



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

Yoshinari Tanaka<sup>1</sup> · Masafumi Yoshino<sup>2</sup>

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## Abstract

Eco-evolutionary feedback can result in periodic shifts with long intervals between alternative community states. Simulations using a food chain model with three trophic levels, namely the resource–prey–predator system, with evolution of an anti-predator trait possessed by the prey (prey trait) have shown long-term oscillations that ecological dynamics alone cannot attain. The alternative community states are characterized by stable states slowly changing with prey trait evolution and fast cycles at the lower two trophic levels. This shift of community dynamical states with large intervals was governed by the evolution of the prey trait. The abrupt state shifts between long and intermittent stationary periods were caused by the interaction between community ecological dynamics and trait evolution. We further examined the effects of genetic variation on the stability of the community. A faster evolutionary rate with larger genetic variance tended to stabilize eco-evolutionary dynamics.

**Keywords** Eco-evolutionary feedback · Tri-trophic food chain · State shift · Anti-predator trait · intermittent cycle · Heterochronic cycle

## 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, the community stability, and the coexistence of competing species (Fussmann et al. 2007; Jones et al. 2009; Dercole et al. 2010; Ellner and Becks 2011; Andreatzi 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 changing ecological interaction (Yamauchi and Yamamura 2005; Mougi and Iwasa 2010, 2011).

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

<sup>1</sup> Graduate School of Global Environmental Studies, Sophia University, Kioi-cho 7-1, Chiyoda-ku, Tokyo 102-8554, Japan

<sup>2</sup> Department of Mathematics, Graduate School of Advanced Science and Engineering, Hiroshima University, Hiroshima 739-8526, Japan

Other studies have indicated that eco-evolutionary dynamics can change the long-term dynamics of purely ecological systems with fixed traits. A key example of this system is the Rosenzweig–McArthur prey–predator system, in which the anti-phase cycle replaces the limit cycles when the prey trait can evolve and the ecological and the evolutionary dynamics work at similar timescales (Yoshida et al. 2003; Ellner and Becks 2011).

On the other hand, some studies on eco-evolutionary dynamics have highlighted the importance of trait evolution to generate long-term periodicity in the community dynamics when the evolutionary change is much slower than the ecological dynamics (Khibnik and Kondrashov 1997; Dercole et al. 2006; Klauschies et al. 2016; van Velzen et al. 2022). In this article we use the word “intermittency” to refer to the time interval of a particular dynamical state (for example, two species periodic oscillation) that occurs discontinuously and repeatedly. And we hypothesize that the evolutionary dynamics of a trait which affects ecological interaction can greatly extend intermittency of some ecological dynamics and cause extremely long periodicity if the evolutionary timescale is much longer than the ecological timescale. As a specific example to verify this hypothesis we present the tri-trophic food chain model which assumes one species at each trophic level, namely the resource (producer)–prey–predator system, and an anti-predator trait of the prey as well.

For the specific case where the predator abundance changes much slower than the resource and prey, the tri-trophic food chain is known to show unique dynamics in which fast cycles of the two species at the lower trophic levels regularly change to slow dynamics of the three species (Hastings and Powell 1991; McCann and Yodzis 1994). We propose that eco-evolutionary dynamics can result in extremely long periodicity of the community dynamics through the effect of trait evolution to slow down the shift between the alternative community states, and refer to such dynamics as “eco-evolutionary oscillation (EEO)” in this article. Our model assumed evolution only for a single prey trait, thereby excluding the possibility of any oscillations caused by coevolution between traits. Therefore, the EEO is exclusively attributed to the interaction between ecological dynamics and trait evolution.

We further examined the effect of genetic variation, which determines the evolutionary rate, on the global stability of the community. Simulations of the present system indicated that a high level of genetic variation and the rapid evolutionary rate resulted in the disappearance of the EEO and the large intermittency, which is compatible with some observed intermittent eco-evolutionary cycles in prey–predator systems (Yamamichi et al. 2011; Coutinho et al. 2016; van Velzen et al. 2022). Trait evolution as fast as ecological dynamics may simplify the community dynamics in terms of turning long complex cycles into short simple cycles, while it has a destabilizing effect in terms of reducing the local stability of a community (Cortez 2016).

## Model description

We used a food chain model of three trophic levels (the tri-trophic model), with a species at each level, namely the resource  $N_1$ , the prey  $N_2$ , and the predator  $N_3$ . 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 assumed for intraspecific competition at the basal level of resources, which was supposed to be an autotroph population by using a logistic growth term. The changes in numerical or biomass abundances of the three species in the timescale  $T$  are

$$\frac{dN_1}{dT} = rN_1 \left( 1 - \frac{N_1}{K} \right) - \frac{A_2 N_1 N_2}{1 + A_2 H_2 N_1} \quad (1)$$

$$\frac{dN_2}{dT} = N_2 \left( \frac{c_2 A_2 N_1}{1 + A_2 H_2 N_1} - D_2 \right) - \frac{A_3(z) N_2 N_3}{1 + A_3 H_3 N_2} \quad (2)$$

$$\frac{dN_3}{dT} = N_3 \left( \frac{c_3 A_3(z) N_2}{1 + A_3 H_3 N_2} - D_3 \right), \quad (3)$$

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 handling time (the inverse of maximum consumption rate),  $c$  is the conversion coefficient,  $D$  is the mortality, and the subscripts denote trophic levels. The consumption efficiency of predator (or the predation efficiency)  $A_3(z)$  is assumed to be a function of the prey trait  $z$  (anti-predator trait), which is a quantitative trait affecting vulnerability to predation.

We transferred Eqs. (1)–(3) into Eqs. (4)–(6) to reduce the number of parameters (Hastings and Powell 1991), by standardizing the biomass of each 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 ( $t = rT$ ),

$$\frac{dn_1}{dt} = n_1 (1 - n_1) - \frac{a_2 n_1 n_2}{1 + a_2 h_2 n_1} \quad (4)$$

$$\frac{dn_2}{dt} = n_2 \left( \frac{c_2 a_2 n_1}{1 + a_2 h_2 n_1} - d_2 \right) - \frac{a_3(z) n_2 n_3}{1 + a_3(z) h_3 n_2} \quad (5)$$

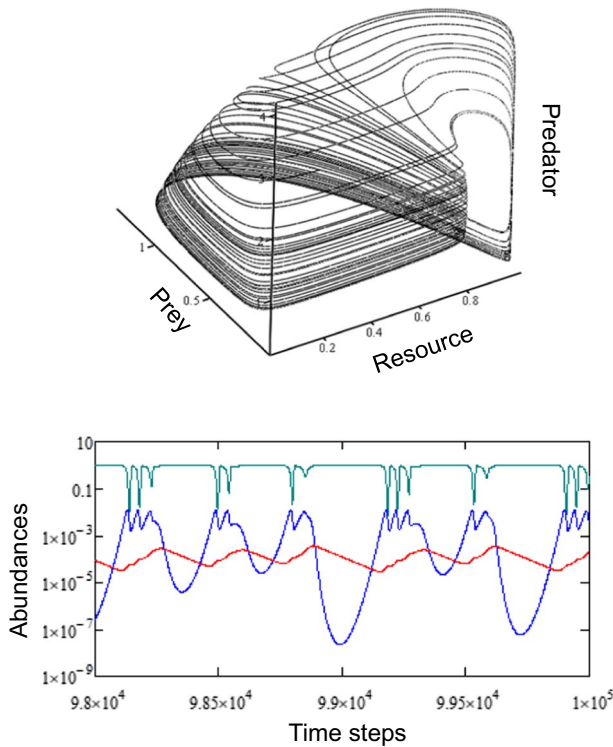
$$\frac{dn_3}{dt} = n_3 \left( \frac{c_3 a_3(z) n_2}{1 + a_3(z) h_3 n_2} - d_3 \right), \quad (6)$$

where  $a_j = A_j K/r$ ,  $d_j = D_j/r$ ,  $h_j = H_j r$  ( $j = 2$  and  $3$ ), and also here the consumption efficiency of predator  $a_3(z)$  is a function of the prey trait  $z$ .

The above tri-trophic system, Eqs. (1)–(3) or Eqs. (4)–(6), is known to have heterochronic cycles, causing intermittent dynamics between slowly changing three-species coexistence and short periodic cycles of the two species for a specific range of parameters (Fig. 1; Hastings and Powell 1991; McCann and Yodzis 1994).

We disregarded the predator trait that would facilitate predation efficiency, because results of simulation when the present model included the predator trait as well indicated that evolution of the predator was much slower than the prey and the coevolutionary process was negligible (Appendix 1). This was followed by the assumption that the prey had a much higher metabolic rate and a much shorter generation time than the predator. We did not observe any considerable alteration of results by using the alternative model that included predator evolution in the parameter region we adopted (Appendix 1). The present study is unlikely to apply for the case in which evolution of the predator trait as fast as the prey trait affects the dynamics and persistence of a community (Dieckmann et al. 1995; Doebeli 1997; Nuismer and Doebeli 2004).

The predation efficiency is assumed to be



**Fig. 1** Trajectories of abundances of three species in the non-evolutionary ecological model with 3-species linear food chain. In the lower graph, the green line: the resource abundance, the blue line: the prey abundance, and the red line: the predator abundance

$$a_3(z) = a_{\max} \exp \left\{ - \left( \frac{z}{s} \right)^{2\gamma} \right\}, \quad (7)$$

where  $a_{\max}$  is the maximum predation efficiency when the prey trait is 0 and the predation efficiency is optimal for the predator,  $s$  measures the scale of the trait in terms of the effect on the predation efficiency (the smaller  $s$ , the larger effect of a change of  $z$ ), and  $\gamma$ , referred to as the slope parameter, takes a positive integer which determines steepness of a curved relationship between  $z$  and  $a_3(z)$ . When  $\gamma$  is 1, Eq. (7) becomes the Gaussian function (with the same shape as the normal distribution). When  $\gamma$  is 2 or larger, non-linear changes of  $a_3(z)$  by  $z$  become steeper than the Gaussian ( $z$  smaller than  $s$  has negligible effect while  $z$  close to  $s$  abruptly reduces the predation efficiency).

The prey trait is assumed to cause a cost for the prey in terms of fitness (the trait cost) as well as bring about a benefit by acquiring defense against predators. The negative selection resulting from the cost is indicated by a component  $W_c$  of the prey fitness. The present analysis used the normal distribution for the cost component of fitness:  $W_c \propto \exp(-\omega z^2/2)$ , in which  $\omega$  is the cost coefficient measuring the trait cost. It is postulated that the cost of prey trait must be the loss of energy that was invested to develop any morphological, behavioral or physiological defense against predators in the sacrifice of investing to growth and reproduction in case without predators. It may also include the loss of time spent

for anti-predator behavior instead of feeding or reproduction. However, we excluded the demographic effect of the trait cost on the prey population (the trait cost does not influence Eq. 5), because we focused on the effect of trait evolution to change interspecific interaction, disregarding the direct effect of trait cost on the prey population abundance. The trait cost may influence relative fitness between individuals within a population (soft selection) and keep its negative effect on the trait evolution without changing the performance of a population as a whole, if increased trait cost is compensated by density dependence and does not impair the population growth.

For the rate of trait evolution, we followed the standard quantitative genetic formulation (Lande 1982; Abrams et al. 1993; Abrams 2001):  $G \frac{\partial(\ln W)}{\partial z}$ , in which  $G$  is the additive genetic variance,  $z$  is the (mean) trait value, and  $\ln W$  is the fitness in the logarithmic scale. The fitness of prey  $W$  with a specific trait value  $z$  consists of two components: one is the demographic benefit through escaping from predators,  $W_n = \exp\left(\frac{1}{n_2} \frac{dn_2}{dt}\right)$ , and the fitness cost of the trait,  $W_c$ . The total fitness,  $W = W_n W_c$ , is specified as  $W = \exp\left(\frac{1}{n_2} \frac{dn_2}{dt} - \frac{\omega}{2} z^2\right)$ . Along with Eq. (5) and  $G$ , it gives the evolutionary dynamics of the prey trait as

$$\frac{dz}{dt} = -G \left\{ \omega z + \frac{a_3'(z)n_3}{(1 + a_3(z)h_3n_2)^2} \right\}, \quad (8)$$

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

## Numerical procedures

The additive genetic variance  $G$  influences the speed of evolution while the cost coefficient  $\omega$  influences the limit of evolution towards stronger defense against predators as well as the evolutionary rate (Eq. 8), because the limit of evolution towards stronger defense is given by the evolutionary equilibrium  $\tilde{z}$  at the balance between the benefit gained from predator avoidance and the trait cost, i.e.  $\tilde{z} = -\frac{1}{\omega} \frac{a_3'n_3}{(1+a_3h_3n_2)^2}$ . The trait cost greatly affects the speed of evolution towards lower cost ( $z=0$ ) when the predator is very rare,  $\frac{dz}{dt} \cong -G\omega z$ . We examined how the limit of evolution towards stronger defense and the evolutionary rate could affect the stability and long-term periodicity of community dynamics by changing the two parameters, the cost coefficient  $\omega$  and the genetic variance  $G$ .

## Parameterization

We used the parameter values set by Hastings and Powell (1991) with minor modifications as the baseline ecological parameters for our simulations:  $a_2=2$ ,  $a_{max}=0.1$ ,  $c_2=c_3=1$ ,  $d_2=0.2$  (varying from 0.1 to 0.3),  $d_3=0.01$ ,  $h_2=2.5$  (varying from 1.67 to 5),  $h_3=20$ . This parameter setting generates chaotic dynamics in the tri-trophic model without evolution,  $z=0$  (Hastings and Powell 1991). The ratio of  $c$  to  $dh$ , which is  $\frac{c_2}{d_2h_2}$  and  $\frac{c_3}{d_3h_3}$  for the prey and the predator respectively, indicates the potential reproductive capacity of a species relative to the mortality. We set the ratio as  $\frac{c_2}{d_2h_2} = 2$  and  $\frac{c_3}{d_3h_3} = 5$ , following McCann and Yodzis (1994) who found that the complex dynamics entailing intermittency was more likely with a lower prey mortality  $d_2$  (equivalent to the metabolic rate in McCann and Yodzis 1994).

The ratio  $c/h$  is the intrinsic growth rate  $b$  by reproduction or body growth when the food is plentiful (Eqs. 4, 5), then  $\frac{c}{dh}$  is the ratio  $b/d$  which is related to the maximum biomass growth of the species. Both the ratio  $b/d$  and the value of  $d$  at the higher two trophic levels greatly influence dynamical properties of the model. A few examples of real systems may justify our parameterization (Appendix 2).

Because the rate of ecological process is largely determined by the mortality and the handling time (the larger  $d$  and the shorter  $h$ , the higher process rate and the shorter generation time), we changed the values of  $d_2$  and  $h_2$  for simulations such that the value of  $\frac{c_2}{d_2 h_2}$  was kept to be 2 (for example, if  $d_2$  was changed from 0.2 to 0.3,  $h_2$  was changed from 2.5 to 1.67) in order to see the net effect of ecological process rate of species 2 relative to that of species 3.

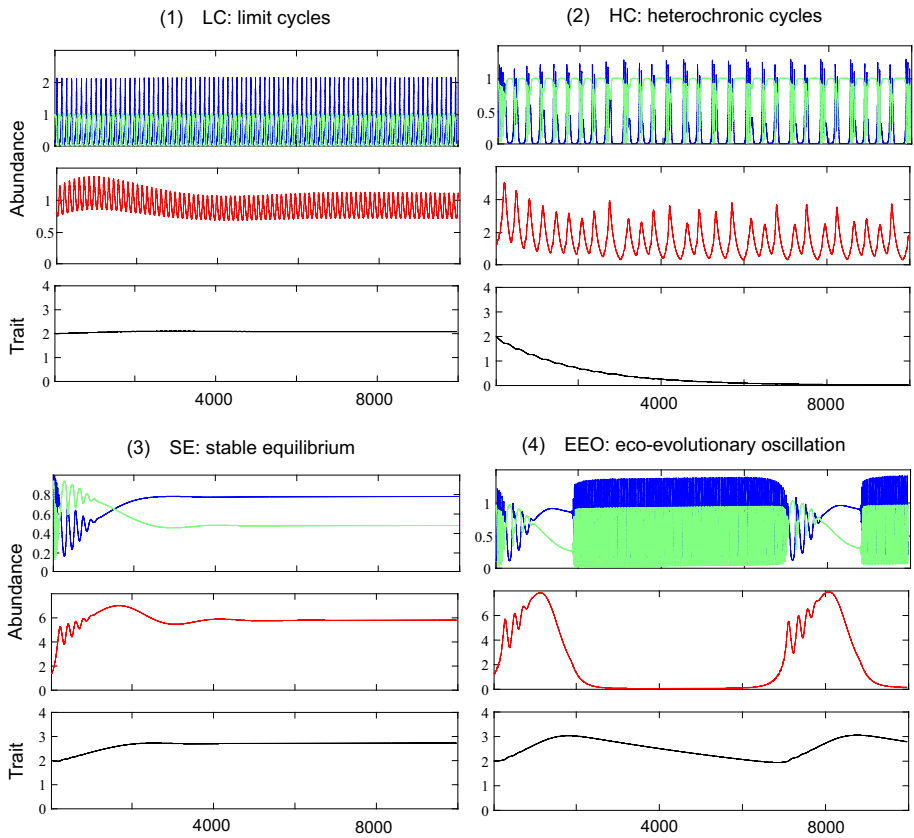
We set the baseline values of parameters related to trait evolution as  $\gamma=1$ ,  $s=2$  and  $G=0.01$ , because these values cause the EEO. To set  $\gamma=1$  and  $s=2$  makes the predation efficiency  $a_3(z)$  the standard normal distribution. This implies that the standard genetic deviation ( $\sqrt{G}=0.1$ ) is as small as 10 percent of the standard deviation of the fitness function ( $\sqrt{s/2}=1$ ), which is compatible with the widely accepted view that stabilizing selection is not detectable or usually weak in nature such that the width of fitness function is much wider than the width of phenotypic or genetic distribution (Lande and Arnold 1983; Endler 1986; Kingsolver et al. 2001, 2012).

## Simulation methods

Numerical integrations were performed for Eqs. (4)–(6) and (8) using the fourth-order Runge–Kutta method from  $t=0$  to  $10^5$  with  $3 \times 10^5$  steps using Mathcad 15 (Parametric Technology Cooperation, Boston, Massachusetts, USA) for each parameter setting. To find the equilibrium abundances and trait values, we used the built-in function of Mathematica 8.0 (Wolfram Research, Inc., Champaign, Illinois, USA). The solver “FindRoot” for differential equations was used for communities with and without evolution.

## Categories of dynamical states

The eco-evolutionary dynamics were categorized into four states according to the dynamical properties of the three species and the trait: the limit cycles (LC), the heterochronic cycles (HC), the stable equilibrium (SE), and the eco-evolutionary oscillation (EEO) (Fig. 2; see Table 1 for more detail and technical definitions). The LC and the HC were distinguished by complexities of the cycles. The LC was defined according to the standard definition of limit cycles as the state in which the two or three species permanently showed fast and regular cycles with a constant period of a cycle. On the other hand, the HC had a more complex structure and we defined it as the state in which the lower two species intermittently exhibited fast cycles resembling the limit cycles and the predator had distinct cycles with much longer period (Hastings and Powell 1991). There were two local unstable equilibria: one included the lower two species and the other had three species that had non-zero values. However, when the prey trait value was 0 at both equilibria, then there was no trait evolution in the HC. The EEO is characterized by shifting dynamical states with very long periodicity and highly extended intermittency coinciding with trait evolution



**Fig. 2** Sample trajectories illustrating four categories of eco-evolutionary dynamic states in a tri-trophic food chain with prey trait evolution. Lines indicate population dynamics over time for resource (blue), prey (blue), predator (red) and the changes in the prey trait value along time (black), respectively. The horizontal axis denotes time steps of simulations in all panels

(Fig. 2). This definition of EEO is compatible with that of the intermittent prey–predator cycles with trait coevolution, which are characterized by interruptions in which predator–prey cycles are strongly dampened or disappear entirely, after which they re-establish themselves (van Velzen et al. 2022).

## Wavelet transform

To elucidate underlying periodicities in the simulation, we performed the wavelet transform for the observed time-series data of the predator abundance. This method, similarly to the windowed Fourier transform, characterizes irregular oscillations, in which different patterns of oscillation appear alternately and the periodicity is not necessarily constant with time (Keitt and Fischer 2006; Cazelles et al. 2008).

The simulated time-series data of predator abundance  $n_3(t)$  at time  $t$  were transformed into the wavelet values at time  $\tau$ ,  $w_L(\sigma, \tau)$ . A wavelet value indicates how well the time-series data fits a short wave consisting of a few cycles. Since each wave, which is given by the mother function, has a peak at a particular time  $\tau$  and a width (scale)  $\sigma$ , wavelet values

**Table 1** Four categories of dynamical states in the eco-evolutionary community simulations

Category	Symbol	Description
Limit cycles	LC	The three species and the trait show fast and uniform cycles like limit cycles. The cases where the trait does not change from the least costly state are included There is only one equilibrium within the orbit, at which the largest eigenvalue of the Jacobian matrix has a positive real part and a pair of large imaginary parts with different signs (complex conjugates)
Heterochronic cycles	HC	The three species exhibit heterochronic cycles with relatively short intermittency accompanying chaotic fluctuations in some cases. The trait does not change from the least costly state There are two (three-species and two-species) equilibria associated with the orbit. At the three-species equilibrium, one of the two dominant eigenvalues of the Jacobian matrix is positive and the other is negative in the real part, indicating that it is a saddle point. Orbits around the two-species equilibrium are indicated to be limit cycles. Then, the entire trajectories around the two equilibria are considered to be connected by heterochronic orbits, which link between a saddle point and other unstable equilibria
Stable equilibrium	SE	The three species and the trait remain permanently at a non-zero equilibrium All eigenvalues of the Jacobian matrix are negative in the real part
Eco-evolutionary oscillation	EEO	The three species and the prey trait exhibit complex cycles with long intermittency and periodicity. The entire trajectories consist of the two-species fast cycles and the slow cycles by the three species and the trait. Shifts between the two dynamical states synchronize with changes of the trait and the predator abundance Orbits around the two-species equilibrium are indicated to be limit cycles. At the non-zero equilibrium of the three species and the trait, all eigenvalues of the Jacobian matrix are positive in the real part with a pair of large imaginary parts with different signs, which indicate that the orbits around this equilibrium are also another limit cycles



with various scales represent underlying cycles with specific periodicities configuring the time-series data.

The wavelet transform was practiced as.

$w_L(\sigma, \tau) = \left\{ \sum_t |\psi(t - \tau, \sigma)|^2 \right\}^{-\frac{1}{2}} \sum_t \psi(t - \tau, \sigma) n_3(t)$ , where  $\psi(t, \sigma)$  is the mother function,  $\tau$  indicates the point at which the data is transformed in the time series, and  $\sigma$  is the scale parameter. Values of  $\sigma$  were set as powers of 2 ( $2^k$ ;  $k=1, 2, 3, \dots$ ) in this study. For  $\psi(t, \sigma)$ , we used the Mexican hat function:  $\psi(t, \sigma) \propto \left(1 - \frac{(2\pi/\sigma)^2 t^2}{2}\right) \exp\left[-\frac{(2\pi/\sigma)^2 t^2}{4}\right]$ , which is one of the most common mother functions (Cazelles et al. 2008).

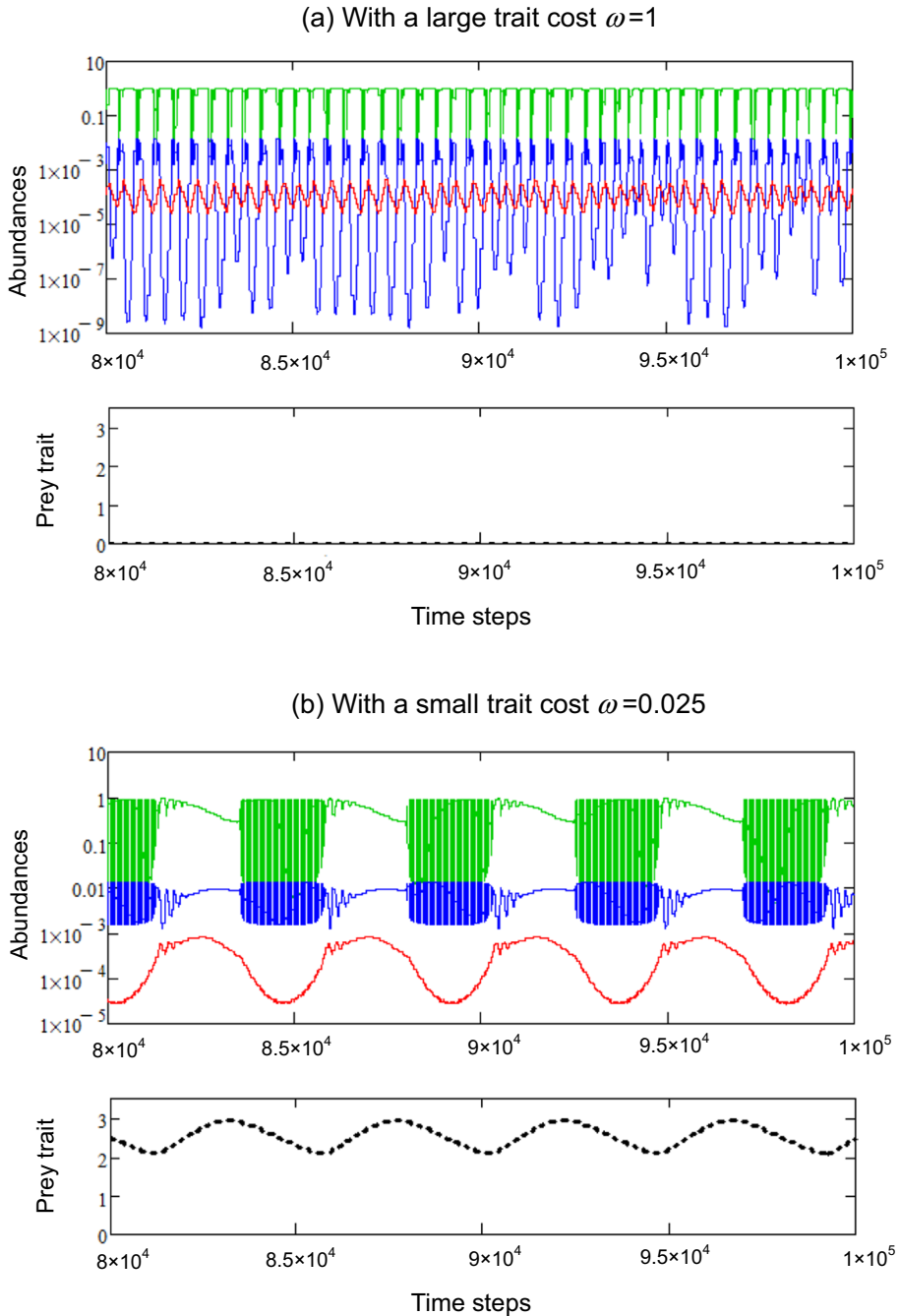
## Results

### Community oscillation induced by trait evolution

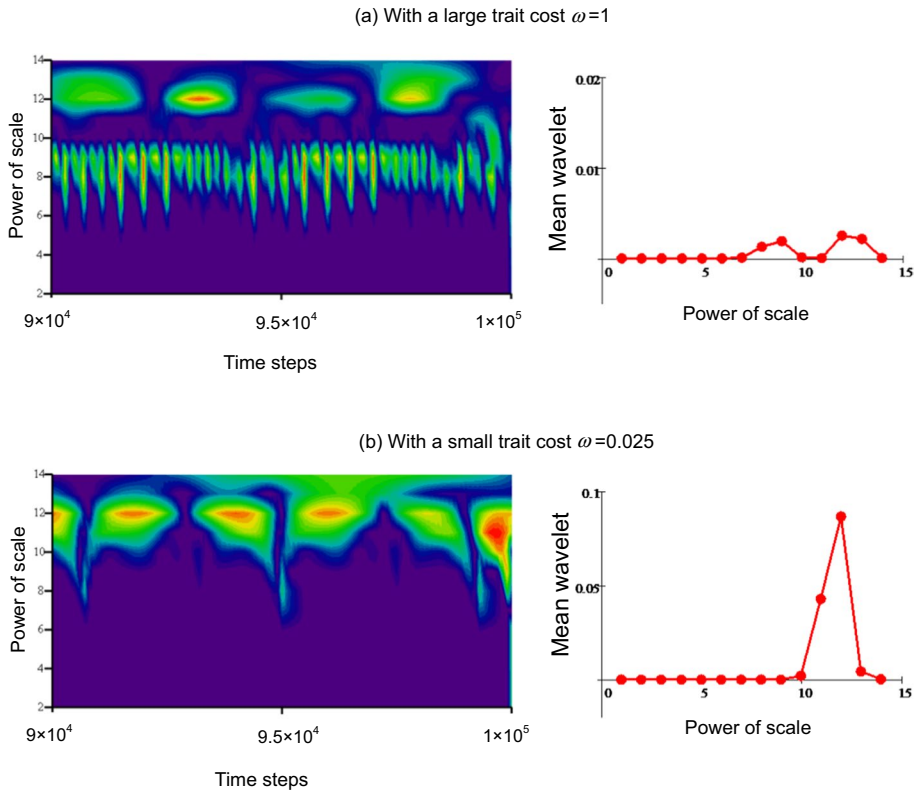
The prey trait evolution stabilized or destabilized the community dynamics depending on the limit of evolution towards stronger defense. When the evolutionary change was inhibited by the large trait cost ( $\omega=1$ ), the community dynamics which was based on the baseline ecological parameters showed heterochronic cycles (Figs. 1, 3). The scale-specific wavelet transform indicated two major periodicities with a shorter cycle at the time scale of about 500 ( $2^9$ ) and a longer cycle at the time scale of about 4000 ( $2^{12}$ ) in terms of the rescaled time unit by the intrinsic growth rate of producer (if  $r$  is 0.5 per day, the time scale 500 corresponds to 250 days) (Fig. 4).

The eco-evolutionary community dynamics showed discrete shifts when the trait cost was gradually reduced. When  $\omega$  was equal to or smaller than 0.047, the three species and the trait reached stable equilibria (Fig. 5). To reduce further the trait cost, with values equal to or smaller than 0.027, caused the EEO, in which the prey trait started a long-term periodic oscillation and retained three-species dynamics similar to the heterochronic cycles (Figs. 3, 5). However, the period (length of a cycle) of oscillation of the predator coincided with that of the trait evolution, and was much longer than that of the heterochronic cycles in the tri-trophic model without evolution (Fig. 3). The time needed for the shifts was much longer with the eco-evolutionary dynamics than with the ecological dynamics without evolution, as indicated by considerably larger wavelet values at the time scale of approximately 4000 ( $2^{12}$ ) (Fig. 4). The period between recurrent resource-prey oscillations increased as the trait cost decreased. Mathematically, there was only one unstable equilibrium for the entire dynamics of three species' abundances and the prey trait. The observed dynamics are long periodic orbits around it, periodically approaching to the two-species limit cycles.

Visual inspection suggested that the predator abundance in the EEO changed during the two-species fast cycles differently from that in the ecological model without evolution, in which the predator abundance gradually increased during the period of the two-species fast cycles and culminated at the end of that period (Fig. 1). In the eco-evolutionary dynamics, however, the predator abundance continued to decline during the first half of the two-species fast cycles and reached its minimum at the midpoint of that period. Then, the predator abundance appeared to show anti-phase dynamics with the resource-prey cycles analogously to the two-species prey-predator system with prey evolution (Yoshida et al. 2003). On the other hand, the prey trait changed similarly to the predator abundance in the tri-trophic model without evolution (Fig. 1) although the direction of change was opposite.



**Fig. 3** Trajectories of eco-evolutionary dynamics **a** with a large trait cost  $\omega=1$  and **b** with a small trait cost  $\omega=0.025$ . The mortality of prey and the genetic variance is respectively set as  $d_2=0.2$  and  $G=0.01$ . In the upper panel, the green line: the resource abundance, the blue line: the prey abundance, and the red line: the predator abundance

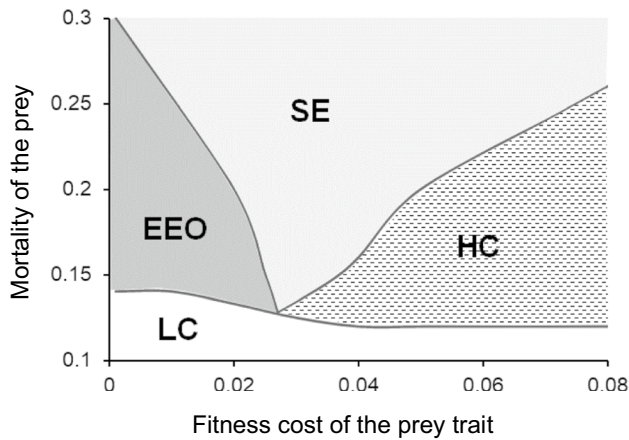


**Fig. 4** The scale-specific wavelet values (left panel) and the time-weighted mean values of scale-specific wavelet values (right panel) for the case of a large trait cost  $\omega=1$  **a** and a small trait cost  $\omega=0.025$  **b**. The other model parameters are subject to Fig. 2a. In the left panel, colors with longer light spectra (red > yellow > green > blue) indicate the larger values of wavelet. The scales are represented as the power coefficient of 2

The prey trait or the predator without prey evolution continued to decrease or increase during the two-species fast cycles and started to recover or decline at the end of that period (Figs. 1, 3). In addition, the prey trait dynamics showed a phase lag with the cycles of the predator abundance.

### A sample trajectory of eco-evolutionary oscillation

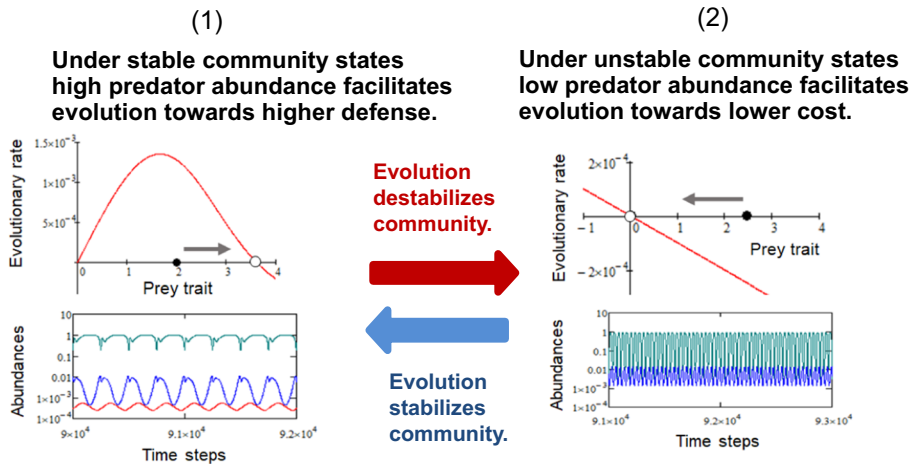
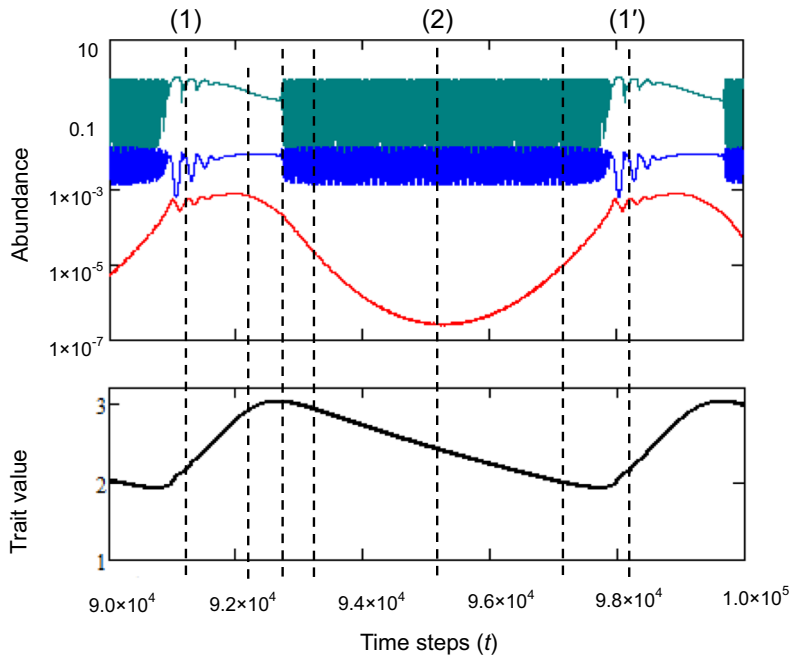
A sample orbit observed in specific time steps ( $t=91,000, 92,000, 92,500, 93,000, 95,000, 97,000$  and  $98,000$ ) of the simulation illustrates the process of the EEO: the parameter values were  $d_2=0.2$ ,  $\omega=0.01$ ,  $G=0.01$ , and the initial values were  $n_1=0.765$ ,  $n_2=0.100$ ,  $n_3=1.308$ ,  $z=2.00$  (Fig. 6; Appendix 3). We used the approximation of fast-ecological dynamics in the similar way as the fast-evolution approach (Cortez and Ellner 2010), to see how the interaction between trait evolution and ecological dynamics drives the EEO. Under this approximation, hypothetically fixing the trait value at a particular time step in the eco-evolutionary simulation made an



**Fig. 5** 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

ecological submodel. The submodel was exactly the same as the eco-evolutionary model (Eqs. 4–6) except for having the fixed trait value and thus a fixed predation efficiency of the predator  $a_3$ , and was used to evaluate the local stability indicating the ecological dynamics and the selection that would act on the trait (see Table A in Appendix 3 for more details).

At the time step (1) in Fig. 6 ( $t=91,000$ ), the number of predators increased because the relatively low prey trait ( $z=2$ ) led to an increased predation efficiency ( $a_3$ ). This increased top-down effect reduced the amplitude of prey oscillations, entering a phase of slow oscillations of the two lower trophic levels with decreasing amplitude. In the next phase, the prey trait restarted the evolution toward stronger defense under the increased predation. However, the predator was still predominant and the lower two species were kept changing very slowly ( $t=92,000$ ). The analysis in Appendix 3 indicated that the ecological subsystem with the fixed trait value at this time step was locally stable and had stable equilibria for the three species' abundances. This ecologically stable state did not persist in the entire eco-evolutionary system, however, because the trait continued to increase, resulting in a decline of the predator abundance ( $t=92,000$ ). Further evolution destabilized the three-species dynamics and especially once the trait value started decreasing, the system entered the phase of high frequency/high amplitude cycles, this was after the predator started decreasing from its peak ( $t=92,500$  in Table A). The decrease of the predator abundance reduced the fitness benefit of the prey trait ( $t=93,000$  in Table A), and when the reduced fitness benefit could not compensate for the trait cost, the net negative selection drove the trait evolution towards lower cost (during the period including the time step (2) in Fig. 6;  $t=95,000$  in Table A). The prey got more edible, thereby increasing the predation efficiency and allowing the predator abundance to increase again, preventing its extinction ( $t=97,000$ ). The prey trait continued to decline until the predator abundance recovered and the anti-predator trait became important again for the prey (the time step (1') in



**Fig. 6** Driving forces of eco-evolutionary dynamics at different phases in a cycle. In the upper panel, the green line: the resource abundance, the blue line: the prey abundance, and the red line: the predator abundance. The vertical broken lines denote the seven referenced time steps. Starting from a high predator abundance and a low prey trait, the ecological dynamics facilitate evolution of the prey trait (1). After the community reaches the relatively stable state ( $t = 9.2 \times 10^4$ ), the further trait evolution makes the predator population drop sharply and destabilizes the community ( $t = 9.3 \times 10^4$ ), in which the trait decreases only due to the fitness cost until the predator population tends to recover

Fig. 6;  $t=98,000$ ). This takes longer if the trait cost is low because it is the only driving force to reduce the trait.

### State diagram

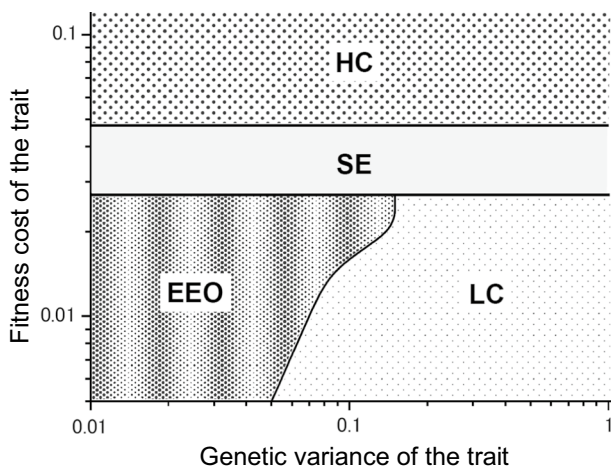
The EEO occurred only when the prey mortality was high, and the trait cost was small (Fig. 5). The trait cost altered the relationship between the trait evolution and community stability. The parameter region of stable equilibria (SE in Fig. 5), in which the abundance of the three species and the prey trait remained unchanged, occupied the region between the EEO and the HC. It is inferred that both a reduction and an increase of the trait cost changes the stable state into one of the unstable states, the EEO or the HC. Whether the trait evolution towards stronger defense, facilitated by the reduced trait cost, stabilized or destabilized community dynamics depended on the previous state of the community. The LC occupied the region where the prey mortality was the lowest in the examined parameter range.

### The shape of the predation efficiency function

We did not find any EEO whenever  $\gamma$  (the slope parameter) was equal to and larger than 2, whereby the predation efficiency function became steeper than the normal distribution. The same conclusion was analytically validated by Yoshino and Tanaka (2013).

### The effect of genetic variance on the eco-evolutionary dynamics

The speed of trait evolution determines the relative process rate between ecological and evolutionary dynamics, which significantly affect the eco-evolutionary feedback (Cortez 2016, 2018; Govaert et al. 2019). We examined the effect of the evolutionary rate by changing the genetic variance and the trait cost. In all cases, the EEO was replaced by



**Fig. 7** Effect of genetic variance of the trait on the regimes of eco-evolutionary dynamics. The abbreviation are subject to Fig. 5

the LC with larger genetic variances (Fig. 7). The trait cost higher than a specific value (about 0.184) kept the HC or SE without inducing the EEO, regardless of the magnitude of genetic variance (Fig. 7). In the region of lower trait cost, higher cost tended to suspend the shift from the EEO to the LC with larger genetic variances, because higher trait costs partly compensated the effect of genetic variance to accelerate the evolution. These results suggest that the evolution is slow and the range of realized trait values by evolutionary changes is wide are necessary for the EEO to appear.

## Discussion

The main theoretical issues in the community eco-evolutionary dynamics include the stabilizing or destabilizing effect of trait evolution on communities (Saloniemi 1993; Abrams and Matsuda 1997; Mougi and Iwasa 2010), the generation of unique oscillations, such as out-of-phase prey–predator cycles, by fast evolution (Yoshida et al. 2003; 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; Andreatzi et al. 2018; Govaert et al. 2019), because the eco-evolutionary feedback can strengthen oscillation or stability of communities, as well as generate intermittent prey–predator cycles (Yoshida et al. 2007; Jones et al. 2009; Mougi and Iwasa 2010; Yamamichi et al. 2011; Hiltunen et al. 2014; Cortez 2016; van Velzen et al. 2022).

The reason why the eco-evolutionary feedback can cause intermittent shifts between different ecological states may be that the ecological and evolutionary subsystems cannot achieve stable states at the same time (Cortez and Ellner 2010; Patel and Schreiber 2015; Patel et al. 2018). This implies that long-periodicity oscillations can emerge when the community dynamics is governed by a trait affecting interspecific interactions, and vice versa. In addition, a time lag is necessary between rapid formation of an adaptive landscape by changes in community states and the slow evolution which will change the community states.

The observed eco-evolutionary oscillation in this article may be a special case of the general rule that intermittent cycles by eco-evolutionary feedbacks can occur when the community state that creates a particular adaptive landscape for evolution is not sustained by the evolution. Yamamichi et al. (2011) exemplified this rule by a prey–predator system, in which the prey consisted of two genotypes which were phenotypically plastic and non-plastic in terms of anti-predator defense. Under the prey–predator limit cycle phase the plastic genotype was more advantageous than the non-plastic genotype, however, the plasticity stabilized the cycles, leading to replacement of the plastic genotype by the non-plastic genotype.

Contrary to the recent attention received on the importance of fast evolutionary changes of traits, we focused on slow evolutionary rates of the prey trait and presented an additional case of intermittent cycles driven by eco-evolutionary dynamics with the three-level food chain. 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; Dercole et al. 2006, 2010). They demonstrated that the prey–predator system, in which a pair of traits possessed by the prey and the predator determined the predation efficiency, could produce eco-evolutionarily driven long-periodicity oscillation (Red Queen Dynamics). However, the genetic subsystem may

have the innate potential to drive long-term oscillations, which is reinforced by interplay with the ecological subsystem. This study first demonstrated that a single trait based on the quantitative genetic inheritance could cause intermittent cycles by interactions with the three-species food chain without trait-by-trait coevolution and phenotypic plasticity of the trait (a review and systematic survey is given by Velzen et al. 2022).

Genetic variance may affect eco-evolutionary dynamics in two ways, namely by changing the local stability of the entire eco-evolutionary dynamics (Ellner and Becks 2011; Mougi and Iwasa 2010, 2011; Cortez 2018), and by affecting the long-term state shifts in communities (Khibnik and Kondrashov 1997; Dercole et al. 2006). In concordance with previous studies (Saloniemi 1993; Yamauchi and Yamamura 2005; Mougi and Iwasa 2010), the present study indicated that faster evolution resulting from larger genetic variances tended to stabilize the community dynamics.

The role of small genetic variance and resultant slow evolution for causing the intermittent state shifts is to reinforce discrepancies in the timescales between trait evolution and ecological dynamics. The lack of observed EEO in this study for the case of the sharply curved predation efficiency function ( $\gamma > 2$  in Eq. 7) partly supports this explanation (Yoshino and Tanaka 2013). Similarly to the fast evolution with a large genetic variance, the sharply curved predation efficiency function allowed quicker increase of the food uptake by the predator with increased edibility of the prey when the predator abundance recovered.

DeLong et al. (2016) compared proportional changes in phenotypic traits and population abundances for many field-based studies and concluded that phenotypic changes, including those due to plasticity, can process at nearly the same timescale as the population dynamics, as supported by some other studies (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 of the prey trait by evolution. This implies that the rate of trait evolution must be two orders of magnitude slower than suggested by the review of DeLong et al. (2016). In laboratory experiments, it is often observed that evolutionary changes of traits occur at a timescale similar to ecological dynamics (Yoshida et al. 2003; Hairston et al. 2005; Johnson et al. 2009; Kopp and Matuszewski 2014). In most natural populations, however, phenotypic changes are likely to be quite slow ( $< 0.05$  standard deviation of traits per generation; Hendry and Kinnison 1999; Hendry 2017). Phenotypic evolution might be hampered even with high heritabilities and directional selection (Price et al. 1988; Kruuk et al. 2001, 2002) by several reasons including genetic correlations with unspecified traits and pleiotropic effects with fitness components (Houle 1991; Hansen and Houle 2008; Agrawal and Stinchcombe 2009; Tanaka 2010). On the other hand, the population abundance of many insect species can increase a few hundred times per generation, and major zooplankton species (like *Daphnia* spp) also can increase at similar rates. This is also inferred from the net reproductive rate  $R$  (the maximal population growth per generation),  $R = \exp(r_m T_G)$ . For example, the fact that the maximum intrinsic growth rate  $r_m$  is about 0.3 (per day) for the majority of *Daphnia* species (Andersen 1997) and the mean generation time  $T_G$  is likely longer than two weeks (Schwartz 1984; Tanaka and Nakanishi 2001; Pietrzak et al. 2010) suggest that  $R$  is 60 or larger. Even many terrestrial mammals may increase more than ten times per generation at maximum if the average generation time is 3 years or longer because  $r_m$  is 0.7 (per year) on average (Hutchings et al. 2012). Therefore, it is likely that trait evolution is considerably slower than demographic dynamics in natural populations.



As well as the large genetic variance of the trait, direct demographic effects of the trait cost may have stabilizing effects on the tri-trophic community. Some supplementary simulations which included reductions of population growth rates of the prey as a consequence of the prey trait evolution (adding the term  $-\omega z^2/2$  into Eq. 5) considerably restrict the parameter region as regards the cost coefficient  $\omega$  (data not shown). This stabilizing effect of the demographic cost of the trait was likely to emerge because the prey population growth was hampered by the cost even when the prey developed the defense trait to avoid the predation pressure and then did not start two-species fast cycles with the resource. Nonetheless, the major conclusions of this article do not largely change because the low fitness cost of the trait, which is essential for EEO, also makes the direct demographic effect of the trait vanish. Systematic and in-depth surveys in future may elucidate sensitivities of eco-evolutionary dynamics on the supposed direct effect of trait fitness cost to population dynamics.

Of course, the fact that real ecosystems have multiple species at each trophic level stands in sharp contrast to current models. However, the simplistic eco-evolutionary models might have some implications in real communities because a single trophic level in a community (e.g., all the prey species) may possibly be summarized by the total abundance and the community-weighted averages (CWA) of traits shared by composite species due to homoplasy or homology (Norberg et al. 2001; Savage et al. 2007; Tanaka and Yoshino 2009; Tanaka 2012). The dynamics of CWA can be driven by ecological processes without evolution, but it must be also influenced by trait evolution of individual species in real communities at the same time. Such a trait-based eco-evolutionary model has a potential to show intermittent cycles as is the case with the present model if the entire trait dynamics resulting from both changes in relative frequencies of species and genotypes is slow.

The eco-evolutionarily driven intermittent state shift may be relevant also for more complex ecosystems with longer time scales. Takahashi et al. (2013) observed intermittent shifts in food web models between alternative community states with different complexities. Considering that the tri-trophic systems generally work as one of the primary modules of many ecosystems (Price et al. 1980; Bascompte 2009; Abdala-Roberts et al. 2019), the factors causing the intermittent state shifts suggested in this study might have a few implications on what can occur in complex food webs and communities in nature. One of the most important implications of the present and previous eco-evolutionary studies is that if long intervals between cyclical state shifts are observed in nature, the feedback between ecological dynamics and trait evolution can be one of the theoretically plausible explanations.

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## Declarations

**Conflict of interest** There is no conflict of interest with any persons or organizations. Code in Mathcad 15 is available upon request.

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