

Eco-evolutionary feedback as a driver of periodic state shifts in tri-trophic food chains

Yoshinari Tanaka (✉ y-tanaka-fo5@sophia.ac.jp)

Sophia University

Masafumi Yoshino

Hiroshima University

Research Article

Keywords: eco-evolutionary feedback, tri-trophic food chain, state shift, anti-predator trait, hetero-chronic cycle, long periodicity

Posted Date: July 5th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1782620/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Evolutionary Ecology on November 12th, 2023. See the published version at <https://doi.org/10.1007/s10682-023-10278-w>.

Abstract

Eco-evolutionary feedback can result in periodic shifts with long intervals between alternative community states. Simulations using a linear food chain model, namely the resource-prey-predator system with prey evolution have shown such an ecologically unfeasible pattern of long-term dynamics. The alternative community states are characterized by stable internal equilibria and fast synchronized perturbations at the lower two trophic levels. This trait-mediated community shift was governed by the evolution of the anti-predator trait of prey and is referred to as “eco-evolutionary oscillation (EEO)”. The observed EEO was interpreted to be because of the interaction between community ecological dynamics and trait evolution. We further examined the effects of genetic variation on the trait-performance relationship on the global stability of the community. The rapid evolutionary rate with high genetic variance and the strong relationship between trait values and predator avoidance tended to stabilize eco-evolutionary dynamics and cause the EEO to vanish.

Introduction

Recent theoretical studies from an evolutionary perspective on community ecology have revealed that adaptive evolutionary changes in the traits responsible for interspecific interaction can affect the dynamical properties, community stability, and the coexistence of competing species (Fussmann et al 2007; Jones et al 2009; Dercole et al 2010; Ellner and Becks 2011; Andreazzi et al 2018; Edwards et al 2018; Kotila and Vetsigiana 2018; Govaert et al 2019). Trait evolution can facilitate or attenuate the stability of communities through ecological interaction (Yamauchi and Yamamura 2005; Mougi and Iwasa 2010, 2011).

Other studies have indicated that eco-evolutionary dynamics can change the long-term dynamics of purely ecological systems with unchanged parameter values without trait evolution. A key example of this system at the basic level is the Lotka–Volterra prey-predator system, in which the phase difference in the limit cycle disappears with the evolution of prey traits (Yoshida et al 2007; Ellner and Becks 2011).

However, few studies on eco-evolutionary dynamics have highlighted the potential of trait evolution to generate long-term periodicity in the context of community dynamics (Khibnik and Kondrashov 1997; Dercole et al 2006). We hypothesize that such long-term periodicity is characterized by a longer evolutionary time scale than the ecological time scale and that it could not be attained by ecological dynamics alone without evolution within the relevant ecological parameters. Oscillation in communities with long periodicity may be a ramification of community interaction between the ecological and evolutionary dynamics.

We propose that eco-evolutionary dynamics could have long-period phase shifts between alternative community states with a linear food chain model with three trophic levels, namely the resource-prey-predator system. The alternative community states are characterized by stable internal equilibria and fast synchronized perturbations at the lower two levels. This trait-mediated community shift is governed by

the evolution of the anti-predator trait at the intermediate trophic level (the prey) and is referred to in this article as the EEO. Our model assumed evolution only for a single prey trait, thereby excluding the possibility of any perturbations caused by co-evolutionary dynamics between traits. The EEO must then be attributed to the interaction between ecological dynamics and trait evolution in communities.

We further examined the effects of genetic variation, which determines the evolutionary rate, on the global stability of the community being examined. Contrary to the local stability effect explored in previous studies (Cortez 2016), we found that the high level of genetic variation and the rapid evolutionary rate resulted in the disappearance of the EEO and tended to stabilize the community dynamics in terms of long-term periodicity. Slow evolutionary rates, rather than rapid trait evolution, changed the dynamic states of the community.

Model description

We used a standard three-species model with a linear trophic link (N_1 : resource, N_2 : prey, and N_3 : predator). Nonlinear functional responses, namely Holling's type II, were assumed for the prey grazing on the resource and the predator preying on the prey. Additional nonlinearity was implemented for intraspecific competition at the basal level of resources, with an autotroph population. The dynamics of the abundance of the three species on the time scale T are

$$\frac{dN_1}{dT} = rN_1 \left(1 - \frac{N_1}{K} \right) - \frac{A_2 N_1 N_2}{1 + A_2 h_2 N_1}$$

1

$$\frac{dN_2}{dT} = N_2 \left(\frac{c_2 A_2 N_1}{1 + A_2 h_2 N_1} - D_2 \right) - \frac{A_3 N_2 N_3}{1 + A_3 h_3 N_2}$$

2

$$\frac{dN_3}{dT} = N_3 \left(\frac{c_3 A_3 N_2}{1 + A_3 h_3 N_2} - D_3 \right)$$

3

where r and K are the intrinsic rate of natural increase and the carrying capacity of the resource, A is the consumption efficiency; h is the inverse maximum consumption rate; c is the conversion coefficient; and D is the mortality. All subscripts denote the different trophic levels.

We simplified the system using Eq. (1)–(3), according to Hastings and Powell (1991), by standardizing the biomass for all species by the resource carrying capacity ($n_i = N_i/K$, $i = 1, 2$ and 3) and by rescaling time with the intrinsic rate of natural increase r of the resource ($t = rT$),

$$\frac{dn_1}{dt} = n_1 (1 - n_1) - \frac{a_2 n_1 n_2}{1 + a_2 h_2 n_1}$$

4

$$\frac{dn_2}{dt} = n_2 \left(\frac{c_2 a_2 n_1}{1 + a_2 h_2 n_1} - d_2 \right) - \frac{a_3 n_2 n_3}{1 + a_3 h_3 n_2}$$

5

$$\frac{dn_3}{dt} = n_3 \left(\frac{c_3 a_3 n_2}{1 + a_3 h_3 n_2} - d_3 \right)$$

6

,

where $a_j = A_j/r$ and $d_j = D_j/r$ ($j=2$ and 3). The original timescale was multiplied by r so that the intrinsic growth rate on the standardized time became 1, and the biomass of the three species was scaled according to the carrying capacity K of the producer (species 1), ensuring the minimum number of model parameters.

In the above tri-trophic system, Eq. (1)–(3) or Eqs. (4)–(6), is known to have heteroclinic cycles, exhibiting chaotic behavior within a specific range of model parameters (Fig. 1; Hastings and Powell 1991; McCann and Yodzis 1994).

We introduced an anti-predator defence trait for the prey and focused on the effect of its evolutionary change on the ecological dynamics of the community. We excluded any predator traits that would facilitate predation efficiency because the evolutionary rate of the predator was likely much slower than that of the prey, allowing the coevolutionary process to be negligible. This was followed by the prey having a much higher metabolic rate and a much shorter generation time than the predator. We observed no altered results in terms of eco-evolutionary dynamics with an alternative model that included predator evolution (simulation data not shown). Therefore, the results of the present study may not hold for cases in which coevolutionary instability significantly affects eco-evolutionary dynamics.

The quantitative trait z of the prey is assumed to be an anti-predator trait that determines vulnerability to predation by the predator. The following predation efficiency function was used in place of a_3 in Equations (5) and (6).

$$a_3(z) = a_{max} \exp \left\{ - \left(\frac{z}{s} \right)^{2\gamma} \right\}$$

7

,

where a_{max} is the maximum predation efficiency when the trait is at an optimal state 0, s measures the scale of the trait and, and γ is the slope parameter of the association between the scaled trait value and predation efficiency (γ is set to unity for all the simulations presented in this article).

The anti-predator trait entailed a cost on fitness as long as it increased the tolerance against predation. The fitness component of the prey that indicated a negative selection of the prey trait was proportional to the following Gaussian cost function: $\exp(-\omega z^2/2)$, in which ω is the fitness cost of the anti-predator trait and was measured in the context of predation not being directly related. We excluded the demographic effect of the cost of the trait on the prey, because preliminary simulations have demonstrated that such a contribution played a lesser role in comparison to the effect of prey trait evolution and is likely to have almost no effect on the behavior of the whole system with the ecological parameter values set in this study.

The rate of evolution of a single trait per unit time is generally the selection gradient, which is the slope of the log mean fitness \bar{W} against the mean trait value \bar{z} , multiplied by the additive genetic variance of the trait G , that is, $G d\ln \bar{W} / d \bar{z}$ (Lande 1982). Applying the selection gradient approximated as $(d\ln W / dz)_{z=\bar{z}}$ (Abrams et al 1993), the fitness of the prey is $W_2 = \exp\left(\frac{dn_2}{n_2 dt} - \frac{\omega}{2} z^2\right)$, which, along with Eq. (5), specifies the evolutionary rate as:

$$\frac{dz}{dt} = -G \left\{ \omega z + \frac{a'_3 n_3}{(1 + a_3 h_3 n_2)^2} \right\}$$

8
,

where a'_3 is the differential coefficient of a_3 by z : $a'_3 = -a_3 \frac{2\gamma}{s} \left(\frac{z}{s}\right)^{2\gamma-1}$.

Numerical procedures

Numerical evaluations of the community model and trait evolution based on Eqs. (4)–(6) and (8), was undertaken to examine the effects of trait evolution on the dynamical properties of the trajectories and periodicity of demographic fluctuations. We focused on how the evolvability or the evolution limit imposed by the fitness cost and evolutionary rate could affect the stability and long-term periodicity of community dynamics.

Parameterization

The set of baseline ecological parameter values used in the simulations, i.e., $a_2 = 2$, $a_{max} = 0.1$, $c_2 = c_3 = 1$, $d_2 = 0.2$ (varying from 0.1 to 0.3) and $d_3 = 0.01$, is known to generate chaotic dynamics in the linear tri-trophic food chain model (Hastings and Powell 1991).

We examined the interaction effect between trait evolution and community dynamics to affect the stability and dynamical properties of the system and elucidated the driving factors by manipulating two parameters, namely the cost coefficient ω and the genetic variance G . The cost coefficient limits the extent of trait evolution by selection pressures arising from predation, and genetic variance determines the process rate of evolution relative to the population dynamics of the prey. The parameters related to trait evolution were set to $\gamma = 1$, $s = 2$ and $G = 0.01$ (a reference value).

The effects of trait evolution on community ecological dynamics may depend on the demographic state of the community without evolution. To characterize the dynamic properties of the community, we used the process rate of the prey population relative to the predator population. This is because previous studies have indicated that the bifurcation in ecological dynamics of the tri-trophic food chain is largely determined by the relative process rate (Hastings and Powell 1991; McCann and Yodzis 1994). McCann and Yodzis (1994) further simplified this system (Eqs. 4–6) in terms of the metabolic rate per unit biomass, which is likely directly associated with or indicated by the mortality rate of the two species, d_2 and d_3 , and the assimilation rate relative to the metabolic rate, $y_2 = \frac{c_2}{d_2 h_2}$ and $y_3 = \frac{c_3}{d_3 h_3}$. Discrepancies in the metabolic rate between the prey and the predator may lead to heteroclinic cycles and chaotic dynamics. Parameters y_2 and y_3 indicate the potential reproductive capacity of the species scaled by the death rate, or the metabolic rate with unlimited consumption and are referred to as the ecological scope. In our simulations, we set the ecological scope to biologically realistic values for the two trophic levels, with two for the prey and five for the predator, followed by other related parameters (Appendix 1). The death rate (metabolic rate) d_2 and the maximum consumption rate h_2^{-1} of the prey were manipulated at the same rate so that the ecological scope of the prey was kept constant. This treatment changed the relative process rate between the prey and predator within the constraint of the ecological scope.

Simulation methods

Numerical integrations were performed according to the fourth-order Runge–Kutta method from $t = 0$ to 10^5 with $3 \bullet 10^5$ steps using Mathcad 15 (Mathsoft) for each parameter setting. To find the equilibrium points of the dynamical systems, we used the built-in function of Mathematica (Wolfram). “NSolve” was used for communities without evolution and “FindRoot” was used for communities with evolution.

Wavelet transform

The nonlinear system comprises four variables with community dynamics at three trophic levels and the evolutionary dynamics of the prey trait, which exhibited complex and chaotic behaviors depending on the parameter values. To objectively and quantitatively present the fluctuation patterns, the simulated sample paths were wavelet-transformed to extract periodicities at multiple time scales. The wavelet transform to

time-series data X_t is $W(\sigma, \tau) = \left\{ \sum_t |\psi(t - \tau, \sigma)|^2 \right\}^{-\frac{1}{2}} \sum_t \psi(t - \tau, \sigma) X_t$, where $\psi(t, \sigma)$ is the mother function, t is the shift parameter (the point of transform in the time series), and σ is the scale

parameter, which was set to powers of 2 (2^h ; $h = 1, 2, 3, \dots$) in this study. For $\psi(t, \sigma)$, we used the following Mexican hat function: $\psi(t, \sigma) \propto \left(1 - \frac{(2\pi/\sigma)^2 t^2}{2}\right) \exp\left[-\frac{(2\pi/\sigma)^2 t^2}{4}\right]$.

Results

Community oscillation induced by trait evolution

The three trophic-level community dynamics with baseline ecological parameters and a large trait cost ($\omega = 1$) showed a heteroclinic cycle (Fig. 1), which was characterized by the coupling of two separate phases. These were the limit cycle-like resource–prey oscillation with a reduced top-down effect from the predator, and the slow recovery of the predator up to the level that effectively suppresses the prey density. The scale-specific wavelet transformed variables (wavelet power spectra) indicated two major periodicities with a shorter cycle as indicated by the phase diagram (scale $\approx 2^9$) and a longer cycle (scale $\approx 2^{12}$) (Fig. 2a). The longer cycle disappeared when the trait evolution was inhibited by setting the genetic variance as 0, implying the existence of a long-term effect of the trait evolution on the ecological dynamics. However, the eco-evolutionary dynamics with that magnitude of fitness cost exhibited almost no discernible difference from non-evolutionary ecological dynamics with the same ecological parameters.

The eco-evolutionary community dynamics showed discrete phase shifts or bifurcation when the trait cost was gradually reduced. When ω was equal to or smaller than 0.047, the chaotic properties disappeared, and the three species and the trait reached stable internal equilibria. By further reducing the trait cost, with values equal to or smaller than 0.027, the prey trait started a long-term periodic oscillation and retained three-species dynamics similar to the heteroclinic cycle (Figs. 1 and 2a). However, the period (length of a cycle) of the oscillation of the predator coincided with that of trait evolution, and was much longer than that of the non-evolutionary tri-trophic system. In addition, the period monotonically increases as the trait cost decreases.

A typical example of such dynamics with $\omega = 0.025$ is shown in Fig. 2b. There was only one internal equilibrium that was locally unstable and the real part of the largest eigenvalue in the Jacobian matrix was positive. The observed trajectories were interpreted as orbits around the internal rest point with a long periodicity. The dynamics comprised shifting between two distinct dynamic regimes with one being dominated by the resource-prey oscillation (apparent limit cycle) which is free from the top-down effect of the predator, and the other being regulated by the top-down effect activated by evolutionary reduction of the prey trait. The coupling of the two phases also characterized the heteroclinic cycles observed in the non-evolutionary tri-trophic model. The eco-evolutionary dynamics had highly different process rates between the slow dynamics driven by the predator and the fast pairwise oscillations governed by the other two species. The frequency of the shifts between the two regimes was affected by the evolutionary rate of prey traits. The time needed to shift between the two regimes was much longer with the eco-evolutionary dynamics than with the non-evolutionary dynamics.

Visual inspection suggested that the periodic dynamics of the predator had a different pattern of coincidence with the limit cycle-like oscillation of the resource and prey in comparison with non-evolutionary ecological dynamics (Figs. 1 and 2). Around the strange attractor in the non-evolutionary system, predator abundance gradually increased during the resource-prey co-oscillation and culminated at the end of the co-oscillation. This was followed by a monotonic decrease in the predator during the collapse of the prey until the resurgence of co-oscillation (Fig. 1). In the eco-evolutionary dynamics, predator abundance continued to decline in the long run during the two-species oscillation and reached its minimum at the midpoint of the co-oscillation period. However, the prey trait behaved like predator abundance in the non-evolutionary ecological dynamics. It continued to decrease during the co-oscillation period and tended to recover over the remainder of the period (Fig. 2).

The present evolutionary model of a single trait excludes the likelihood that trait evolution alone would drive any periodic fluctuations. A purely ecological model without evolution cannot explain this long periodicity. It is inferred that the long-term cycle observed was caused by the interaction between ecological and evolutionary dynamics through eco-evolutionary feedback processes. Eco-evolutionary dynamics that are characterized by shifting phases with a long periodicity are referred to as EEO in this study.

The eco-evolutionary dynamics at stationary states with specific sets of parameter values were categorized into four regimes according to the dynamical properties of the three species and the trait. These were the limit cycle (LC), the heterochronic cycle (HC), the stable equilibrium (SE), and the EEO (see Table 1). The distinction between the LC and the HC was based on the three-dimensional orbit by the community dynamics of the three species. LC was defined as the case where the circular orbit was not folded and the heterochronic orbit was not visible. Meanwhile, the HC was defined as the case where the circulating or quasi-circulating (for the case of chaotic fluctuation) orbit was intricately folded such that the heterochronic orbit between two basins of attraction was clearly identified. The EEO required far longer to pass through the heterochronic orbit because the system behavior was influenced by the prey trait, which slowly changed with evolution.

Table 1

Six categories of phases in the eco-evolutionary community dynamics observed in the simulations

Category	Symbol	Description
Limit cycle	LC	The three species exhibit limit cycles while the trait does not change by evolution.
Heterochronic cycle	HC	The three species exhibit heterochronic cycles accompanying chaotic fluctuations. The trait does not change.
Stable equilibrium	SE	The three species and the trait remain permanently at an internal equilibrium.
Eco-evolutionary oscillation	EEO	Transitions between orbits around two ecological equilibria are derived by trait evolution.

As indicated by the phase diagram (Fig. 3), which depicts each region of the regimes along the metabolic rate of the prey and the fitness cost of the trait, EEO occurred when the metabolic rate was higher for the prey ($x_2 > 0.13$) than for the predator ($x_3 = 0.1$), and the fitness cost of the trait was small.

The relationships between the trait evolution and community stability were reversed according to the fitness cost of the trait. The parameter region attained stable equilibria (SE in Fig. 3), in which the abundance of the three species and the prey trait remained unchanged, which was adjacent to the parameter region of EEO and HC. It was then inferred that EEO or HC, both of which are unstable, could be generated from the stable eco-evolutionary state SE if a reduction or an increase in the fitness cost of the trait enhanced or inhibited the evolution. EEO or HC could lead to a stable state of SE if an increase or a reduction in the fitness cost of the trait inhibited or enhanced the evolution. Facilitated evolvability could stabilize or destabilize community dynamics depending on the previous states.

There was a trend for the region of SE to become wider with a higher metabolic rate for the prey. The low metabolic rate of the prey (less than 0.13) diminished the stabilizing or destabilizing effect of evolution, according to the transition between the regimes, and led to the disappearance of the EEO from the system.

The shape of the predation efficiency function

We did not find any EEO with predation efficiency functions more sharply convex than the Gaussian ($\gamma > 2$) for all the parameter sets examined in this study (cf. Yoshino and Tanaka 2013).

Sample paths

The inspection of the separate dynamical phases along a typical sample path may elucidate the process behind the EEO (Fig. 4). A sample path was chosen to have the specific parameter values $d_2 = 0.2$, $\omega = 0.01$, and $G = 0.01$, and the initial conditions were $n_1 = 0.765$, $n_2 = 0.100$, $n_3 = 1.308$, and $z = 2.00$. This combination of parameter values and initial conditions resulted in three unstable equilibria, $(\tilde{n}_1 \tilde{n}_2 \tilde{n}_3 \tilde{z}) = (0.20.800)$, $(0.960.131.640)$, and $(0.260.852.122.77)$, all of which had the largest positive eigenvalues. The first and second equilibria are fulfilled when the prey trait almost diminishes and the system converges with the purely ecological model, which has the maximum predation efficiency. However, the community and trait circulated between the vicinities of these unstable equilibria rather than resting at one of those equilibria.

To unravel the internal forces causing the dynamics of the EEO in terms of the interaction between the two subsystems, trait evolution, and ecological dynamics, we used the fast-ecological dynamics approximation. Under this approximation, the trait value was hypothetically fixed at a particular time step for the eco-evolutionary dynamics. The ecological dynamics that temporarily excluded the evolutionary change of the trait were examined for the local stability of the subsystem and the selective force on the trait (see Table A1 in Appendix A). This approach may provide intuitive insight, in the same way as the fast-evolution approach, which may present a general method to predict whether trait evolution would stabilize or destabilize predator-prey dynamics (Cortez and Ellner 2010). The inverse approximation in our

analyses may be justified by the assumption that the trait evolution processes occur at much slower rates than the ecological dynamics.

The evolution of prey traits affected the ecological dynamics regime by reducing the maximum predation efficiency. The adaptive landscape for the prey trait depended on the regime of the ecological dynamics, which was approximated by the non-evolutionary community dynamics, with the predation efficiency corresponding to a specific trait value at a particular time step of the entire eco-evolutionary trajectory (Fig. 4; Table A1).

At an arbitrary starting point ([1] in Fig. 4; $t = 91000$ in Table A1), the number of predators increased because of the reduced prey trait value ($z = 2$) and the increased predation efficiency (a_3). The oscillations of the lower two species were checked using the top-down effects of the predator. The evolutionary rate was accelerated by the increasing predator abundance and achieved nearly a maximum rate. However, the ecological dynamics of the three species depicted an orbit between the two saddle points. The lower two species coexisted or the top predator was predominant (Table A1), whereas the trait remained at low values. At time step (2) in Fig. 4 ($t = 92000$ in Table A1), the predator reached its peak abundance where the ecological dynamics had locally stabilized. However, this ecologically stable state did not persist because the trait was not stable simultaneously. The stable evolutionary equilibrium was larger than the temporal state of the trait ([2] in Fig. 4; $t = 92000$ in Table A1). Further evolution destabilized the three-species demographic equilibrium and brought about a crash in predator abundance due to reduced predation efficiency ([3] in Fig. 4; $t = 92500$ in Table A1). The asymptotic state of the ecological dynamics shifted from the three-species system to the two-species limit cycle under release from the predation pressure. In the eco-evolutionary system, a considerable decrease in the predator abundance reduced the adaptive value of the prey trait in terms of resisting predation. When the reduced adaptive value could not compensate for the fitness cost of the trait, the net negative selective force caused the evolutionary degeneration of the trait. The reduced prey trait allowed the recovery of potential predation efficiency, thereby preventing extinction of the predator. Although the two species at lower trophic levels exhibited quasi-limit cycles, the prey trait continued to decrease at a slow rate if the fitness cost was low ([4] in Fig. 4; $t = 93000$ in Table A1). This phase would be replaced by two inverse shifts into stable ecological equilibrium followed by three-species oscillation in the ecological subsystem ($t = 95000$ and 97000 in Table S1). In the eco-evolutionary system, the prey trait continued to decline until the system returned to its initial state ([5] in Fig. 4; $t = 98000$ in Table A1).

At the first inverse shift, the evolutionary degeneration of the trait recovered the predation efficiency, and the ecological dynamics reached a stable equilibrium ($t = 95000$ in Table A1). In the eco-evolutionary dynamics, the predator did not fully recover from the sharp drop and could not prevent the degeneration of the trait. The three-species ecosystem did not remain in the same basin of attraction. Further evolutionary reduction of the trait caused the three-species system to exhibit long-term oscillations around an internal saddle point. During this period, the selective force on the prey trait changed from negative to positive ($t = 97000$ and 98000 ; Table A1). The trait started to increase with a time lag following the dynamics of the predator, and the eco-evolutionary system returned to its original state ($t =$

91000 in Table A1) where we started the observation, which was regarded as the completion of an eco-evolutionary cycle.

Periodicities of community dynamics and trait evolution

The priority of one eco-evolutionary cycle predominantly depends on the relative strengths of the selection caused by ecological interaction with the selection caused by adaptation to the non-biotic environment, namely the fitness cost. The mean periodicity was defined as the average time steps required for the trajectories of the eco-evolutionary dynamics to return to the same prior state, which was measured as the average time step between adjacent peaks of predator abundance inspected from the long-term cycles. In the case of stable equilibria, the periodicity was assigned as 0 because it is indefinable. Mean periodicity depended on the fitness cost of the trait (Fig. 5). For a high fitness cost (≥ 0.1), the periodicity was shorter and comparable to the periodicity of the ecological subsystem without evolution. Meanwhile, the periodicity was substantially extended by approximately one order of magnitude when a smaller fitness cost of the trait triggered the EEO (Fig. 5).

The effect of genetic variance on the eco-evolutionary dynamics

The evolutionary rate of the consumer trait determines the relative process rates between community ecological dynamics and evolutionary dynamics, which significantly affect the regime of eco-evolutionary feedback (Cortez 2016, 2018; Govaert et al 2019). We examined the effect of the evolutionary rate by manipulating the genetic variance and fitness cost of the prey trait. In all cases, the EEO was replaced by LC with larger genetic variance (Fig. 6). Higher fitness costs, which limit the evolvable ranges of the trait, maintain the regime of HC or SE, regardless of the magnitude of genetic variance. This result, coupled with the effects of genetic variance, indicated that a slower rate of evolution and higher evolvability were the necessary conditions for the eco-evolutionary oscillation with long periodicities (EEO).

Discussion

The main questions to be addressed in the theoretical issues with community eco-evolutionary dynamics are the stabilizing or destabilizing effect of trait evolution on community dynamics (Saloniemi 1993; Abrams and Matsuda 1997; Mougi and Iwasa 2010), the generation of unique oscillations, such as out-of-phase prey-predator oscillation, by fast evolutionary dynamics (Yoshida et al 2007; Jones et al 2009; Hiltunen et al 2014), and the effects of genetic variance on the interaction between trait evolution and community dynamics (Johnson et al 2009; Cortez 2016, 2018). The concept of eco-evolutionary feedback provides a key perspective on these questions (Fussmann et al 2007; Andreazzi et al 2018; Govaert et al 2019). Cortez and Ellner (2010) presented an analytical framework based on fast evolution and slow ecological dynamics approximation, which can predict shifts between different dynamical properties of ecological systems driven by separation by the trait from a critical manifold at the evolutionary equilibria. Eco-evolutionary feedback, which is realistic because the evolutionary timescale is often comparable with that of ecological dynamics (Kopp and Matuszewski 2014), can strengthen oscillation or stabilize

communities, as well as generate cryptic dynamics leading to out-of-phase oscillation or less explicit ecological dynamics (Yoshida et al 2007; Jones et al 2009; Hiltunen et al 2014). Contrary to the attention received on the importance of fast evolutionary changes in traits, we focused on the slow evolutionary rates of the prey trait that cause unusual community dynamics.

Results from the present analysis indicated that a special case of eco-evolutionary dynamics in the three-level linear food chain can occur when the demographic process rate of the pair of resources and prey is much faster than that of the predator. Environment-driven natural selection that does not occur through interspecific interactions acting on the anti-predator prey trait is weak, and the evolutionary rate of the trait is constrained. The resultant eco-evolutionary oscillation (EEO), is characterized by periodic shifts with a long periodicity between two community states, namely intermittent short periodic synchronous cycles by the pair of lower species with reduced population density of the predator, and relatively slow community dynamics with the recovered abundance of the predator. These unique community dynamics are inherent in tri-trophic systems, which depict heterochronic orbits, and are characterized by longer periodicity than in the two-species predator-prey system. In line with the linear tri-trophic food chain in this study, evolution-driven periodic shifts in three-species communities with intraguild predation were also identified by Patel and Schreiber (2015), who assumed the presence of a predator trait governing the relative strength of intraguild predation and the exploitation of common resources. Even in two-species predator-prey systems, prey trait evolution can cause intensified oscillation between two alternative extremes, namely the prey-dominated and the predator-dominated states (Mougi and Iwasa 2010; Cortez 2016), which did not require long periodicities.

Khibnik and Kondrashov (1997) highlighted the importance of slow-fast dynamics in a pair of interacting species in the context of causing the Red Queen oscillation (slow evolution alongside rapid ecological dynamics; *c.f.* Dercole et al 2006, 2010). They demonstrated that the predator-prey system, in which a pair of traits possessed by the predator and the prey determined the predation efficiency, could produce eco-evolutionarily driven long-periodicity oscillation (Red Queen Dynamics). This was characterized by cyclical and long-term epochs of highly different ecosystem states. The genetic subsystem has the innate potential to drive long-term oscillations while being reinforced by interplay with the ecological subsystem. The three-species system in this study assumed a single evolvable trait assigned to the intermediate prey species, which did not include trait-by-trait coevolution, which could generate dynamical instability.

A mechanistic explanation for the eco-evolutionary feedback that causes regular or irregular intermittent shifts between different ecological states may be given by the heterochrony of stable states between the ecological and evolutionary subsystems (Cortez and Ellner 2010; Petal and Schreiber, 2015; Petal et al 2018; see Fig. 7 for a simplified schematic explanation). One of the most important factors triggering the shifts between the alternative states observed in this study is the combination of prey traits and predator density because it determines the predation pressure. The eco-evolutionary system can cause feedback loops between the community state and trait evolution. In the stable community, the trait evolves towards the equilibrium that is determined by the balance between the fitness cost and the benefit of increased predator avoidance (Fig. 7; from the upper right to the lower right graph). However, the community shifts

from a stable to an unstable state, driven by trait evolution, before the trait reaches an evolutionary equilibrium because of slow evolution (Fig. 7; from the lower right to the upper left graph). The shifted community structure changes the adaptive landscape for the trait at a moment, and under an unstable community, the prey trait slowly degenerates by the tradeoff (fitness cost) (Fig. 7; from the upper left to the lower left graph). The stable community was recovered when the trait was reduced to a certain level that allowed the recovery of the predator (Fig. 7; from the lower left to the upper right graph).

This implies that long-periodicity oscillations could occur whenever the community demographic dynamics are governed by a trait affecting the strength of interspecific interactions. The adaptive landscape for the trait is formed with time lags by the demographic state of the composite species in communities. The eco-evolutionary oscillation observed suggests a special case of the generic rule that eco-evolutionary feedbacks can occur when the community state that creates a particular adaptive landscape defining an evolutionary equilibrium is not sustained by the evolution of the trait approaching that equilibrium. Local stability can be systematically examined by combining the local stabilities of the composite subsystems (Cortez 2018).

The interval between state shifts is determined by the evolutionary rate of the trait, which is constrained by genetic variance. Genetic variance may affect eco-evolutionary dynamics in two ways, namely as a determinant of the local stability of the evolutionary subsystem and the entire eco-evolutionary stability (Ellner and Becks 2011; Mougi and Iwasa 2010, 2011; Cortez 2018), and as a factor governing the long-term state shifts in communities (Khibnik and Kondrashov 1997; Dercole et al 2006).

The effect of genetic variance can be reinforced by discrepancies between the timescales of trait evolution and the population dynamics. DeLong et al (2016) compared proportional changes in phenotypic traits and population abundance for many field-based studies and concluded that phenotypic changes, including those due to plasticity, can process at nearly the same timescale at one fourth on average as the population changes, which is compatible with the recent recognition of the rapid evolutionary rates relative to ecological dynamics (e.g. Hairston et al 2005; Fussmann et al 2007; Kopp and Matuszewski 2014). In the present simulations, the maximum proportional change in the prey population was approximately three orders of magnitude faster than the maximum proportional change in the prey trait by evolution if the genetic variance was smaller than 0.1. The present simulations implied that the relative rate of trait evolution had to be at least two orders of magnitude slower than the observed rates to drive the eco-evolutionary oscillation with long periodicity. The phenotypic evolution in some species can be regarded as a several percent improvement of the mean trait value per generation, while the population abundance of the species can increase more than ten-fold per generation at the maximum.

In the two-species predator-prey system, state shifts with long periodicity are far less likely than in the tri-trophic system with trait evolution, because during the phase of reduced predator abundance due to the prey trait evolution, the (time-weighted) mean abundance of prey would be regulated in comparison to the two-species predator-prey system, in which the prey abundance was almost unchecked until the predator

abundance recovered. During the process of temporarily decoupled resource-prey oscillations, the prey trait changes (degenerates) slowly depending on the genetic variance and fitness cost (trade-off) of the trait. This is because the prey population under the check by oscillation can efficiently avoid predation pressure, whereas in the two-species system the predation pressure quickly recovers by the increased functional response per predator individual, thereby regenerating selection pressure on the prey trait. The lack of observed long periodicity eco-evolutionary oscillation (EEO) in the case of the sharply convexed predation efficiency function ($\gamma > 2$) may coincide with this explanation (Yoshino and Tanaka 2013). This is because the higher sensitivity of predation efficiency against trait evolution is likely to expedite the recovery of predation pressure under the phase of increased prey abundance.

A complex eco-evolutionary food web model with trait evolution in a resource niche revealed intermittent shifts between alternative community states differing in complexity and average link length (Takahashi et al 2013). In contrast to the present simulation, the drivers of such complex adaptive dynamic systems include mutations, selection, speciation, and extinction. Considering that the tri-trophic system may function as one of the primary modules of the ecosystem (Price et al 1980; Bascompte 2009; Abdala-Roberts et al 2019), the substantial process causing long periodic state shifts may be shared by our model, although it has contrasting simplicity.

The present analysis suggests that if long intervals between cyclical state shifts are observed in real communities, feedback between ecological interactions and trait evolution may be one of the theoretically feasible explanations.

Declarations

This study was supported by a grant-in-aid by Japan Society for the Promotion of Science to the author. There is no conflict of interest with any persons or organizations. Code in R is available upon request.

Acknowledgments

This study was partly supported by a grant-in-aid (23570040) by Japan Society for the Promotion of Science to YT.

References

1. Abdala-Roberts L, Puentes A, Finke DL et al (2019) Tri-trophic interactions: bridging species, communities and ecosystems. *Ecol Lett* 22:2151–2167
2. Abrams PA, Matsuda H (1997) Prey adaptation as a cause of predator–prey cycles
3. *Evolution* 51:1742–1750
4. Abrams PA, Matsuda H, Harada Y (1993) Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evol Ecol* 7:465–487

5. Andreazzi CS, Guimarães PR Jr, Melián CJ (2018) Eco-evolutionary feedbacks promote fluctuating selection and long-term stability of antagonistic networks. *Proc R Soc B* 285:20172596
6. Bascompte J (2009) Disentangling the web of life. *Science* 325:416–419
7. Brown JH, Gillooly JF, Allen AP et al (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
8. Cortez MH (2016) How the magnitude of prey genetic variation alters predator-prey eco-evolutionary dynamics. *Am Nat* 188:329–341
9. Cortez MH (2018) Genetic variation determines which feedbacks drive and alter predator-prey eco-evolutionary cycles. *Ecol Monogr* 88:353–371
10. Cortez MH, Ellner SP (2010) Understanding rapid evolution in predator-prey interactions using the theory of fast-slow dynamical systems. *Am Nat* 176:E109–E127
11. Dercole F, Ferriere R, Gagnani A et al (2006) Coevolution of slow-fast populations: evolutionary sliding, evolutionary pseudo-equilibria and complex Red Queen dynamics. *Proc R Soc B* 273:983–990
12. Dercole F, Ferriere R, Rinaldi S (2010) Chaotic Red Queen coevolution in three-species food chains. *Proc R Soc B* 277:2321–2330
13. DeLong JP, Forbes VE, Galic N et al (2016) How fast is fast? Eco-evolutionary dynamics and rates of change in populations and phenotypes. *Ecol Evol* 6:573–581
14. Edwards KF, Kremer CT, Miller ET et al (2018) Evolutionarily stable communities: a framework for understanding the role of trait evolution in the maintenance of diversity. *Ecol Lett* 21:1853–1868
15. Ellner SP, Becks L (2011) Rapid prey evolution and the dynamics of two-predator food webs. *Theor Ecol* 4:133–152
16. Fussmann GF, Loreau M, Abrams PA (2007) Eco-evolutionary dynamics of communities and ecosystems. *Func Ecol* 21:465–477
17. Govaert L, Fronhofer EA, Lion S et al (2019) Eco-evolutionary feedbacks -Theoretical models and perspectives. *Func Ecol* 33:13–30
18. Gliwicz ZM (1990) Food thresholds and body size in cladocerans. *Nature* 343:638–640
19. Hairston NG Jr, Ellner SP, Geber MA et al (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecol Lett* 8:1114–1127
20. Hastings A, Powell T (1991) Chaos in a three-species food chain. *Ecology* 72:896–903
21. Hiltunen T, Hairston NG Jr, Hooker G et al (2014) A newly discovered role of evolution in previously published consumer-resource dynamics. *Ecol Lett* 17:915–923
22. Johnson MTJ, Vellend M, Stinchcombe JR (2009) Evolution in plant populations as a driver of ecological changes in arthropod communities. *Phil Trans R Soc B* 364:1593–1605
23. Jones LE, Becks L, Ellner SP, Hairston NG Jr et al (2009) Rapid contemporary evolution and clonal food web dynamics. *Phil Trans R Soc B* 364:1579–1591

24. Khibnik A, Kondrashov AS (1997) Three mechanisms of Red Queen dynamics. *Proc R Soc B* 264:1049–1056
25. Kopp M, Matuszewski S (2014) Rapid evolution of quantitative traits: theoretical perspectives. *Evol Appl* 7:169–191
26. Kotila SE, Vetsigiana K (2018) Emergence of evolutionary stable communities through eco-evolutionary tunneling. *Nat Ecol Evol* 2:1644–1653
27. Kreutzer C, Lampert W (1999) Exploitative competition in differently sized *Daphnia* species: a mechanistic explanation. *Ecology* 80:2348–2357
28. Lande R (1982) A quantitative genetic theory of life history evolution. *Ecology* 63:607–615
29. McCann K, Yodzis P (1994) Biological conditions for chaos in a three-species food chain. *Ecology* 75:561–564
30. Mougi A, Iwasa Y (2010) Evolution towards oscillation or stability in a prey-predator system. *Proc R Soc B* 277:3163–3171
31. Mougi A, Iwasa Y (2011) Green world maintained by adaptation. *Theor Ecol* 4:201–210
32. Patel S, Schreiber SJ (2015) Evolutionarily driven shifts in communities with intraguild predation. *Am Nat* 186:E98–E110
33. Patel S, Cortez MH, Schreiber SJ (2018) Partitioning the effects of eco-evolutionary feedbacks on community stability. Available from <https://doi.org/10.1086/695834>
34. Price PW, Bouton CE, Gross P et al (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annu Rev Ecol Syst* 11:41–65
35. Saloniemi I (1993) A coevolutionary predator–prey model with quantitative characters. *Am Nat* 141:880–896
36. Takahashi D, Brännström Å, Mazzucco R et al (2013) Abrupt community transitions and cyclic evolutionary dynamics in complex food webs. *J Theor Biol* 337:181–189
37. Yamauchi A, Yamamura N (2005) Effects of defense evolution and diet choice on population dynamics in a one-predator-two-prey system. *Ecology* 86:2513–2524
38. Yodzis P, Innes S (1992) Body size and consumer-resource dynamics. *Am Nat* 139:1151–1175
39. Yoshida T, Ellner SP, Jones LE et al (2007) Cryptic population dynamics: Rapid evolution masks trophic interactions. *PLoS Biol* 5(9):e235. doi:10.1371/journal.pbio.0050235
40. Yoshino M, Tanaka Y (2013) Global properties of evolutionary Lotka-Volterra system. *Adv Pure Math* 3:709–718

Figures

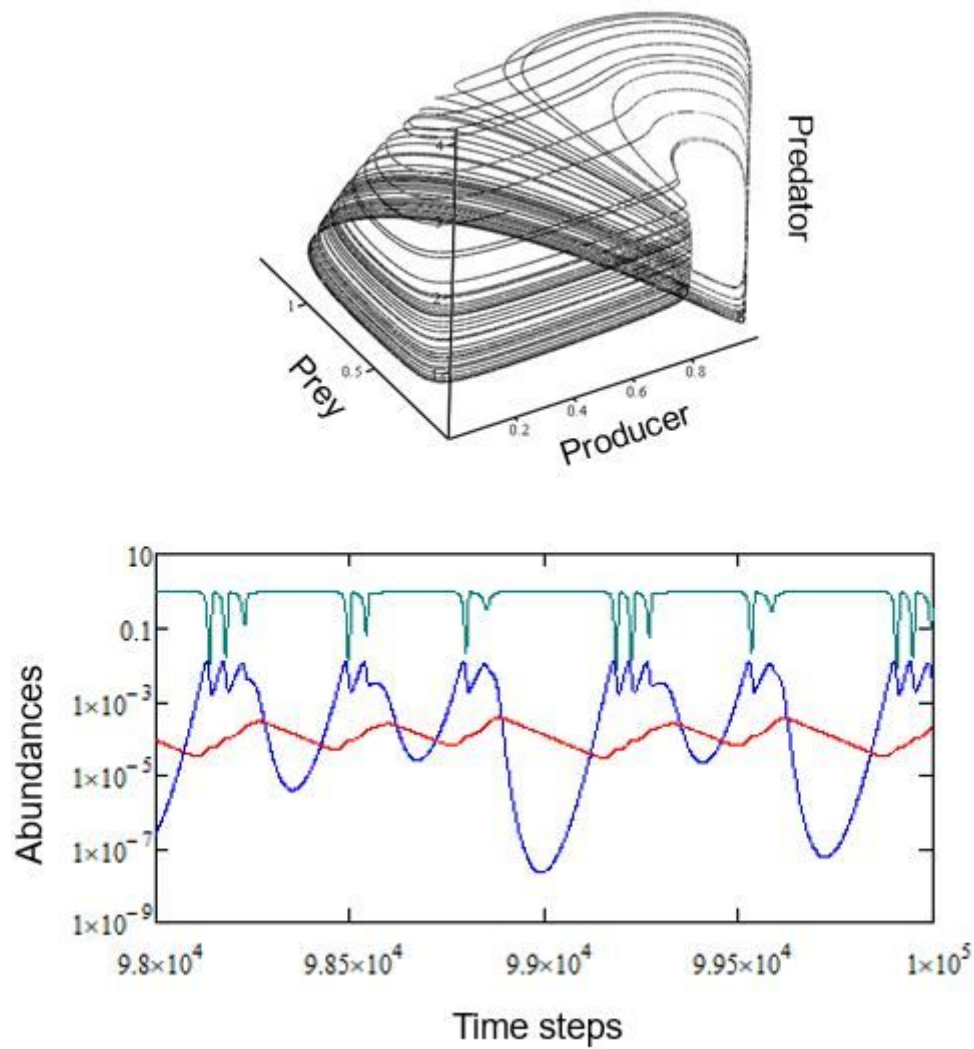


Figure 1

Trajectories of abundances of three species in the non-evolutionary ecological model with 3-species linear food chain. The green line in the lower graph denote the resource population, the blue line the prey, and the red line the predator.

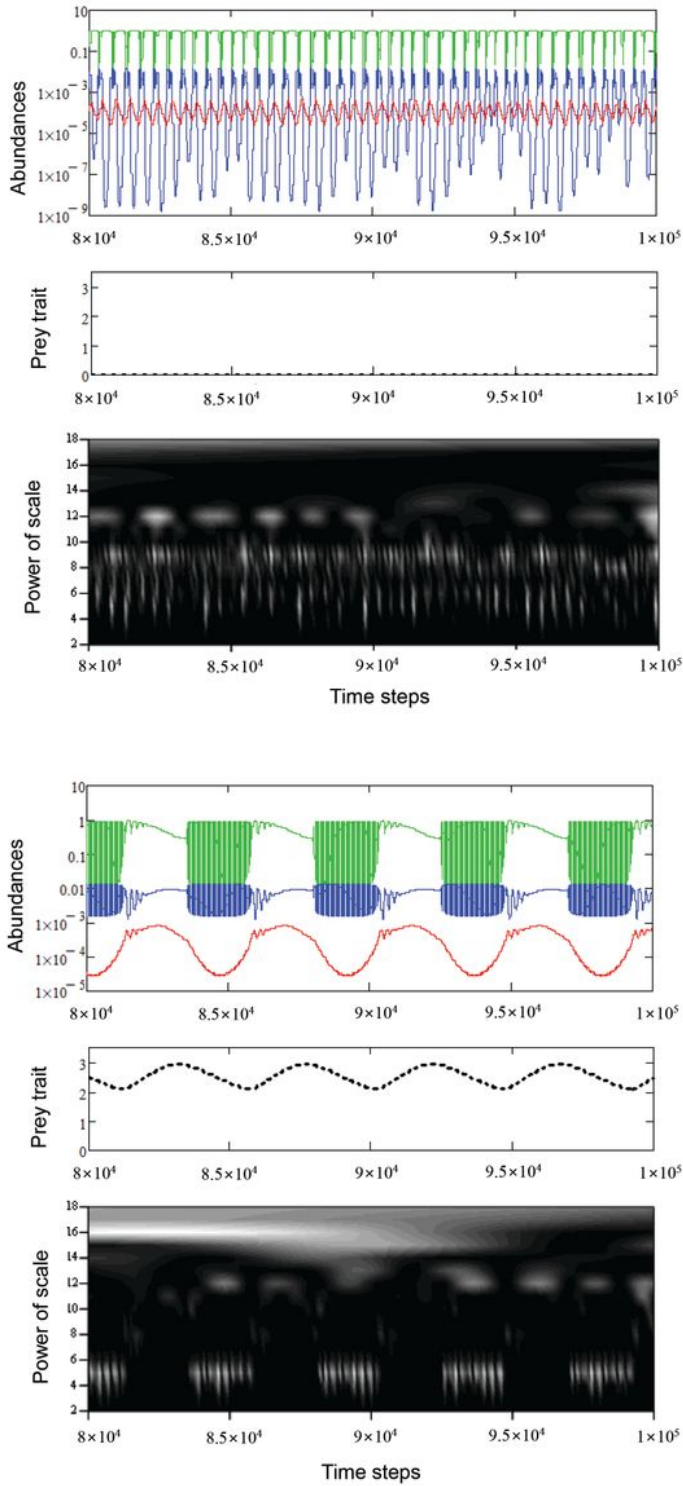


Figure 2

Trajectories of eco-evolutionary dynamics with a large fitness cost (a) $w=1$, and a small fitness cost (b) $w=0.025$. The mortality of prey and the genetic variance is respectively set as $d_2=0.2$ and $G=0.01$. The wavelet spectra are graphed at the lowest panel. The lighter regions indicate higher values of spectrum. The scale is indicated as the power coefficient of 2.

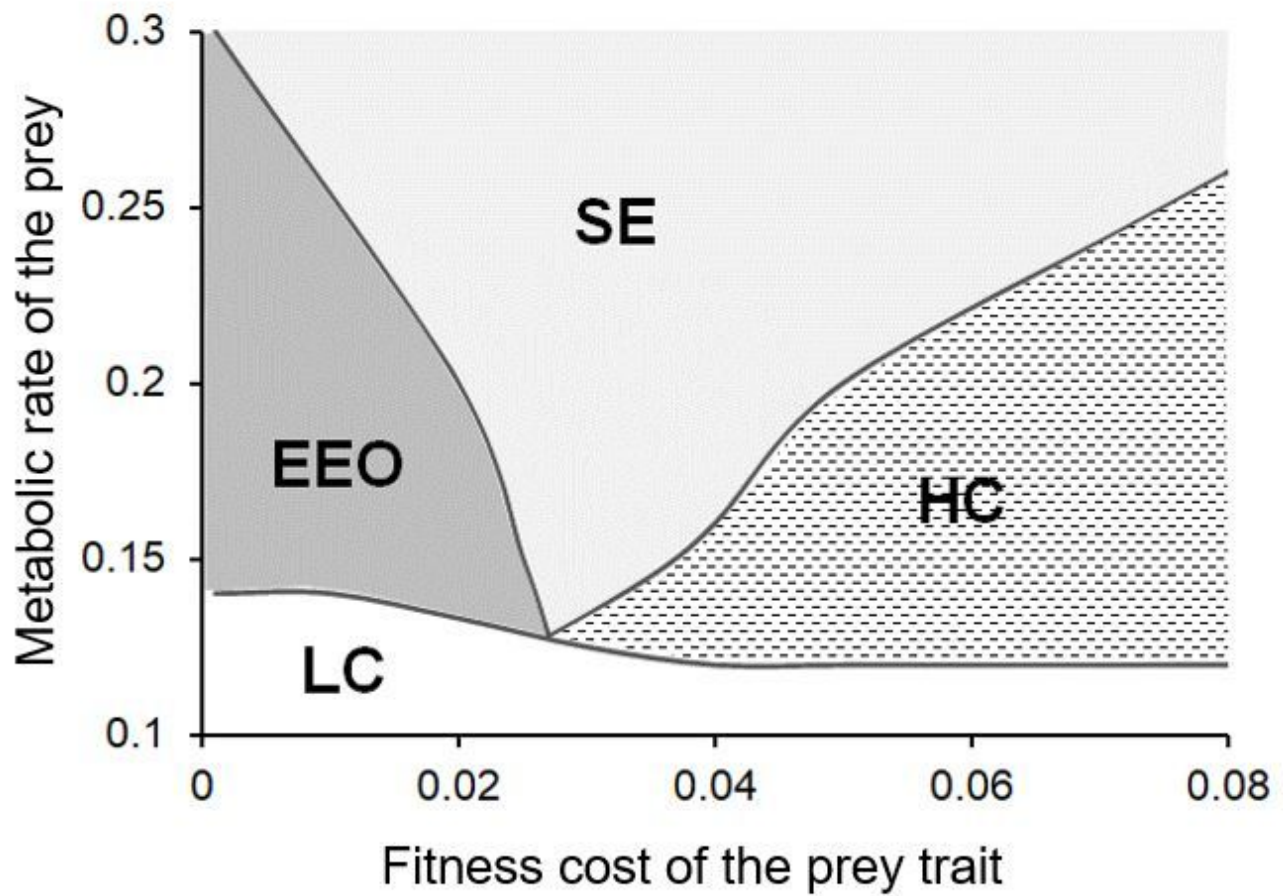


Figure 3

A phase diagram of the eco-evolutionary dynamics along two parameter axes, fitness costs of the prey trait and metabolic rates of the prey (equivalent to the prey mortality d_2). The abbreviations indicate EEO: eco-evolutionary oscillation, HC: heterochronic cycle, LC: limit cycle, and SE: stable equilibrium.

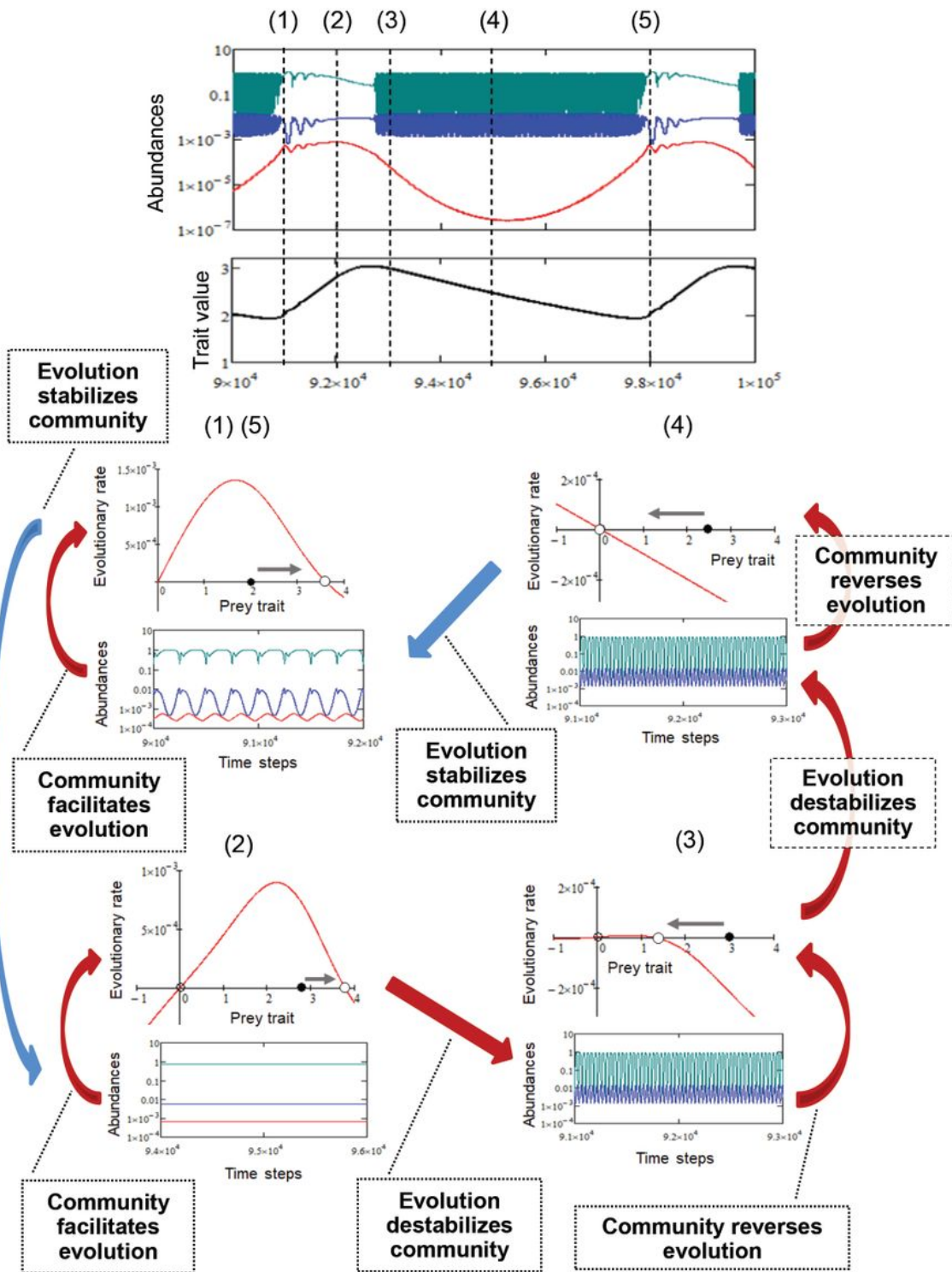


Figure 4

Driving forces of eco-evolutionary dynamics at different phases in a cycle. Starting from the situation of a high predator abundance and a low value of the prey trait, the ecological dynamics facilitates evolution of the prey trait (1) and (2). After the community reaches the stable equilibrium, the further trait evolution makes the predator population dropping sharply and destabilizes the community (3), in which the trait decreases only due to the fitness cost (4) until the predator population tends to recover.

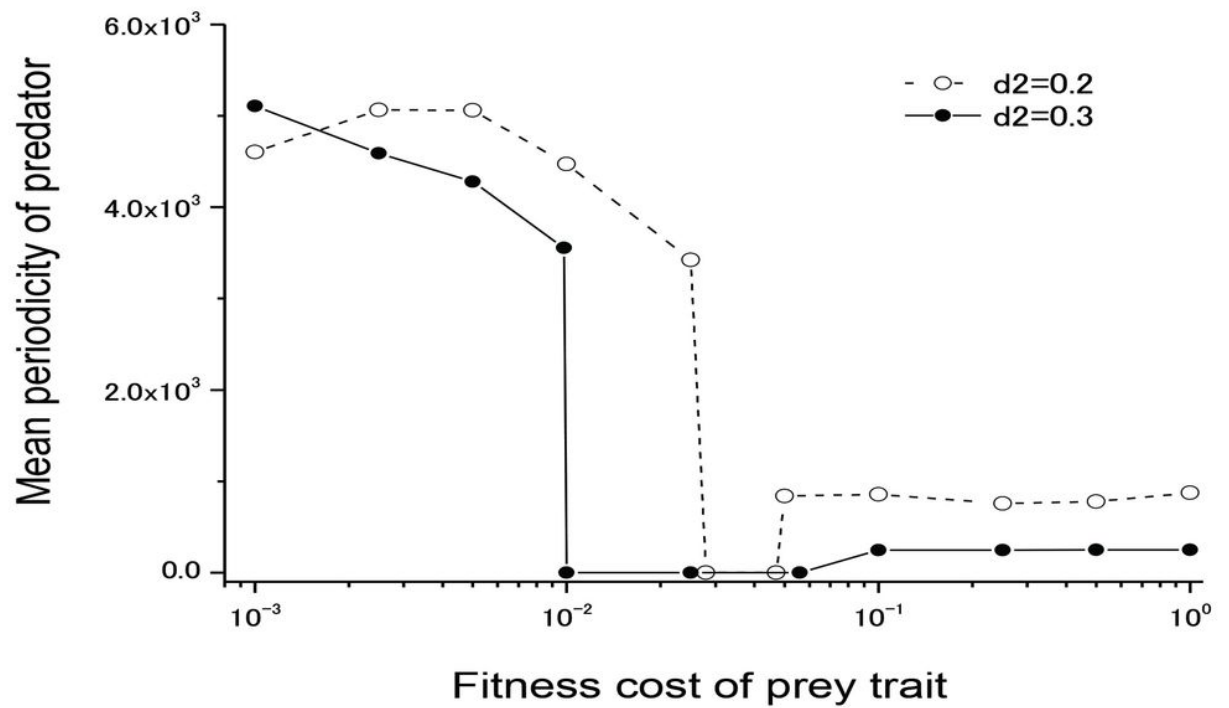


Figure 5

Relationship between cycle lengths of the eco-evolutionary dynamics and fitness cost (tradeoff) of the prey trait. The cycle length is defined as the mean periodicity of the top predator abundance.

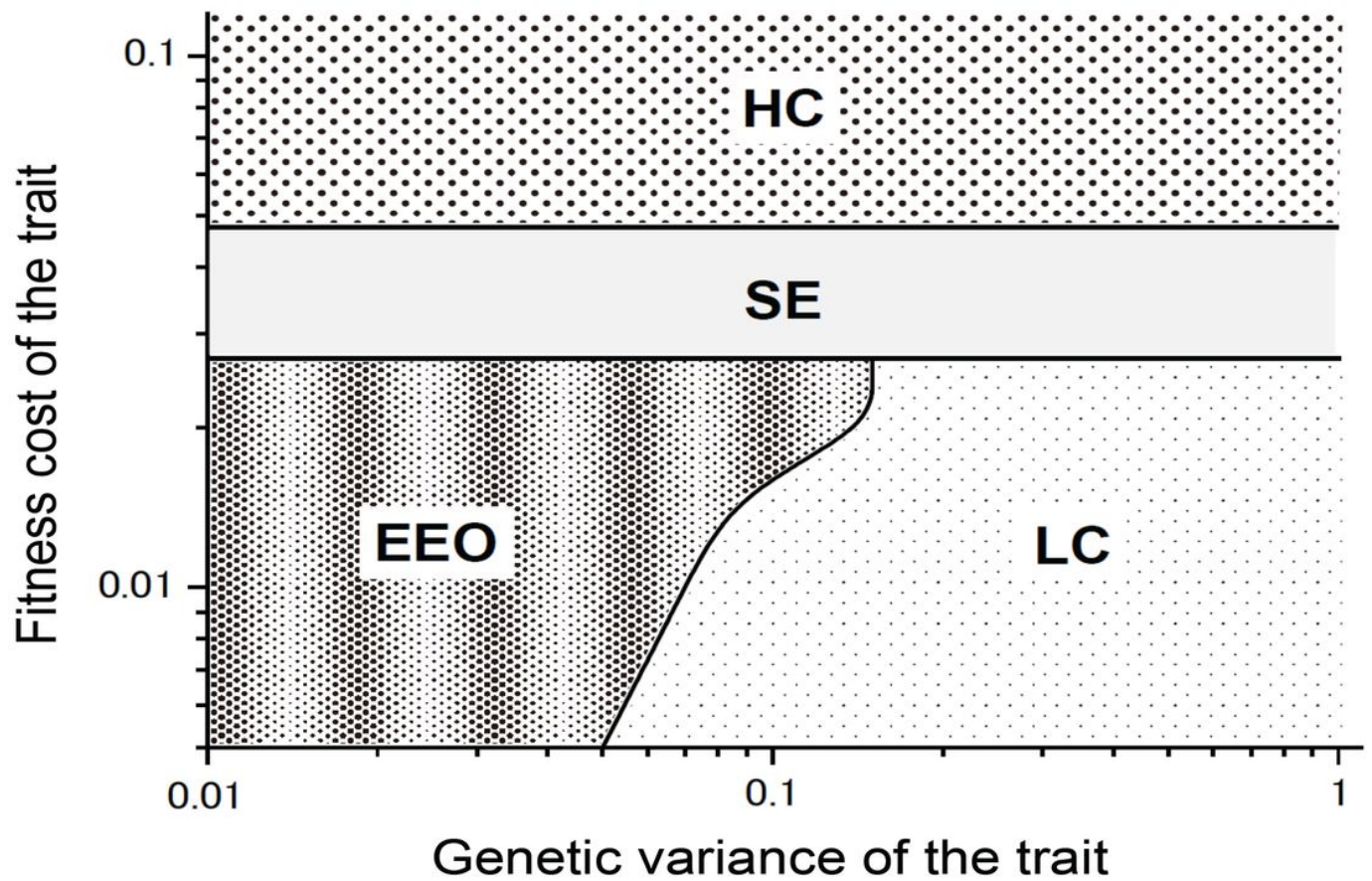


Figure 6

Effect of genetic variance of the trait on the regimes of eco-evolutionary dynamics. The abbreviations are subject to Fig. 3.

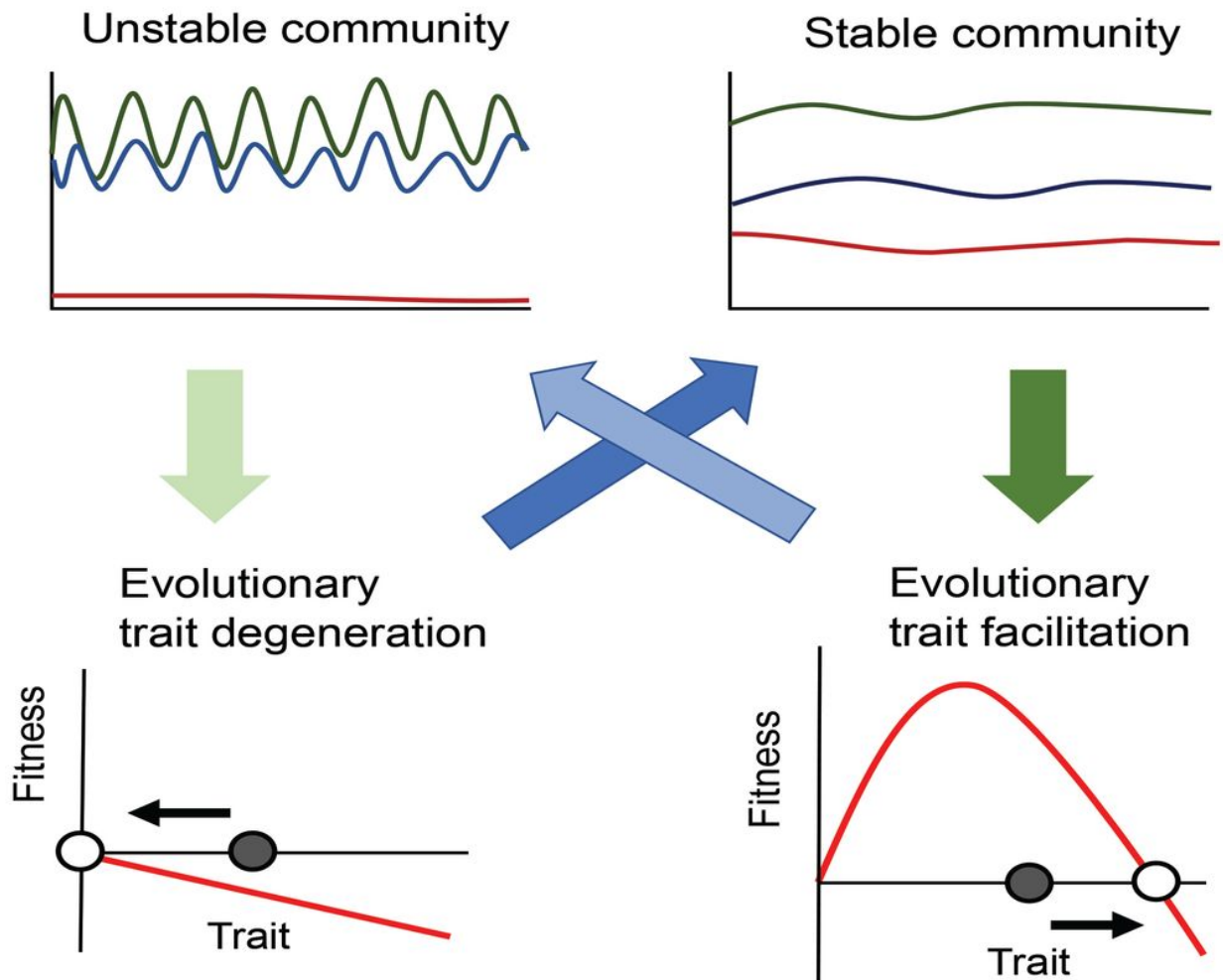


Figure 7

A schematic drawings of interactions between the ecological and the evolutionary subsystems to cause the eco-evolutionary oscillation.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementraymaterialTanakaandYoshino.docx](#)