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Abrupt community transitions and cyclic evolutionary dynamics in complex food webs

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Abrupt community transitions and cyclic evolutionary dynamics in complex food webs

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Abstract

Understanding the emergence and maintenance of biodiversity ranks among the most fundamental challenges in evolutionary ecology. While processes of community assembly have frequently been analyzed from an ecological perspective, their evolutionary dimensions have so far received less attention. To elucidate the eco-evolutionary processes underlying the long-term build-up and potential collapse of community diversity, here we develop and examine an individual-based model describing coevolutionary dynamics driven by trophic interactions and interference competition, of a pair of quantitative traits determining predator and prey niches. Our results demonstrate the (1) emergence of communities with multiple trophic levels, shown here for the first time for stochastic models with linear functional responses, and (2) intermittent and cyclic evolutionary transitions between two alternative community states. In particular, our results indicate that the interplay of ecological and evolutionary dynamics often results in extinction cascades that remove the entire trophic level of consumers from a community. Finally, we show the (3) robustness of our results under variations of model assumptions, underscoring that processes of consumer collapse and subsequent rebound could be important elements of understanding biodiversity dynamics in natural communities.

Keywords: individual-based model; extinction cascade; trophic-level evolution; consumer collapse

1 Introduction

Biodiversity emerges over time through speciation and extinction. Species evolve subject to ecological constraints, which stem from the interactions among them. A recent study of environmental change and species extinction suggests that the dynamical change of species interactions is an important proximate cause of species extinction (Cahill *et al.*, 2012), thus highlighting the importance of understanding the eco-evolutionary processes and mechanisms that maintain evolved 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 (Caldarelli *et al.*, 1998; Drossel *et al.*, 2001, 2004; Christensen *et al.*, 2002; Yoshida, 2002, 2006; Rossberg *et al.*, 2005, 2006, 2008; Stauffer *et al.*, 2005; He & Yu, 2006; Ito & Ikegami, 2006; Bell, 2007; Rikvold, 2007, 2009; Rikvold & Sevim, 2007; Guill & Drossel, 2008; Guttenberg & Goldenfield, 2008; Pękalski *et al.*, 2008; Ingram *et al.*, 2009; Ito *et al.*, 2009; Powell & Boland, 2009; Murase *et al.*, 2010; see also 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. A surprising finding in many studies is that communities sometimes exhibit a sudden transition from one evolutionary state to another (Christensen *et al.*, 2002; Ito & Ikegami, 2006; Rikvold 2007, 2009; Guill & Drossel, 2008; Rossberg *et al.*, 2008; Murase *et al.*, 2010).

Using an individual-based model of evolutionary food-web emergence without adaptive foraging, Rikvold (2009) found a sudden transition between two states: a community with multiple trophic levels and a community with only producer species. Although that study suggested that the emergence of intraspecific 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. Ito & Ikegami (2006) also found evolutionary transitions between highly diversified and poorly diversified communities. Other authors observed fluctuating dynamics of species richness without significant transitional dynamics (Rossberg *et al.*, 2008; Guill & Drossel, 2008). So far, however, no mechanistic explanation of the intermittent evolutionary dynamics observed in all those models has been provided.

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 (Drossel *et al.*, 2001, 2004; Christensen *et al.*, 2002; Yoshida, 2002, 2006; Rossberg *et al.*, 2005, 2006, 2008; Stauffer *et al.*, 2005; He & Yu, 2006; Bell, 2007; Rikvold, 2007; Rikvold & Sevim, 2007; Guill & Drossel, 2008; Guttenberg & Goldenfield, 2008; Pękalski *et al.*, 2008;

Ingram *et al.*, 2009; Powell & Boland, 2009; Murase *et al.*, 2010). 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.

Here, we investigate trophic interactions in a multi-dimensional 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 Methods

We 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 leads to the emergence of clusters of related individuals in trait space, which we identify as species. These species, together with the trophic interactions among them, define the food web, of which we analyze the structure, stability, and certain network properties. The details of our model are described below.

2.1 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 ith individual, f_i, represent 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, we 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, we consider this space as an abstract representation of all relevant biological traits.

2.2 Demographic dynamics

We consider birth and death events, which increase and decrease the total population abundance by 1, respectively. Events are realized sequentially one after the other, and average waiting times are exponentially distributed, following a Poisson process.

We implement the resulting stochastic demographic dynamics using the Gillespie algorithm (Gillespie, 1976, 1977). Event rates depend on the intensities F and I of foraging and interference competition, respectively. We 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,

$$\begin{aligned} F(f_i, v_j) &= \exp(-\| f_i - v_j \|^2 / 2\sigma_{\mathrm{F}}^2) / \sqrt{2\pi}\sigma_{\mathrm{F}} \\ I(f_i, f_j) &= \exp(-\| f_i - f_j \|^2 / 2\sigma_{\mathrm{I}}^2) / \sqrt{2\pi}\sigma_{\mathrm{I}}, \end{aligned} \tag{1}$$

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.

To prevent runaway selection, we furthermore assume a cost for vulnerability traits that increases quadratically with their distance from the origin, $D(v_i) = \| v_i \|^2$. We assume the availability of an external resource, with vulnerability trait vector v_{R} and abundance N_{R} For simplicity, we 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 ith individual are given by

$$\begin{aligned} r_{\mathrm{b}i} &= aC_{\mathrm{F}} \sum_j F(f_i, v_j) + aC_{\mathrm{F}} F(f_i, v_{\mathrm{R}}) N_{\mathrm{R}}, \\ r_{\mathrm{d}i} &= C_{\mathrm{F}} \sum_j F(f_j, v_i) + C_{\mathrm{I}} \sum_j I(f_i, f_j) + C_{\mathrm{D}} D(v_i) + d. \end{aligned} \tag{2}$$

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.

2.3 Evolutionary dynamics

As we assume haploid individuals with asexual reproduction, mutation is the only source of phenotypic variation. We assume a mutation rate proportional to the reproduction rate of each individual (Stauffer *et al.*, 2005; He & Yu, 2006; Bell, 2007; Rikvold & Sevim, 2007; Rikvold, 2007, 2009; Powell & Boland, 2009; Murase *et al.*, 2010), with the ratio of those rates being given by a mutation probability. Rossberg *et al.* (2006) argued, based on their analysis of empirical data, that the mutation rate of foraging traits tends to be much higher than that of vulnerability traits. We therefore consider different mutation probabilities for the foraging and vulnerability trait vectors, μ_{f} and μ_{v}, respectively, with $\mu_{\mathrm{f}} > \mu_{\mathrm{v}}$. We assume that the occurrences of mutations in foraging and vulnerability traits are independent of each other, so mutations that alter both foraging and vulnerability trait vectors occur with probability $\mu_{\mathrm{f}}\mu_{\mathrm{v}}$. 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.

2.4 Parameter values and initial conditions

Table 1 lists the parameter values we use in our 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, we assume that the foraging kernel is considerably wider than the competition kernel.

We start our 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.

2.5 Species determination

Determining what constitutes a species is not trivial when mutational steps are small and reproduction is asexual. However, in our model, distinct clusters tend to form in trait space, and the strains in a cluster are mostly close relatives of each other. We 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, we 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 some strains, which results in isolated strains being detected as outliers.

Those outlier strains are treated as species consisting of a single trait type.

2.6 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,

$$t_i = 1 + \sum_j w_{ij} t_j . \tag{3}$$

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. Eqs. (3) define a linear system in which the trophic levels $t_1, t_2, ...$ 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 our model community tend to cluster around integer trophic levels; we can thus naturally classify species by their trophic level as producers ($1 \le t_i < 1.5$), trophic-level-2 consumers ($1.5 \le t_i < 2.5$), trophic-level-3 consumers ($2.5 \le t_i < 3.5$), and so on.

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. 1), similar to the flip-flop dynamics reported by Rikvold (2009). These ranges correspond to two characteristic community states. We 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 producers, while trophic-level-2 consumers are rare and ephemeral (Fig. 1a). In contrast, an HTL community comprises also higher-trophic-level consumers (Fig. 1b).

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

We now describe these findings in turn. All model parameters used for this investigation are specified in Table 1 (for the parameters used for the robustness checks, see Section 3.4).

3.1 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 1 shows the typical structures of the emerging communities. In the HTL state, communities include producers and higher-trophic-level species, exhibiting three distinct trophic levels (Fig. 1b).

3.2 Community-level evolutionary cycles

Figure 2 shows the total abundance of individuals in the community on a long time scale. This abundance tends to remain around either of two levels for long periods, each corresponding to one of the characteristic community states shown in Fig. 1. As the presence of trophic-level-2 consumers effectively regulates the abundance of the producers, the HTL producer community tends to have lower total abundance than the

LTL producer community. Occasional mutations from producers to trophic-level-2 consumers do occur in the LTL state, but they typically fail to establish.

Transitions between these states are relatively fast (Fig. 2a), and we consistently observe cyclic evolutionary dynamics (Fig. 2b). The distributions of durations of both LTL and HTL states better match exponential distributions than power-law distributions (Fig. 2c, d), suggesting that transitions between the two states are triggered by rare random events that occur with constant probabilities per unit time.

3.3 Understanding the evolutionary cycles

We now present a detailed analysis of the observed evolutionary cycles (Fig. 2b). Starting from the LTL state, Figure 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, producers 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 producers during the preceding HTL state. Gradually, however, the number of those clouds decreases through random extinctions. Also, the occasional and temporary emergence of a trophic-level-2 consumer imposes strong foraging pressure on one of those clouds, and thereby increases its risk of random extinction. Because of those processes, only a few vulnerability clouds survive the LTL period. 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 producers to avoid being foraged by other producers.

The 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 producer species. This mutant tends to be the offspring of a producer 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 producer species, making it a sort of generalist. Consumer control now regulates producer abundance, leading to increasing producer evenness (Fig. 4a). The proportion of foraged producers very quickly increases from 0 to 1 (Fig. 4b). Because of the foraging pressure, the abundances of the producers quickly decrease, leading to the eventual (stochastic) extinction of a number of producers due to overexploitation, in what can be viewed as a top-down process.

The extinction of some producers leads to mounting foraging pressure by the generalist consumer on the remaining producers, generating a strong selection pressure towards a diversification of their vulnerability traits. This promotes differentiation of the vulnerability trait vectors within the producer community. The foraging traits of the trophic-level-2 consumer undergo a corresponding specialization, resulting in the emergence of trophic-level-2 consumers each specialized on one producer species. Because we 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 producers. This is the HTL community state. The HTL producers are diversified in their foraging trait vectors (because of interference competition) as well as in their vulnerability trait vectors (because of foraging pressure). The trophic-level-2 consumers 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 producers are not, i.e., because of the absence of predation). The high evenness among producers suggests that producer abundances are strongly controlled by consumers (Fig. 4a,c). A generalist trophic-level-3 consumer foraging on trophic-level-2 consumers can also emerge. More complex communities rarely evolve in our model, except for extreme parameter settings ($a = 0.9$, Fig. S2), because the strongly decreasing abundance of the higher-trophic-level species makes their persistence less likely.

The random extinction of a trophic-level-2 consumer initiates the transition from the HTL state to the LTL state. Since producers are mostly foraged on by specialists, the extinction of such a specialist consumer removes the foraging pressure from the corresponding producer. As a consequence, the abundance of this producer quickly increases, which, in turn, increases the level of interference competition exerted by it. Strong interference competition effectively decreases the abundance of the other producers, and consequently, the abundance of the corresponding trophic-level-2 consumers, threatening their survival (and the survival of all higher-trophic-level consumers). This destabilization of the producer level manifests itself in terms of decreasing producer evenness, which slightly precedes the decrease in consumer richness (Fig. 4c). As more and more higher-trophic-level species become extinct, the proportion of producers that are free from foraging pressure increases (Fig. 4d), and so does the competitive pressure on the remaining pairs of producers and trophic-level-2 consumers. Ultimately, only a few producer species survive, which means that the community has reverted to its initial state. 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 producer species.

3.4 Robustness of the evolutionary cycles

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

First, we relax the assumption that the cost minimum for vulnerability traits coincides with the vulnerability trait of the external resource (Fig. S1). We find that the re-emergence of the trophic structure becomes difficult when this difference is made large, but at the same time we can confirm that the results presented here remain valid for small to moderate differences.

Second, we investigate the effect of altering the trait-space dimensionality on the cyclic evolutionary dynamics (Fig. S2). We 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), we 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, we 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, larger species richness, and higher trophic levels evolve (Fig. S3). Larger 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 a trophic-level-2 consumer.

Fourth, we 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. S4). We 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. S5). 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 extinction.

Sixth, we relax the assumption that the offspring trait distributions have the same variances for foraging and vulnerability traits (Fig. S6). Introducing separate variances for foraging and vulnerability traits, $\sigma_{\mathrm{m,f}}^2$ and $\sigma_{\mathrm{m,v}}^2$, respectively, by fixing $\sigma_{\mathrm{m,v}} = 0.03$ and varying $\sigma_{\mathrm{m,f}}$ to equal 0.01 or 0.09, we 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 latter case, consumers can switch their resource more easily, keeping the producers under consumer control and thus preventing the community's collapse, while in the former case, producers can more easily evolve away from their consumers, freeing them from consumer control and thus triggering the community's collapse. While the waiting time until community collapse is thus changing, the overall community dynamics remain largely the same.

Seventh and finally, we introduce handling times, by considering a Holling-type-II functional response instead of a linear functional response (Fig. S7). If the handling times are sufficiently small, we observe the same evolutionary cycles as with the linear response; otherwise, the evolved consumer species tend to become extinct quickly, and the HTL state is not established.

4 Discussion

In this study, we have 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 lead to the establishment of large interconnected ecological communities with three to four trophic levels. The subsequent evolutionary dynamics are characterized by relatively long periods that the community spends around either of two characteristic states, occasionally punctuated by fast transitions during which the composition of the community is altered by mass extinctions and rapid diversification, respectively.

To the extent that similar transitions happen in natural communities, they might be triggered more or less easily than in our model. Because of constraints on computational time, our 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 in community dynamics, in particular for species at higher trophic levels. This demographic stochasticity might facilitate the triggering of community-level transitions. On the other hand, in natural communities these transitions might alternatively be triggered by environmental stochasticity or random external impacts, such as the occasional release from a natural enemy (Keane & Crawley, 2002); such external drivers are not included in our model. At any rate, once events have been set in motion towards a transition, the resultant cascade of coevolutionary changes might well be a community's principal cause of extinctions.

A key element in any model of food-web evolution are the trait values that characterize an individual. Loeuille & Loreau (2005) and Brännström *et al*. (2011) used the maximum body size of species as the evolving trait. Guill & Drossel (2008) and Ingram *et al*. (2009) considered an abstract one-dimensional niche space. In the Webworld model (Caldarelli *et al*., 1998; Drossel *et al*., 2001, 2004) and the Tangled-Nature model (Christensen *et al*., 2002; Rikvold, 2007, 2009; Rikvold & Sevim, 2007), many traits determine both foraging ability and vulnerability, and the acquisition or loss of such traits are considered as evolutionary steps. Our model is grounded in a different school of thought, which has traditionally emphasized abstract vulnerability and foraging traits (Rossberg *et al*. 2006, 2010; see also Rossberg *et al*. 2008, which partly bridges between these two schools). In an effort to better understand the structure of food webs, Rohr *et al*. (2010) carried out a statistical analysis of twelve empirically documented food webs and found that body size only partially captures the trophic information embodied in a food web, while the inclusion of latent traits representing foraging and vulnerability drastically improved statistical fits. In good alignment with the conclusions of our study, they found that basal species mainly diversify their vulnerability traits, whereas top predators mainly diversify their foraging traits. These results support the findings presented here and underscore the importance of considering both foraging traits and vulnerability traits.

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. In the present study, we have elucidated the detailed eco-evolutionary mechanisms underlying the entire cyclic dynamics, including the transitional processes, using a full model featuring an emerging number of species. Our results suggest that IGP is not a major factor for explaining successive extinctions. If IGP were a major factor, transitions should be much slower than observed by Rikvold (2009) and in our model. Furthermore, non-specialist consumers are very rare in the high-trophic-level (HTL) community state, since the distances among the producer vulnerability clouds are relatively large. 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 competition-based explanation of cyclic community dynamics we propose here therefore could also be applied to explaining the flip-flop dynamics observed by

Rikvold (2009).

It is instructive to compare the cyclic community dynamics of consumer emergence and collapse reported here to the classical phenomenon of predator–prey cycling. From this perspective, a community that mainly consists of producers, being in the low-trophic-level (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 is which predator and prey temporarily coexist at relatively high abundance, analogous to the high-trophic-level (HTL) state of our 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 our model consumer species start to go extinct once they have reached a high diversity, owing to foraging-induced extinctions of their resource species.

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 producer- and consumer-abundant communities in predator–prey cycling, which contrast with the relatively long durations of the LTL and HTL states we have observed. The main reason for this difference is that our 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 study is that the HTL state is unstable: in this state, 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 become extinct. Evolution towards unstable community states, as observed in the model of Rand *et al.* (1995) and in our model, highlights the potential for community crashes to occur as the outcome of the evolutionary dynamics of interspecific interactions.

Altering several parameters in our model results in communities that differ in terms of their species richness, total abundance, and maximum trophic level. Yet, as we 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 our results, an important challenge for future research is to infer reasonable parameter ranges from empirical data. The most immediate concern might be to improve empirical estimates of the intensities of foraging and interference competition, as these two parameters have a particularly strong effect on the presence or absence of cyclic transitions.

As we increase the number of trait-space dimensions, we 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 producers on which they forage, which results in the emergence of consumer-free producers and triggers the transition to the LTL state with increasing frequency. For host–parasite systems, such evasive evolution has been theoretically analyzed by Gilman *et al.* (2012).

Although we observe large intermittent evolutionary avalanches, i.e., successive speciation and extinction at transitions, we do not find other signatures of self-organized criticality as defined by Bak *et al.* (1988, 1989), which has been used to explain the large fluctuations observed in evolutionary food-web models (Rossberg *et al.*, 2006, 2008; Guill & Drossel, 2008; Rikvold, 2009). Since both HTL and LTL states have a characteristic species richness, the stochastic transitions between HTL and LTL states result in the stochastic occurrence of fixed-sized extinction and speciation cascades, which does not agree with the $1/f$ noise expected by Bak *et al.* (1988) and Bak & Sneppen (1993). However, the fact remains that the HTL structure investigated in this study, into which the system evolutionarily organizes itself so predictably, represents a fragile community state that, equally predictably, will be destabilized by eventual random abundance fluctuations.

Evolutionarily emerging food webs can be seen as examples of adaptive networks. Another example are gene-regulatory networks, in which the evolutionary need to balance phenotype conservation and phenotype innovation leads to critical dynamics, so that perturbations of gene expression neither amplify nor die out (Torres-Sosa *et al.*, 2012). We can similarly explain the intermittent dynamics observed in our model by a sort of conservation–innovation balance, if we liken consumers remaining specialized on their resource (caused by small mutational variance in foraging traits) to phenotype conservation, and evolutionary resource switching (enabled by large mutational variance in foraging traits) to phenotype innovation. Conservative evolution in this sense tends to the LTL state, while innovative evolution favors the HTL state; the fact that the community cyclically switches from one state to the other can be interpreted as an evolutionary attempt to balance conservation and innovation. This analogy should be taken with a grain of salt, however, since the underlying model details are rather different. In particular, the selection scheme of gene-regulatory networks, i.e., selection on the entire network structure and dynamics, is different from that in food webs, in which selection acts at the individual level, and thus, separately impacts each network node.

Our current model assumes a well-mixed community and does not incorporate extinction–invasion dynamics. On the population-dynamical time scale, local extinctions and invasions can alter the set of coexisting species (Leibold *et al.*, 2004). Migration to and from neighboring communities can lead to the extinction of consumer species, before an abundance explosion of prey species induces secondary extinctions, and the trophic structure of the whole metacommunity is stabilized. Understanding the effects of occasional invasions from other ecological communities is important and would be a worthwhile extension of the work presented here.

In this study, we have demonstrated the evolutionary emergence and breakdown of complex food webs through the coevolution of generic foraging and vulnerability traits. We 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.

Acknowledgements

We thank Michio Kondoh, Maurice Sabelis, Arndt Telschow, Shigeo Yachi, Norio Yamamura, and Katsuhiko Yoshida for discussions, insightful comments, and suggestions. This research was supported by the Global Center of Excellence Program A06 at Kyoto University, by the Japan Society for the Promotion of Science (JSPS) Core-to-Core Program (20004), and by KAKENHI (11007744) from JSPS to A.Y. D.T. gratefully acknowledges financial support by a JSPS Research Fellowship for Young Scientists. U.D. gratefully acknowledges financial support by the European Science Foundation, the Austrian Science Fund, the Austrian Ministry of Science and Research, and the Vienna Science and Technology Fund, as well as by the European Commission, through the Marie Curie Research Training Network FishACE and the Specific Targeted Research Project FinE.

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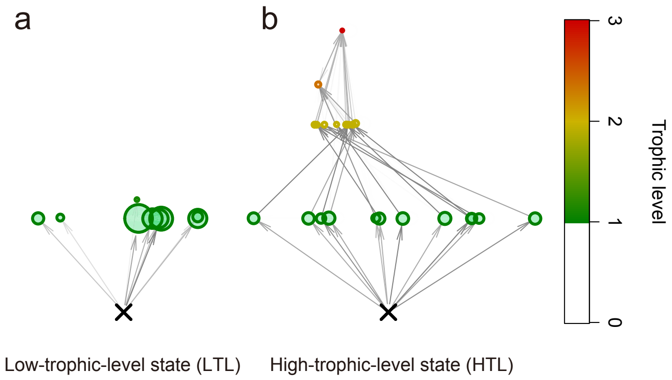
Figures



Low-trophic-level state (LTL) High-trophic-level state (HTL)

Figure 1: Examples of the two distinct community states observed in this study. Each circle represents a species, with their areas being proportional to the species' abundance, their colors 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.

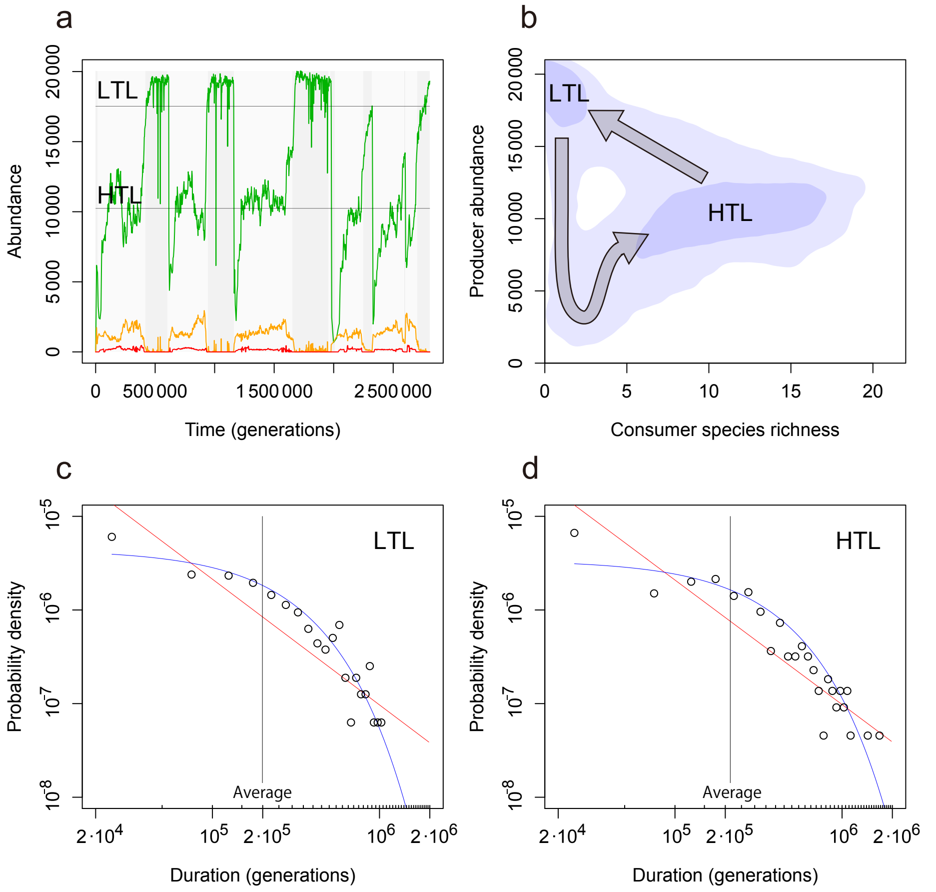
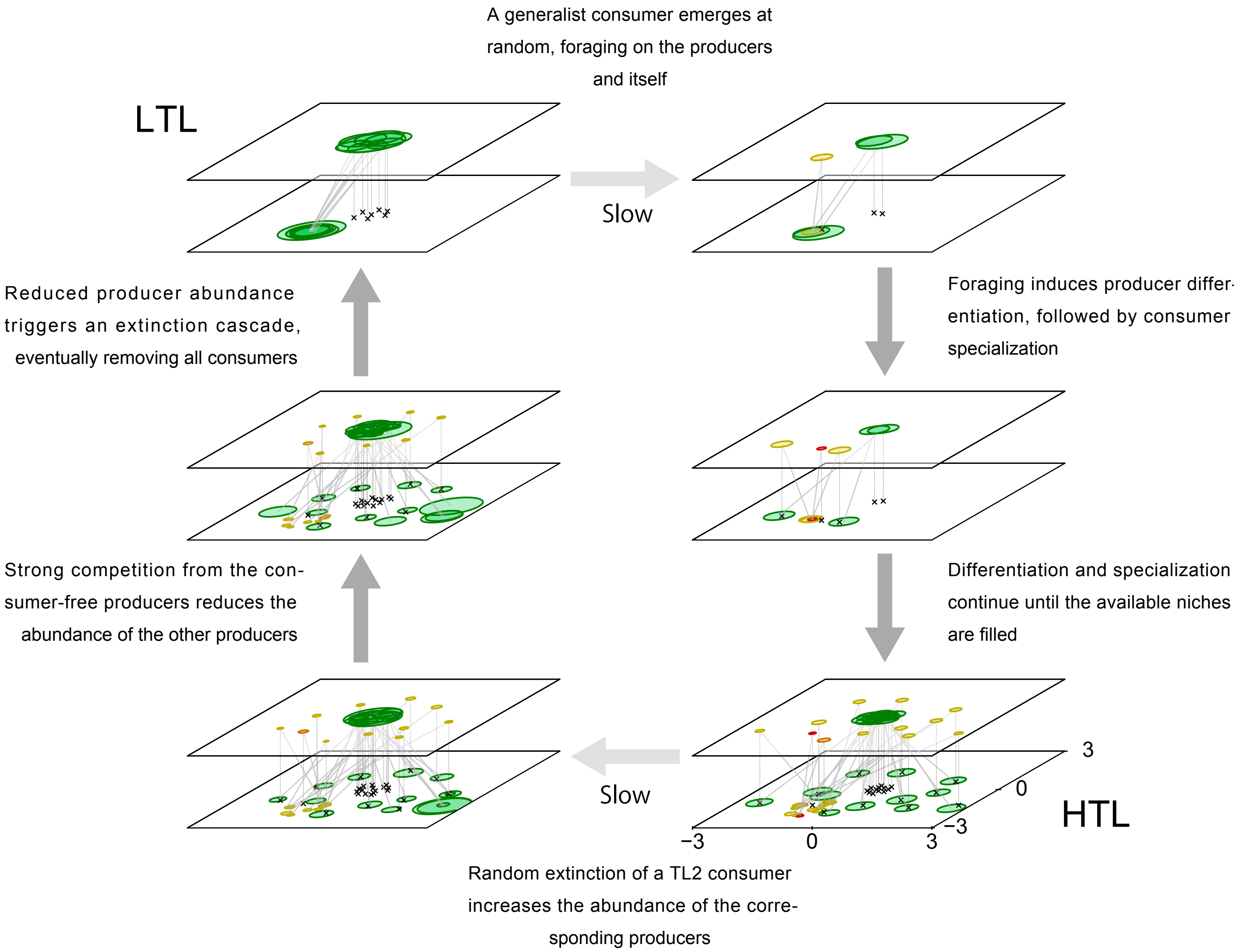


Figure 2: Cyclic evolutionary transitions between the two community states. (a) Continuous curves represent the total abundance of producers (green), trophic-level-2 consumers (orange), and trophic-level-3 consumers (red). (b) Frequency distribution of community states: 99% of community states are observed 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, red and blue curves 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.



A generalist consumer emerges at random, foraging on the producers and itself

Foraging induces producer differentiation, followed by consumer specialization

Differentiation and specialization continue until the available niches are filled

Random extinction of a TL2 consumer increases the abundance of the corresponding producers

Strong competition from the consumer-free producers reduces the abundance of the other producers

Reduced producer abundance triggers an extinction cascade, eventually removing all consumers

Figure 3: Mechanistic explanation of the cyclic evolutionary transitions between the low-trophic-level (LTL) state and the high-trophic-level (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 indicates 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 and potentially concurrent transitions, while light arrows indicate slow transitions triggered by rare random events.

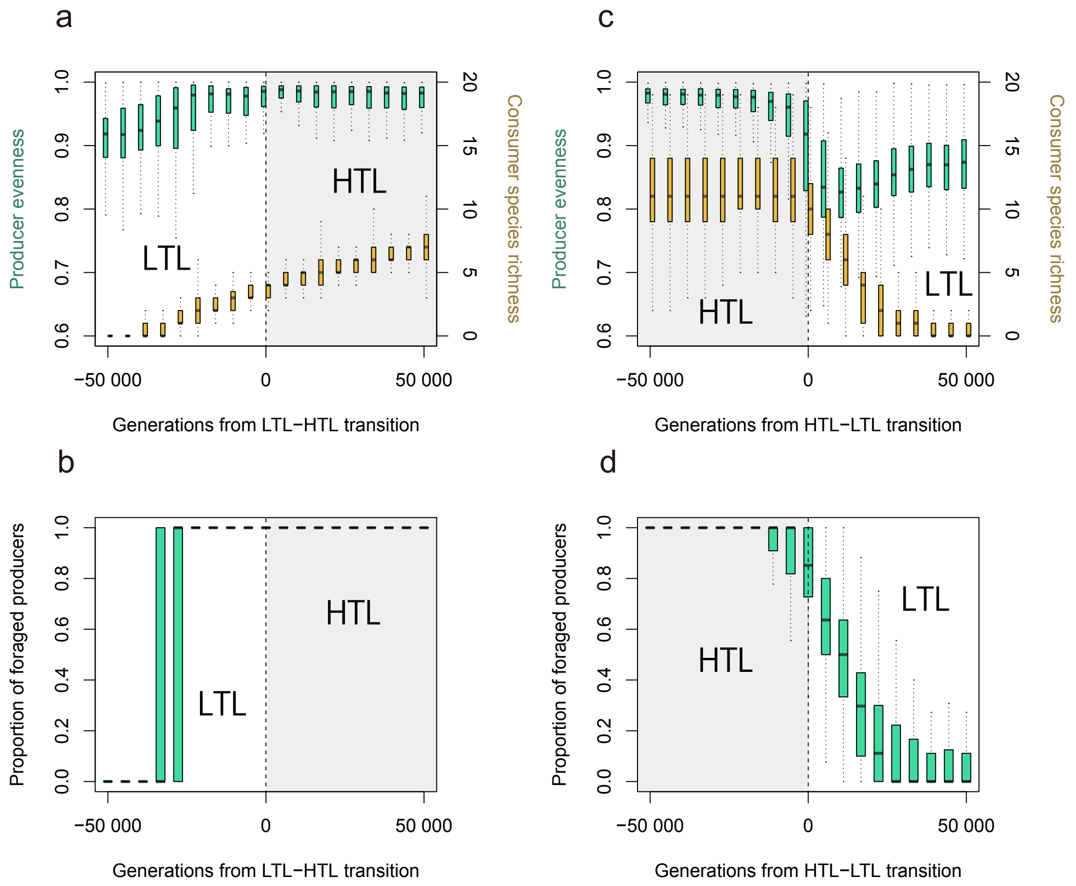


Figure 4: Transient dynamics associated with the cyclic evolutionary transitions between the two community states. Panels (a, b) show the time course during consumer emergence, while panels (c, d) show the time course during consumer collapse. Shaded areas highlight the HTL state. (a, c) Green and yellow boxes indicate producer evenness (Pielou, 1966) and consumer species richness, respectively. (b, d) Green boxes indicate the proportion of producer species foraged by trophic-level-2 consumers. 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 trophic-level-3-or-higher species. 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.

Description	Symbol	Value
Abundance of external resource	N_{R}	4,500
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 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.

Supplemental information:

Abrupt community transitions and cyclic evolutionary dynamics in complex food webs

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Robustness checks

As summarized in Section 3.4 of the main text, we test the effects of different choices of the cost minimum for vulnerability traits (Fig. S1), trait-space dimensionalities (one-dimensional and three-dimensional foraging and vulnerability trait vectors, Fig. S2), larger trophic efficiency ($a = 0.9$; Fig. S3), larger abundance of the external resource ($N_\mathrm{R} = 9{,}000$; Fig. S4), 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. S5a,b). Furthermore, we 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. S6). Finally, we introduce handling times, leading to a Holling-type-II functional response instead of a linear functional response; based on this model extension, we investigate large and small handling times ($h = 1/8000$, and $1/800$; Fig. S7). As discussed in Section 3.4 of the main text, cyclic transitions are observed in nearly all resultant evolving communities.

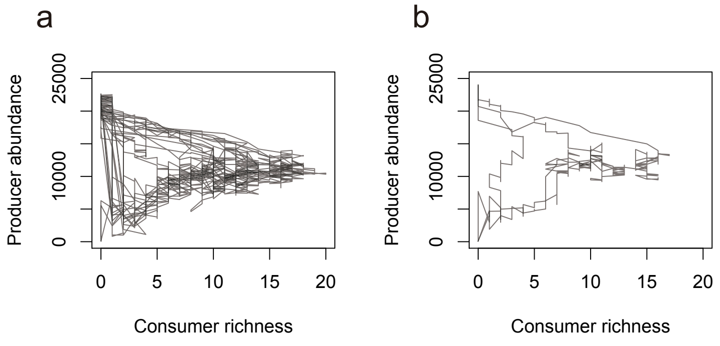

Fig. S1. Robustness with respect to altering the cost minimum for vulnerability traits. The choices (a) $(1,0)$ and (b) $(2.5,0)$, respectively, correspond to a moderate distance and a large distance of the cost minimum from the vulnerability trait vector of the external resource. For moderate differences, the result remains qualitatively unchanged (a), whereas larger differences make the re-emergence of the trophic structure difficult (b).

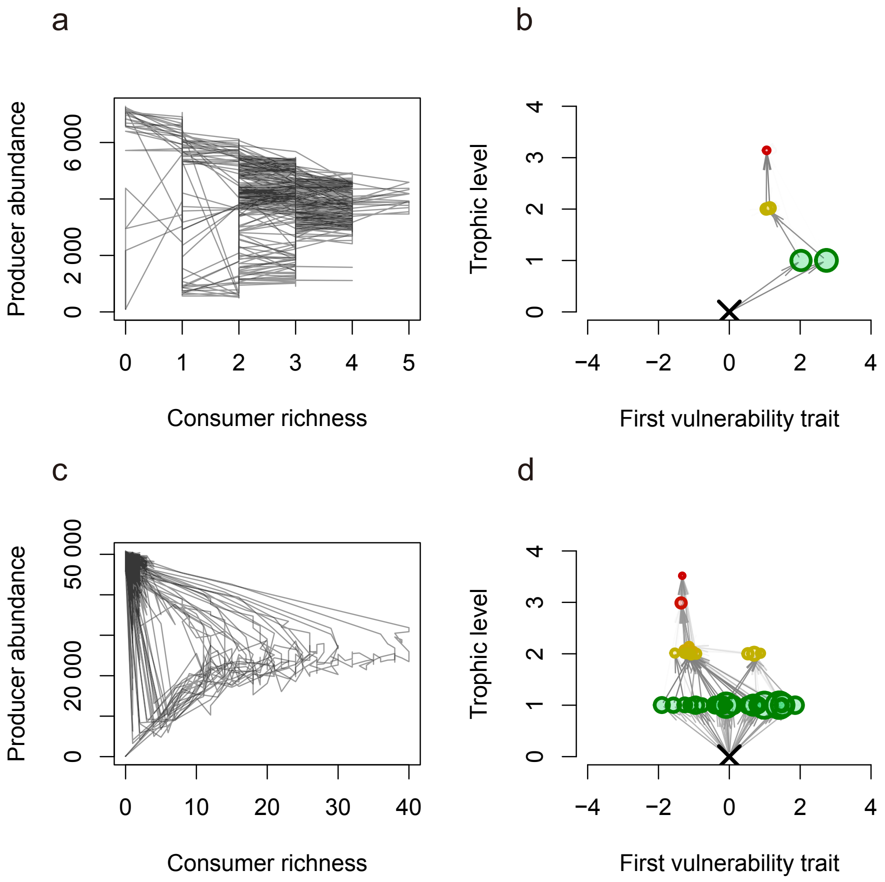

Fig. S2. Robustness with respect to altering the trait-space dimensionality. We show results for a one-dimensional trait space (a, b) and a three-dimensional trait space (c, d). (a, c) Curves show the time course of consumer richness and producer abundance. Each time course is obtained from three independent model runs. (b, d) Circles represent species, with their areas being proportional to the species' abundance, their colors 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).

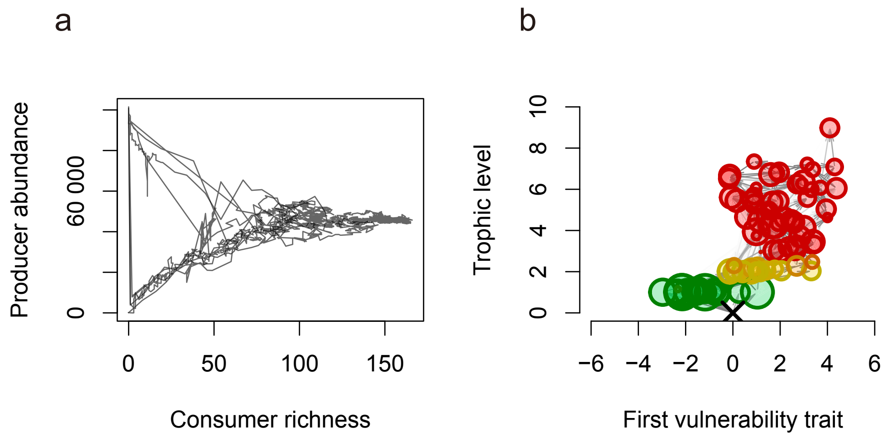

Fig. S3. Robustness with respect to increased trophic efficiency, $a = 0.9$. (a) The curve show the time course of consumer richness and producer abundance obtained from a single model run. (b) Circles represent species, with their areas being proportional to the species' abundance, their colors indicating 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.

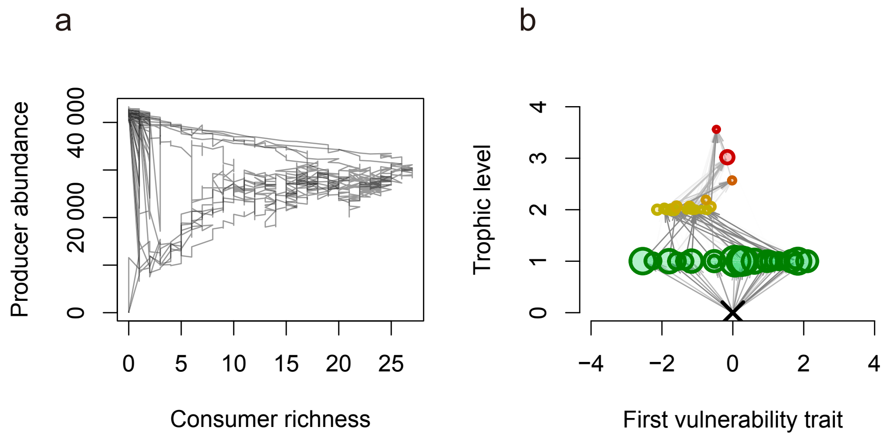

Fig. S4. Robustness with respect to increased abundance of the external resource, $N_{\mathrm{R}} = 9{,}000$. (a) The curve shows the time course of consumer richness and producer abundance obtained from three independent model runs. (b) Circles represent species, with their areas being proportional to the species' abundance, their colors 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.

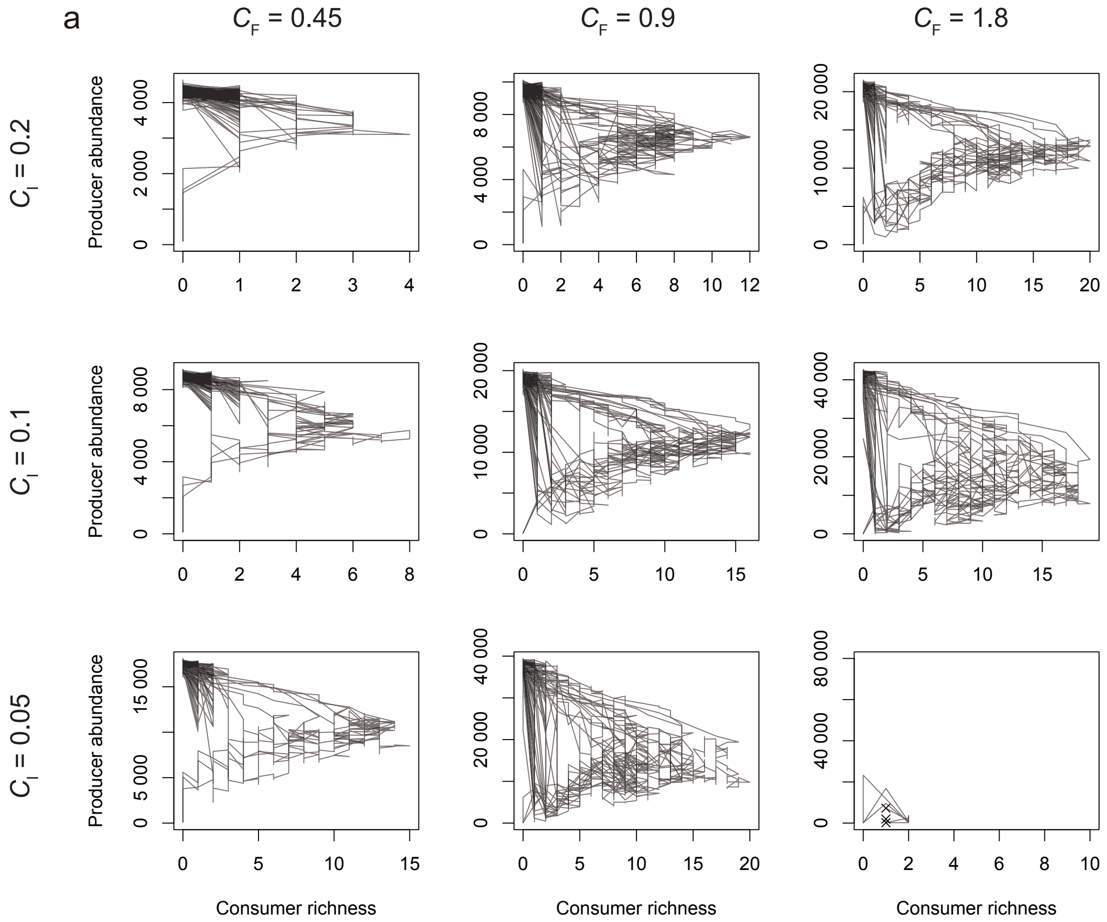

Fig. S5a. Robustness with respect to altering the scales of foraging intensities and interference-competition intensities: effect on cyclic dynamics. Curves show the time course of consumer richness and producer abundance obtained from three model runs. Consumers tend not to re-emerge when foraging intensities 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.

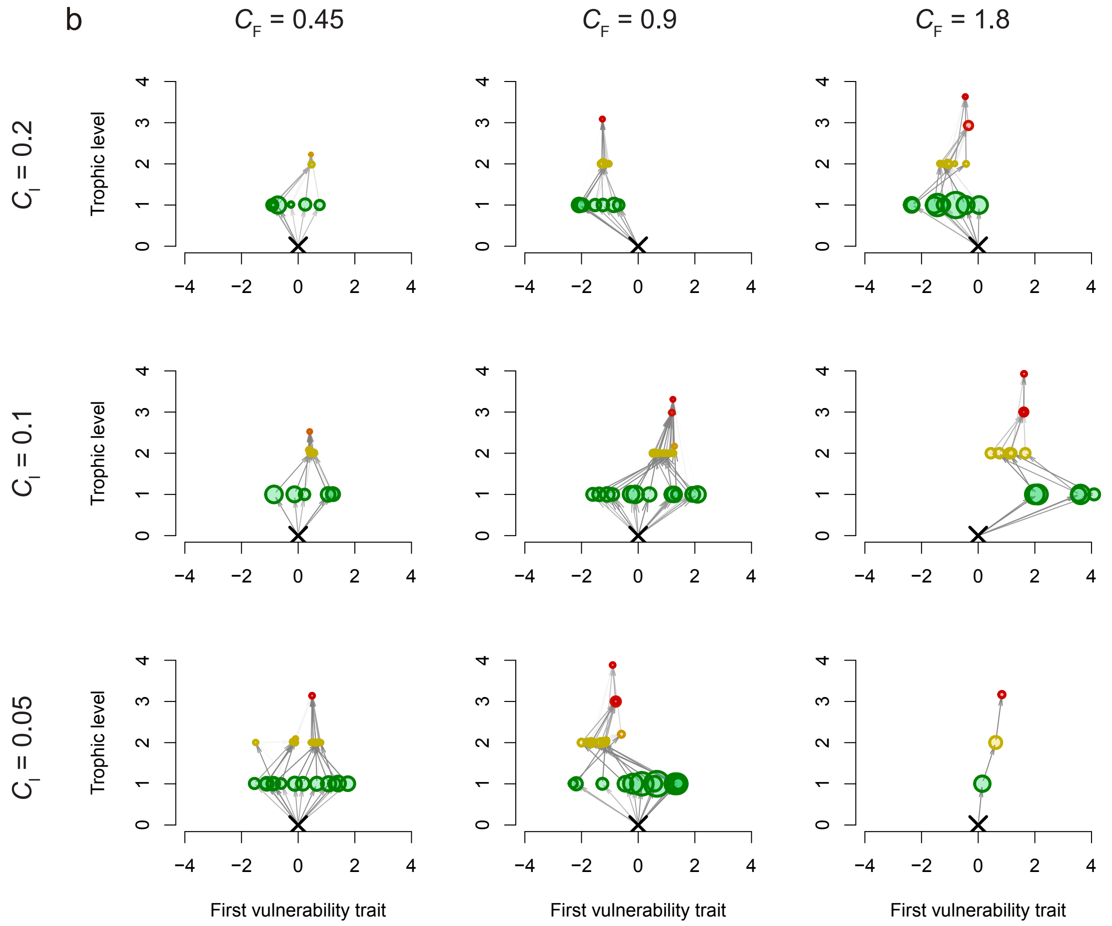

Fig. S5b. Robustness with respect to altering the scales of foraging intensity and interference-competition intensity: effect on community structure. Circles represent species, with their areas being proportional to the species' abundance, their colors indicating the species' trophic level, and their 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. S5a). Low foraging intensities tend to reduce the maximum trophic level.

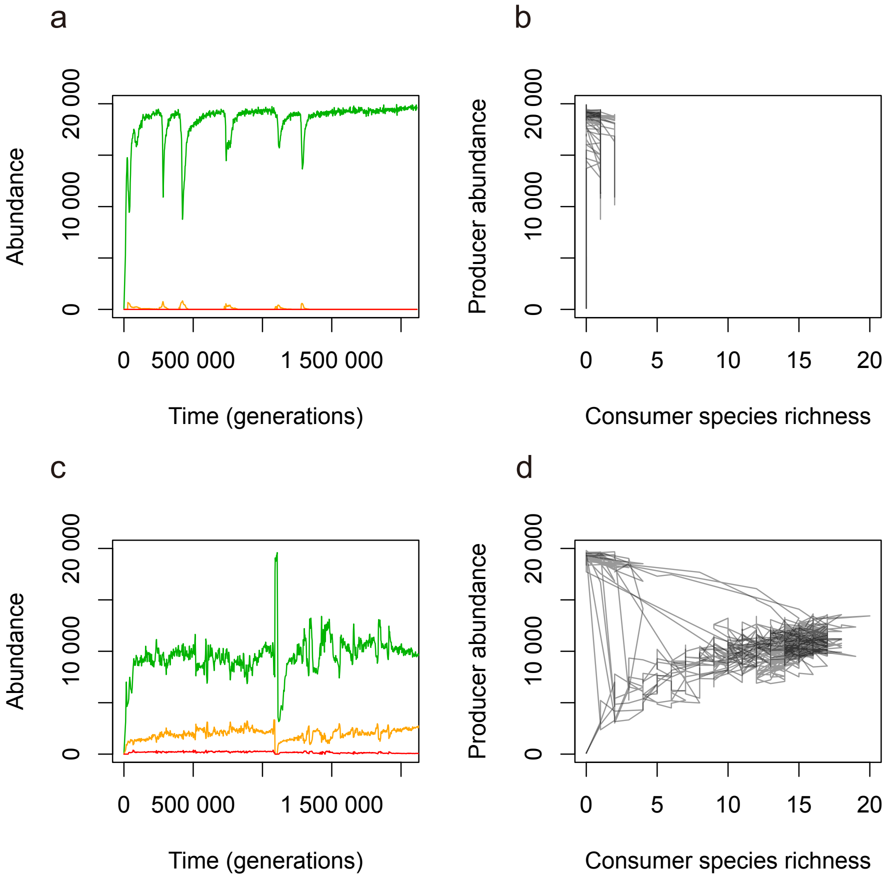

Fig. S6. Robustness with respect to altering the variances of the offspring trait-distributions for foraging and vulnerability traits. With $\sigma_{\mathrm{m,v}} = 0.03$, we show results for (a, b) $\sigma_{\mathrm{m,f}} = 0.01$ and (c, d) $\sigma_{\mathrm{m,f}} = 0.09$. (a, c) Curves show the time course of the abundances of producers (green), trophic-level-2 consumers (yellow), and higher-trophic-level consumers (red). (b, d) Curves show the time course of consumer richness and producer abundance. All curves 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).

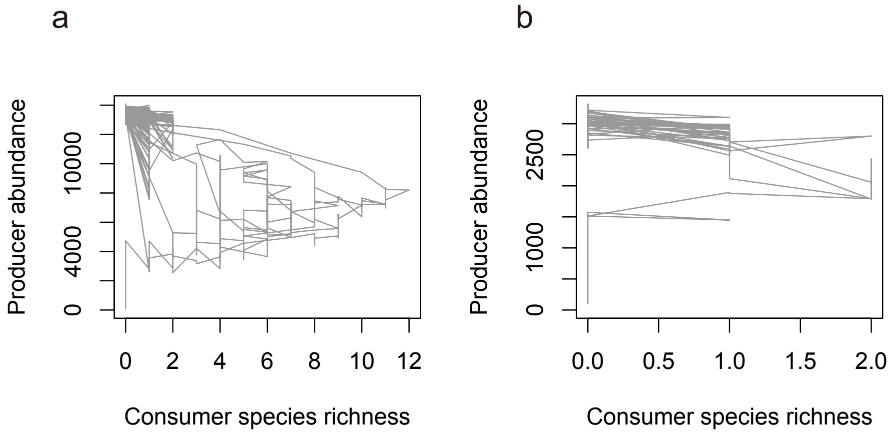

Fig. S7. Robustness with respect to introducing handling times, leading to a nonlinear functional response. We consider a Holling-type-II functional response with an attack rate of 1 and different handling times, (a) $h = 1/8{,}000$ and (b) $h = 1/800$. Curves show the time course of consumer richness and producer abundance obtained from a single model run. If handling times are sufficiently small (a), we observe the same evolutionary cycles as with the linear response.