speciation and extinction, and the process of population dynamics can be investigated in the same time scale. Although those evolutionary and population dynamics are sometimes considered as dynamics with different time scales, empirical evidence of evolution has been accumulating which suggests that evolutionary dynamics may be as fast as population dynamics (Yoshida *et al*., 2003; reviewed at Jones *et al*., 2009). Therefore, we cannot presume separate time scales for those two processes. As an individual-based model, the present model determines all dynamics from the dynamics of each individual based on the inter-individual interactions. Although it does not assume the existence of species a priori, the result indicates the evolutionary dynamics of clusters in the trait space, which can be interpreted as an individual-based explanation of species dynamics.

Therefore, the present model includes the species-formation process, which is implicitly assumed at the model that based on the dynamics of species. It will give the eco-evolutionary bases of evolutionary dynamics that was investigated by species-based models.

Early works using a simple theoretical model (Bak & Sneppen, 1993; Bak & Paczuski, 1997) suggested the evolutionary dynamics within a large community could be a cycle of intermittent bursts interposed with stable periods. After the pioneer work of the Bak & Sneppen (1993), some previous theoretical research of the food-web evolution indicated the sudden collapse of a complex community even without any disturbance from outside of the system (Christensen *et al*., 2002; Guill & Drossel, 2008; Ito & Ikegami, 2006; Rossberg *et al*., 2008; Rikvold, 2007, 2009; Rikvold & Sevim, 2007; Sevim & Rikvold, 2005). The sudden community collapse implies that the coevolution of species potentially brings a community to a certain fragile state, in which a large secondary extinction after the trigger event (e.g., a species extinction or other intrinsic disturbances) happens. However, its mechanism has not been clarified, and further investigations are inevitably necessary to understand these dynamics. To understand the detailed processes and mechanisms of the cycle and the sudden collapse, a model that is based on more detailed dynamics is needed. Using an individual-based model, instead of species-based models that have been used by most of previous theoretical works, I investigated those mechanisms, based on the birth and the death of an individual. To explain the eco-evolutionary process of food web dynamics, the detailed eco-evolutionary process should be clarified by using the individual-based model.

In chapter 2, I investigated the individual-based model of evolving food webs and reveal the detailed eco-evolutionary processes of emergence and collapse of a community, which had been overlooked by previous species-based models. When a complex community emerges, the strong foraging pressure promotes differentiation of a

plant species, which is followed by the adaptation and speciation of an herbivore species. When it corrupts, an extinction of an herbivore species releases a plant species from foraging pressure, which eventually induces the secondary extinction of herbivores by competition-induced abundance-decrease of other plant species. In other words, these observed results are a consequence of the tight relationships among the lowest-trophic-level species (i.e., plants) and their direct consumers (i.e., herbivores).

The analysis in chapter 2 revealed the existence of two qualitatively different states of a community and eco-evolutional processes during the state transition of a community. However, the model considered the dynamics on a single community, where all species are introduced by speciation within a community. In general, the migration among multiple communities can also be a source of a new species. The migration of a novel species from a parapatric community has been considered as one of the ecological mechanisms to increase biodiversity of a community (e.g., Hubbel's neutral theory that based on speciation, extinction and migration, Hubbel, 2006). However, empirical studies suggest that the applicability of this simple view is unclear in particular when the migration occurs in the same time scale as the trait evolution (Fukami *et al*., 2007; Urban *et al*., 2008). These studies indicate that both evolution and migration should be included in the model of a community to understand the dynamics of a community. Unlike a species introduced by mutations, migrations can introduce a species that are not relatives of resident species. Therefore, the interactions between the immigrant species and other species may also be dissimilar from any resident species. If a migrant is significantly different from any of the resident species, the migrant can alter the dynamics of the immigrated community by introducing new interspecific interactions.

Therefore, the effect of migrants on the eco-evolutionary dynamics of a community should be included in addition to the mutations. By extending the model into the metacommunity scale, in chapter 3, I investigated the effect of migration on the

dynamics of a community. I indicated the frequent community collapse at the intermediate levels of migration rate, where migrations are rare enough to allow species in a community to evolve almost independently from species in other communities. As shown in chapter 2, the evolutionary change in trophic interactions can potentially result in an emergence of plants free from herbivory pressure in a community, which can trigger a collapse of the community. It is the opposite result from the previous theoretical models with evolution of competitive ability (Loreau *et al*., 2003; Gonzalez *et al*., 2009), where those models predict the highest species richness at the intermediate migration rate. Experimental research using bacteria supported it assuming the dynamics are purely determined by competition (Fukami *et al*., 2007; Urban *et al*., 2008), however, the effect of trophic interactions on the community dynamics was overlooked in these studies. The present result, i.e., low richness at intermediate migration rate, indicates that the existence and evolution of trophic interactions can totally alter the community's response to the migrants. Therefore, the trophic interaction cannot be ignored when we consider the biodiversity and metacommunity structure.

The driving forces behind a community's state transitions

For every evolutionary and population dynamic, the major driving force at work is an essential question to understand these dynamics. In the present model, the interactions between plant and herbivore promotes the state transition of a community, and the migration of enemy-free plants explains the instability of a complex metacommunity. Those results suggest the potential importance of evolution-determined interactions between plants and herbivores to understand the mechanism of emergence and collapse of an empirical community and the dynamics of that metacommunity.

On the emergence of a complex community, empirical research has revealed that the types of defensive chemical, which could be interpreted as vulnerability traits, correlate to the phylogeny of the plants (Agrawal, 2007; Liscombe, *et al*., 2005; Wink,

2003; Wink & Mohamed, 2003). It suggests that the diversification process observed in the present model emphasizes the potential importance of coevolution between the plant defense and herbivore counter-adaptation on the emergence of diverse community. Indeed, the phylogenies of host plants and herbivores tend to be correlated each other (Mitter *et al*., 1991), suggesting that the present scenario of coevolutionary diversification of plants and herbivores is one of the important factor to explain the diversity of the natural communities.

On the other hand, the present result also indicates the importance of plant–herbivore interactions for the collapse process of a complex community. Similar to the community collapse process in the present model, Ebenman *et al*. (2004) theoretically showed that the removal of an herbivore would have much larger risk to start a cascade of secondary extinction than the removal of predators. They suggested that the existence of interspecific competition among plants might be a cause of a larger effect of an herbivore removal than that of a predator. By direct investigation of the processes of community collapse, I also theoretically revealed that the secondary extinction of consumers is driven by the decreased abundance in the host plants, which is caused by the strong competitive pressure from the enemy-released plant.

The bacteria–bacteriophage system is an experimental model system of eco-evolutionary process, which is driven by prey–predator interactions (Campbell, 1961; Lenski & Levin, 1985; reviewed at Bohannan & Lenski, 2000). A bacteriophage evolves its infectious ability, while in turn a bacteria evolves resistance against phages. Based on an experiment, Bohannan & Lenski (2000) proposed a scenario of a community's evolutionary trajectory, the trait diversification was followed by a sudden "mass extinction" when a costless-resistant mutant appeared. Their scenario is similar to the scenario that I suggest in this thesis, by considering bacteria and phage as producers and herbivores. However, the interference competition, which is a key mechanism to drive community collapse at the present model, seems to be weak in the bacterial

system. Instead, the scramble competition between costless-resistant mutant and others is considered to be a cause of the mutant's dominance in the bacterial community (Bohannan & Lenski, 2000). However, the similarity between their scenario and the present eco-evolutionary process suggests that the difference of these two mechanisms of competition do not largely effect on the applicability of the present result.

Self-organization of species by eco-evolutionary process

Although the present model is individual-based and does not postulate the existence of species, the resultant individuals' distribution in a trait space is self-organized into clusters. Each cluster consists of individuals that share the same trophic traits. Therefore, the cluster formation can be regarded as an evolutionary emergence of a trophic species, which is a functional group of taxa that share the same set of predators and prey and is widely accepted in theoretical food-web studies (Dunne *et al*., 2002; Pimm *et al*., 1991; Williams & Martinez, 2000). The species-formation process that is observed in the present model corresponds to the cluster formation, which is reported by Ito & Ikegami (2006) and Ito *et al*. (2009). Although their simulations focused on a model with a one-dimensional-foraging trait and a one-dimensional-vulnerability trait only, the present models show that similar species formation processes are possible in individual-based models on a multiple-dimensional-trait space, even with migrantions. The process of each co-speciation of plant and its herbivore in the present analysis agrees with the coevolutionary dynamics of a one-predator-one-prey system (Doebeli & Dieckmann, 2000), i.e., a prey species initially diversifies its vulnerability, and a predator species substantially adopts its foraging trait to the diversified prey species.

Counterintuitively, the stochastic evolution can help the formation of clusters in the trait space. Rogers *et al*., (2012) indicated a theoretical background of the maintenance of the clusters in a trait space, i.e., species, from the stochastic nature of the model. They theoretically examined the cluster formation of competing organisms,

and found the clustered distribution tends to be maintained when the demographic stochasticity is strong, compare to the fluctuation induced by mutations. It suggests that the gradual evolution with small effect of mutations is a key assumption in the present model for the evolutionary-time-scale maintenance of distinctive species on the trait space.

Constraints and limitations of the model

The assumptions of the present model are based on our ecological knowledge, e.g., birth–death process based on the trophic interactions. However, it is not possible to include all aspects of the natural community in the model, and to greater or less extent, those assumptions need to be simplified due to the computational demand. Those simplifications may result in drawbacks of the model, so that I need to care about their interpretations. One of those simplifications is the absence of the intrinsic distinction between producers (individuals that can use external resource) and consumers (individuals that can forage on other individuals instead of external resource). This is one of the common assumptions of the theoretical model of evolutionary-food web (e.g., Caldarelli *et al*., 1998; Christensen *et al*., 2002; Drossel *et al*., 2001, 2004; Guill & Drossel, 2008; Ingram *et al*., 2009; to *et al*., 2009; Rikvold, 2007, 2009; Rikvold & Sevim, 2007; Rossberg *et al*., 2005, 2006), which potentially allows the evolution of producers to be a consumer and vice versa. It may be unrealistic that producer and consumer species change their own trophic positions each other. However, it should be noted that such a transition is not frequent even in the present model. In the model, after the community collapse, producers that share the similar vulnerability traits eventually become dominant. In this case, the benefit of resource switching becomes high due to the severe interference competition, which can trigger the reemergence process of consumers from producers. On the other hand, when herbivores exist, plant species differentiate their vulnerability traits due to the disruptive selection caused by the strong

foraging pressure. As a consequence, vulnerability traits of a plant population are divided into many vulnerability clusters, abundances of which clusters and consumer species are too small to facilitate evolutionary switching of plant species to utilize other organisms. Accordingly, in this case, organisms are unlikely to switch their trophic positions, suggesting a rareness of reciprocal evolution between plants and animals after a complex community starts to emerge. This may corresponds to rareness of evolution between producers and consumer in nature.

By using the individual-based model, the present model naturally introduces demographic stochasticity into the population dynamics within a community. However, environmental parameters, e.g., the quantity of external resource, were treated as constants during a realization. Theoretical studies have shown the structure of the evolved community also depends on the intensity of the environmental stochasticity, e.g., the quantity of external resource (Loreau *et al*., 2003) and the frequency of random background extinction (Hironaga & Yamamura, 2010). While the present analysis propose the biological mechanisms of the complex dynamics of a local community and a metacommunity, the effect of environmental stochasticity on these dynamics is needed to investigate in future.

Instead of a community with both specialist and generalist consumers, the most of the consumers (herbivores in particular) in the community, which are evolved from the present model, are specialists. The evolution of those specialists is driven by the differentiation of producers and adaptation of consumers. In the present study, I assume that an individual can utilize resource with a restricted range of vulnerability, which prevents the evolution of generalists after the diversification of prey species, in particular, producers. Indeed, in both mutualistic interactions and antagonistic interactions, specialists are common, although many communities have been considered to have generalist species to some degree (Poisot *et al*., 2011). The compiled empirical observations suggest that the specialization on different resource has been remarkably

successful in explaining patterns of animals' diversity, but less successful for plant species (Miller *et al*., 2005; Poisot *et al*., 2011), which suggests a tendency of a consumer to be a specialist. In addition, many apparent generalists can be in fact a group of specialist individuals (Bolnick *et al*., 2002). Therefore, the present analysis that tends to result in specialists can contribute to understand the dynamics of real communities.

The evolution of trophic traits of species can be in fact very rapid (Grant & Grant, 2002; Jones *et al*., 2009; Yoshida *et al*., 2003). An experimental investigation suggests that tens of generations are enough to evolve an escape-ability in a prey population (O'Steen *et al*., 2002). However, the present model takes more than ten thousand generations to complete the transition from LTL-state communities to HTL-state community by the prey–predator coevolution (see chapter 2, Fig. 2.4a,b). One reason of this mismatch between the speed of those rapid evolution and the speed of the transitional process after the emergence of herbivore may come from the selected parameter set, where I assumed relatively small probability of mutation due to the computational constraint. In addition, these observations focused on the single adaptation event, whole the accumulation of those prey–predator adaptations including speciation of those species are needed for the transition process from the LTL-state community to the HTL-state community. Therefore, even though every evolution of prey and predator is fast, the transition of a community state may take quite a long time compared to each evolutionary adaptation.

Conclusion

There is a growing evidence of dynamic relationships between evolution and ecology within a community (Fussman *et al*., 2007; Johnson & Stinchcombe, 2007; Pelletier *et al*., 2009; Post & Palkovacs, 2009). These relationships indicate the generality of the eco-evolutionary process in natural communities, therefore, the research on the dynamic

aspect of a community should include both ecological and evolutionary viewpoints. The model presented in this thesis derives the evolutionary dynamics of species, e.g., speciation and extinction, and the composition in an evolved community (or in a metacommunity), from ecological process, i.e., birth and death of an individual by trophic and competitive interactions. Therefore, the present model has ability to investigate the detailed processes and mechanisms of evolutionary dynamics of a community.

In the evolutionary time scale, previous theoretical models of evolutionary-food web showed the collapse and reemergence of complex communities (Alhoff & Drossel 2013; Christensen *et al*., 2002; Guill & Drossel, 2008; Ito & Ikegami, 2006; Rossberg *et al*., 2008; Rikvold, 2007, 2009; Rikvold & Sevim, 2007; Sevim & Rikvold, 2005), suggesting the evolutionary emergence of unstable communities. Alhoff & Drossel (2013) theoretically indicated that the larger degree of freedom of the evolution could result in the evolution of a complex but unstable community, which may correspond to the evolution to the unstable community observed from the present model. On this thesis, I clarified a mechanism of the unstable dynamics by investigation on the intermittent collapse and reemergence of a complex community.

In addition, I suggest that instability can significantly alter the dynamics of the metacommunity. Even when the model is extended to the metacommunity scale, the present results show the intermittent collapse and the reemergence of local communities. However, the evolutionary dynamics of local communities depends on the frequency of migrations. Frequent migrations synchronize local communities, while rare migration allows differentiation of species compositions of local communities. The analysis indicates that the probability of migration-induced-community collapse is maximized when the migration is intermediate range that is rare enough to allow differentiation of local communities but frequent enough to disturb migrated community. The clarified mechanisms of those dynamics indicate that evolutionary changing of interspecific

interaction is an important determinant of the metacommunity dynamics.

The result that presented here indicates the importance of the balance between the diversification of the forging traits and that of the vulnerability traits on the dynamics and persistence of a community. (1) When the evolution in a local community is a major source of diversity, the foraging traits should evolve sufficiently more rapid than vulnerability traits to construct a complex food web. (2) On the other hand, when migrants exist, plant migrants contribute to the increase of vulnerability-traits diversity while consumer migrant do not always contribute the diversity of foraging traits due to the lack of its target resource. As a consequence, some mechanisms that increase the diversity of foraging traits, e.g., even more rapid evolution of the foraging traits, will be needed. These indicate that the empirical identification and quantification of those trophic traits are the important challenge for future research to understand the long-term fate of a community.

Those two present models start from assumptions of the eco-evolutionary processes and observe the emergence of complex communities and dynamics of them. The dynamics of these two models are complex, but ecological and evolutional mechanisms explain both of them. Therefore, results of the present analysis contribute to the mechanistic understanding of the eco-evolutionary dynamics on the emergence and maintenance of food web.

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Appendix A. Robustness of the abrupt community-state transition

In this appendix, I show the robustness of the intermittent eco-evolutionary dynamics of a single community that is indicated and analyzed on the chapter 2 is illustrated. As summarized in Section 2.3.4 of the main text, I test the effects of different choices of the cost minimum for vulnerability traits (Fig. A.1), trait-space dimensionalities (one-dimensional and three-dimensional foraging and vulnerability trait vectors, Fig. A.2), larger trophic efficiency ($a = 0.9$; Fig. A.3), larger abundance of the external resource ($N_{\mathrm{R}} = 9{,}000$; Fig. A.4), and different combinations of the scales of foraging intensities ($C_{\mathrm{F}} = 0.45$, 0.9, and 1.8) and interference-competition intensities ($C_{\mathrm{I}} = 0.05$, 0.1, and 0.2; Fig. A.5a,b). Furthermore, I relax the assumption of equal variances of the offspring trait distributions for foraging and vulnerability traits ($\sigma_{\mathrm{m,f}} = 0.01$ and 0.09 with $\sigma_{\mathrm{m,v}} = 0.03$; Fig. A.6). Finally, I introduce handling times, leading to a Holling's type-II functional response instead of a linear functional response, in which large and small handling times ($h = 1/8{,}000$, and $1/800$; Fig. A.7). As discussed in Section 2.3.4 of the main text, cyclic transitions are observed in nearly all resultants evolving communities.

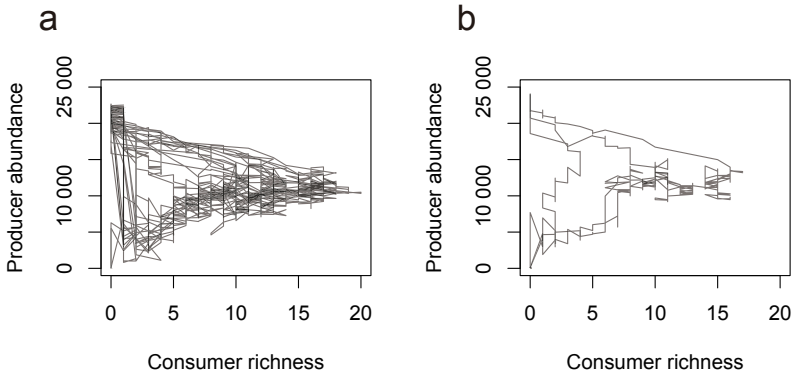

Figure A.1: Robustness with respect to altering the cost minimum for vulnerability traits. The choices of the position of the cost minimum of panels (a) and (b) are $(1,0)$ and $(2.5,0)$, respectively, correspond to a moderate distance and a large distance of the cost minimum from the vulnerability trait vector of the external resource. For moderate distance, the result remains qualitatively unchanged (a), whereas larger distance makes the re-emergence of the trophic structure to be difficult (b).

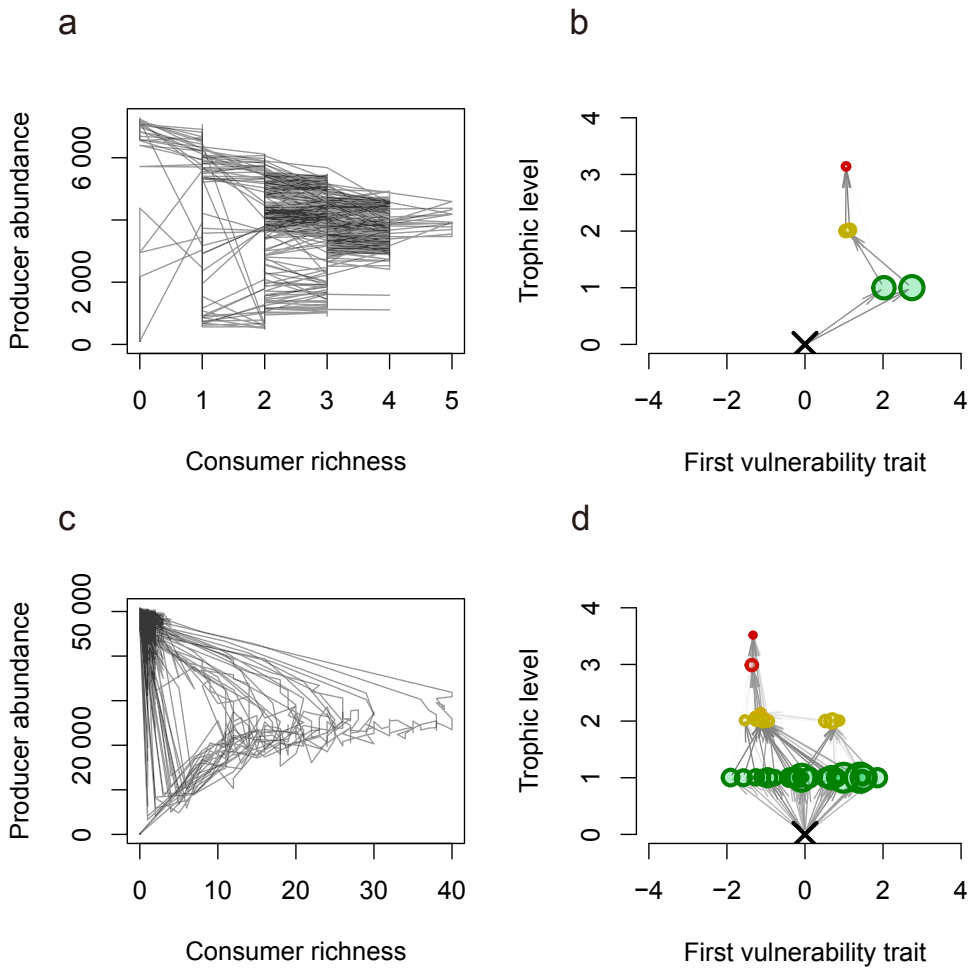

Figure A.2: Robustness with respect to altering the trait-space dimensionality. We show results for a one-dimensional trait space (a, b) and a three-dimensional trait space (c, d). (a, c) Trajectories show the time course of consumer richness and producer abundance. Each time course is obtained from three independent model runs. (b, d) Circles represent species, with their areas being proportional to the species' abundance, their vertical positions indicating the species' trophic level, and their horizontal positions indicating the species' first vulnerability trait. The cross at trophic level 0 represents the external resource. Arrows indicate trophic links, with darker colors indicating stronger interactions. Cyclic transitions between the HTL state and the LTL state are observed both for a one-dimensional trait space (a, b) and for a

three-dimensional trait space (c, d), with the relative duration of the LTL state increasing with the dimensionality. Snapshots of the corresponding HTL states show that species richness significantly increases with trait-space dimensionality (b, d).

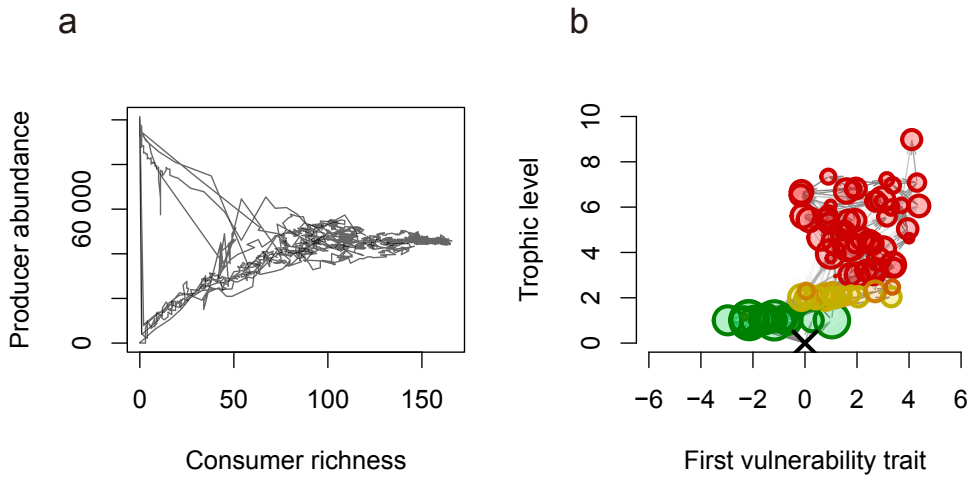

Figure A.3: Robustness with respect to increased trophic efficiency, $a = 0.9$. (a) Trajectories show the time course of consumer richness and producer abundance obtained from a single model run. (b) Circles represent species, with their areas being proportional to the species' abundance, their vertical positions indicating the species' trophic level, and their horizontal positions indicating the species' first vulnerability trait. The cross at trophic level 0 represents the external resource. Arrows indicate trophic links, with darker colors indicating stronger interactions. The community's overall behavior remains the same, except for higher trophic levels and larger species richness.

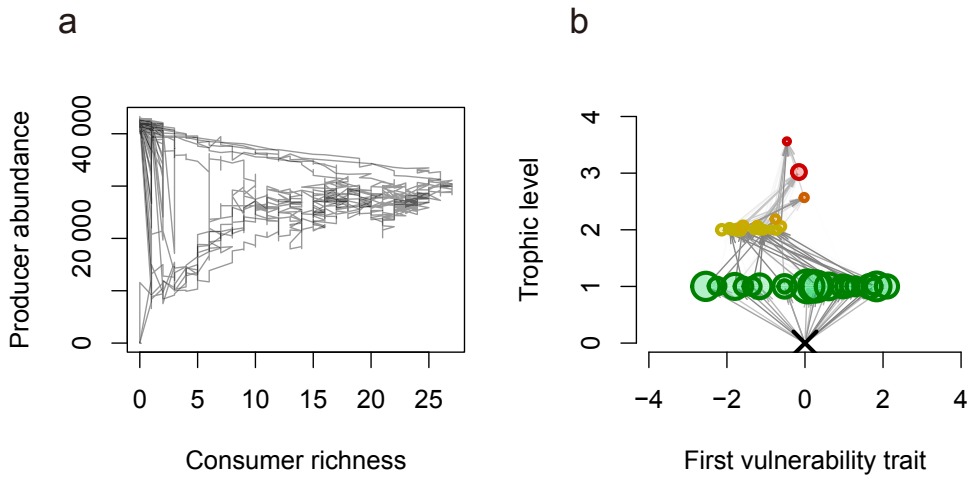

Figure A.4: Robustness with respect to increased abundance of the external resource, $N_R = 9{,}000$. (a) Trajectories show the time course of consumer richness and producer abundance obtained from three independent model runs. (b) Circles represent species, with their areas being proportional to the species' abundance, their vertical positions indicating the species' trophic level, and their horizontal positions indicating the species' first vulnerability trait. The cross at trophic level 0 represents the external resource. Arrows indicate trophic links, with darker color indicating stronger interactions. The community's overall behavior remains similar, except for a prolonged duration of the HTL state.

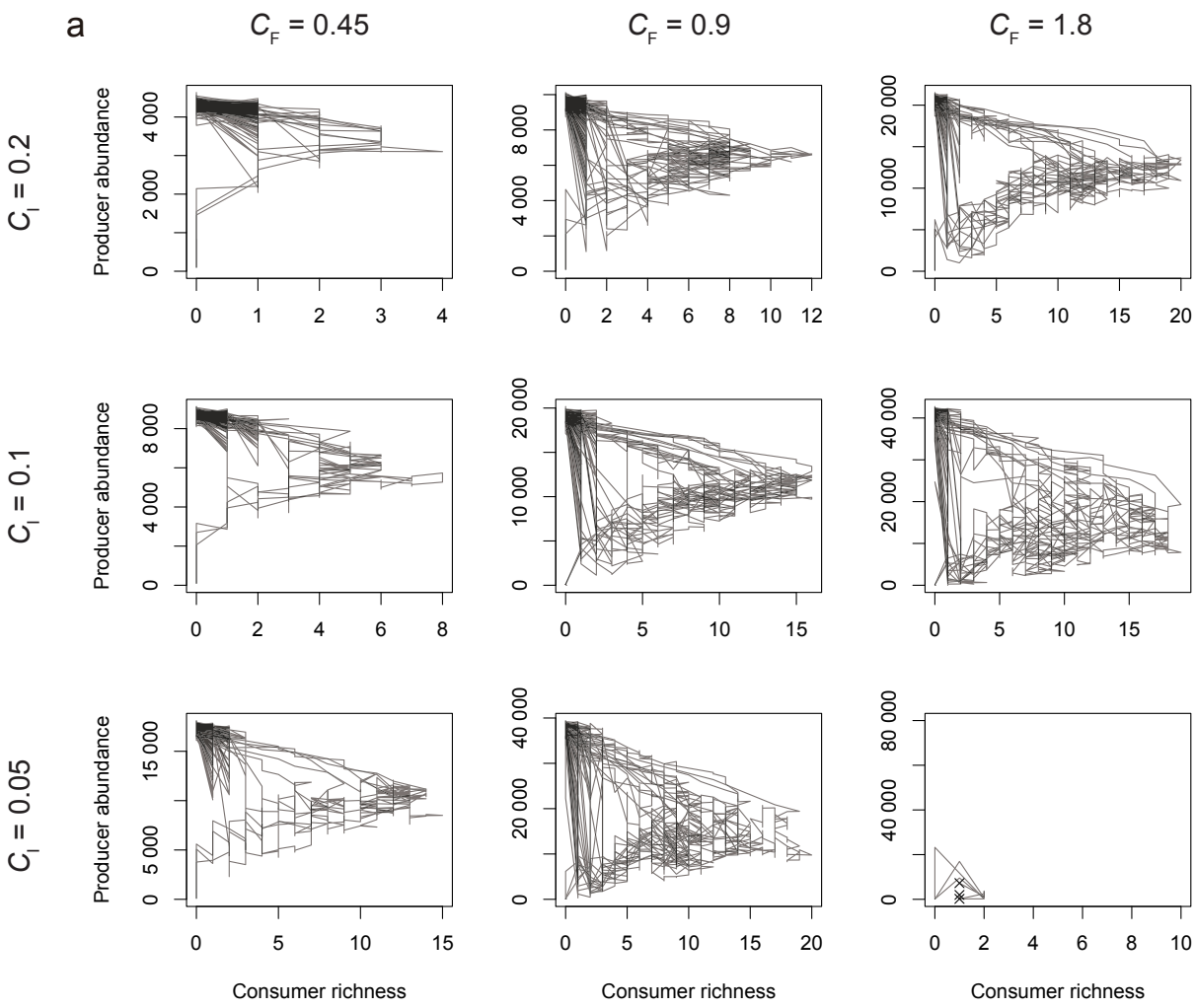

Figure A.5a: Robustness with respect to altering the scales of foraging intensities (C_F) and interference-competition intensities (C_I): effect on cyclic dynamics. Trajectories show the time course of consumer richness and producer abundance obtained from three model runs. Consumers rarely re-emerge when foraging intensities are low and interference competition is strong ($C_F = 0.45$ and $C_I = 0.1$, 0.2). Communities quickly become extinct (cross marks) when foraging intensities are high and interference competition is weak ($C_F = 0.2$ and $C_I = 0.05$). Otherwise, cyclic transitions between the HTL state and the LTL state are observed.

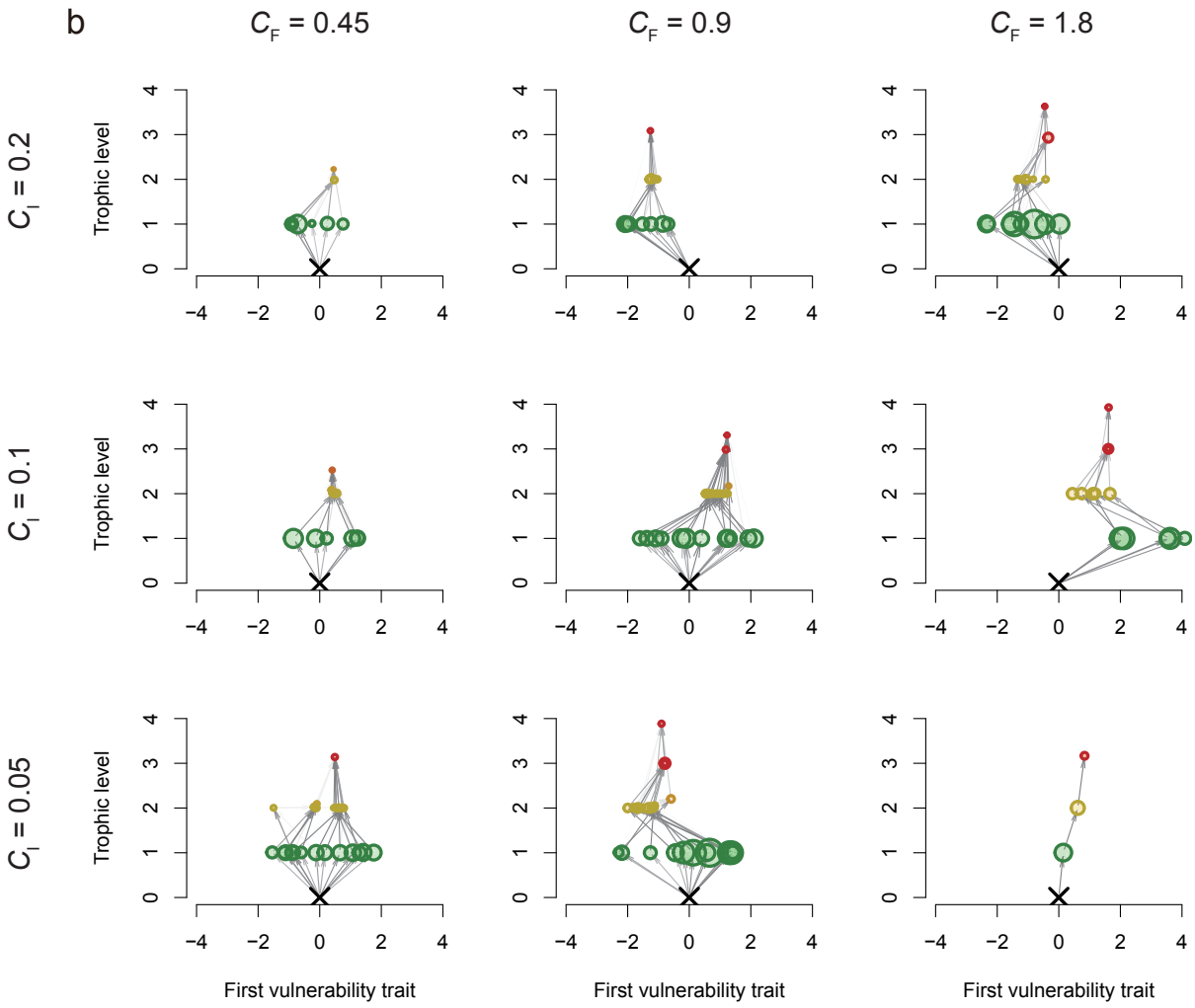

Figure A.5b: Robustness with respect to altering the scales of foraging intensity (C_F) and interference-competition intensity (C_I): effect on community structure. Circles represent species, with their areas being proportional to the species' abundance, their vertical positions indicating the species' trophic level, and their horizontal positions indicating the species' first vulnerability trait. The cross at trophic level 0 represents the external resource. Arrows indicate trophic links, with darker color indicating stronger interactions. The bottom-right panel shows a community just before its extinction (see also the corresponding panel in Fig. 2.A5a). Low foraging intensities (small C_F) tend to reduce the maximum trophic level.

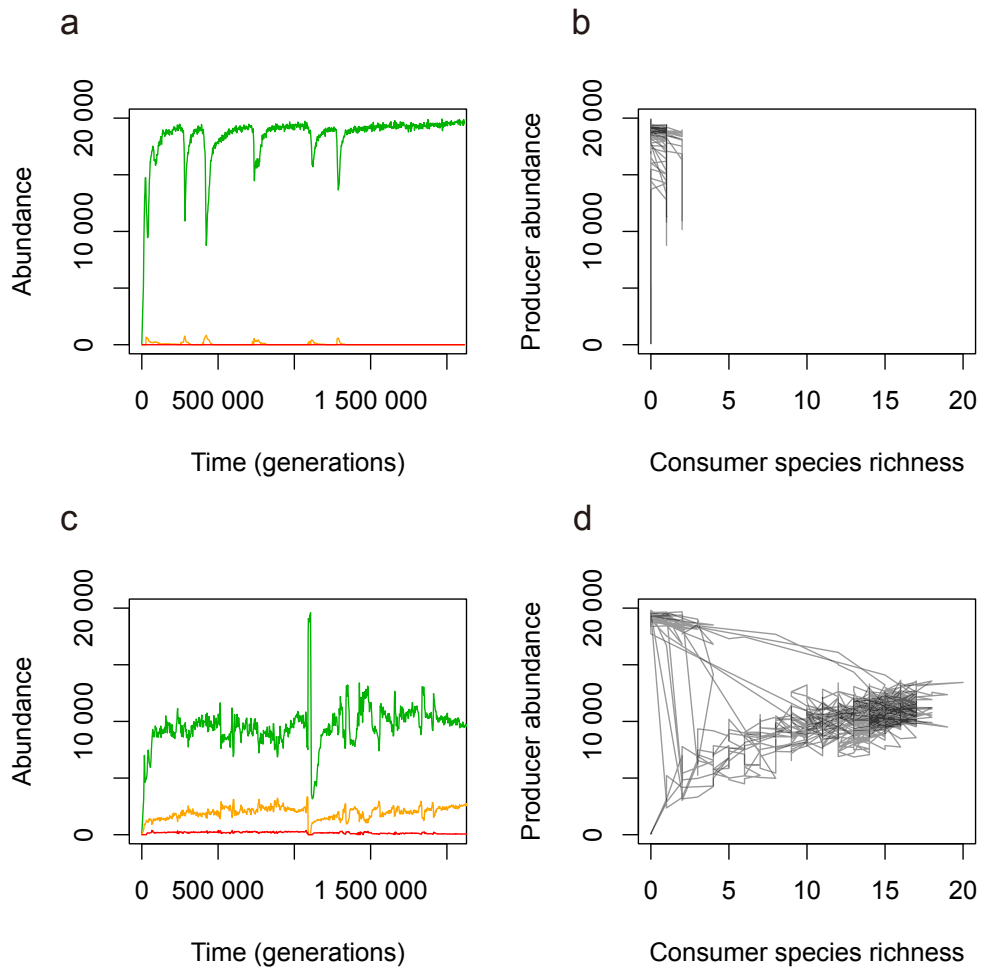

Figure A.6: Robustness with respect to altering the variances of the offspring trait-distributions for foraging and vulnerability traits ($\sigma_{m,f}$ and $\sigma_{m,v}$, respectively). With $\sigma_{m,v} = 0.03$, I show results for (a, b) $\sigma_{m,f} = 0.01$ and (c, d) $\sigma_{m,f} = 0.09$. (a, c) Curves show the time course of the abundances of producers (plants, green), trophic-level-2 consumers (herbivores, orange), and higher-trophic-level consumers (predators, red). (b, d) Trajectories show the time course of consumer richness and producer abundance, which are obtained from three independent model runs. Larger variances for foraging traits stabilize the HTL state and shorten the recovery time from the LTL state (c, d).

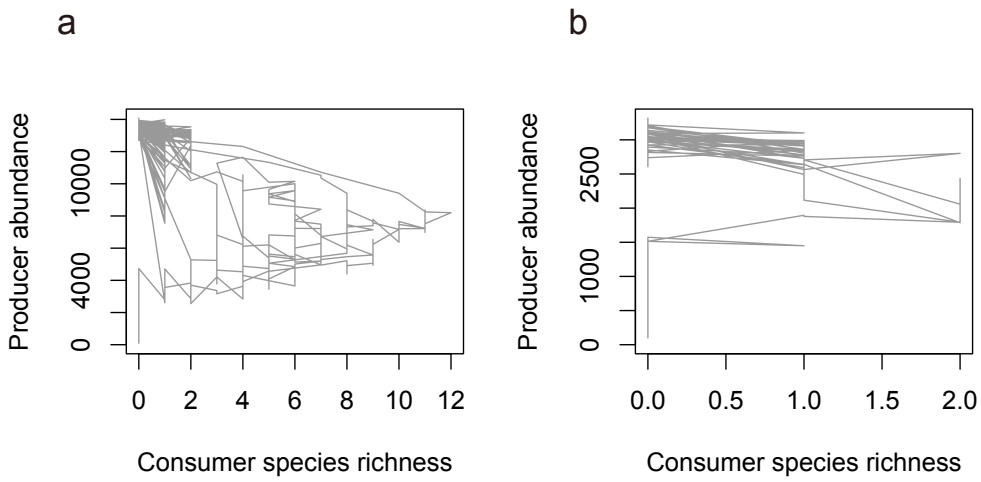

Figure A.7: Robustness with respect to introducing handling times, leading to a nonlinear functional response. We consider a Holling's type-II functional response with an attack rate of 1 and two handling times, (a) $h = 1/8{,}000$ and (b) $h = 1/800$. Trajectories show the time course of consumer richness and producer abundance obtained from a single model run. If the handling time is sufficiently small (a), the evolutionary cycle is similar to that with the linear response.