The eco-evolution and diversification in antagonistic and mutualistic interactive populations

Abstract

Understanding the generation and maintenance of our ecosystem and biodiversity is of utmost importance as we are currently seeing the disturbances in the long-term formed ecological and evolutionary systems and also facing the loss of diversity across the globe. In particular, the ecological structures, the coevolution and the biodiversity of ecosystems with interactive functional species need our investigation as they dictate ecosystem functionality and stability. Here we set out to explain the eco-evolutionary dynamics that generate functional coevolution and diversification, mediated by (1) within-trophic-level competitive interactions for resources, (2) between-trophic-level antagonistic and mutualistic interactions, and (3) the interactions with the abiotic environments. We design an eco-evolutionary and trait-based model of three interacting trophic levels where the functional traits of species determine the focused three integrations. We use the adaptive dynamics approach to simulate adaptation and diversification in traits as a response to the three interactions.

We find that typically, higher positive interactions (i.e., higher mutualism-related abiotic or biotic interactions) increase the interactive population sizes, and also drive the evolutionary traits towards the direction to interact more with other biotic populations in the system, and less with the abiotic environment; whereas higher negative interactions (i.e. antagonism related abiotic or biotic interactions) have the opposite effect. We also find that a higher abiotic ecological opportunity, less intense competition, and a higher interactive range between the plants and antagonistic herbivores or mutualistic pollinators can generate a higher level of diversification in herbivores and pollinators. That means typically, a mild condition either abiotic or biotic can promote diversification, while a harsh condition impedes diversification. Our research includes the considerations of three main interactions in the eco-evolutionary system which helps to understand the general mechanism in the interactive dynamical ecosystem in the aspects of the change of population sizes, traits evolution and diversification. The finding could also be useful in understanding the present urgent issues, such as the responses of changing environmental conditions (e.g., climate change, loss of natural habitats) on the eco-evolutionary dynamics and the loss of diversifications and can be applied and tested in many specific ecosystems.

Keywords: Eco-evolutionary response, adaptation, diversification, interaction, antagonism, mutualism, herbivore, pollinator.

Introduction

Nowadays, we are benefiting from the continuous development of biotechnology- better genes are engineered for higher agricultural plant production and their better tastes (Akter., 2016); pesticides or herbicides are used to kill pests and unwanted competitive plants (Popp., 2013); and antibiotics as medicine are useful in preventing bacterial infections in human bodies (Hutchings., 2019). However, we are, at the same time, changing the environment, the ecology, the biological adaptation and biodiversity that have been gradually formed over a long period of time (Miller., 2005). Organisms living inside the environment and ecology are experiencing a substantial change in their interactive surroundings. The biological population constitution among species changes gradually due to the changing environment and the ongoing coevolution in these populations. Some organisms might burgeon, whereas others might shrink and even go extinct. The human-directed changes toward certain specific short-term outcomes rather than maintaining the existence of many existing species and the biodiversity (e.g., intensifying certain agricultural species rather than promoting diversified natural plant species), are found to be generating unprecedented change in the ecosystem and loss of biodiversity (Díaz et al., 2006, Hilderbrand et al., 2010). This is considered not good for the long-term maintenance of a good-functioning and healthy environmental or ecological dynamical system (Cardinale., 2012, Naeem., 2002; Loreau et al., 2022).

Although understanding the maintenance of ecological systems and biodiversity is vitally important nowadays, progress in understanding the processes that underlie the complex ecosystem and the diversity patterns has however been slow and riddled with controversy (Pontarp et al TREE). One reason for the slow progress is arguably the complexity with which ecological interactions and evolutionary processes interact. Organisms not only interact within their own populations, interact among trophic-level populations both positively and negatively, but also interact with the abiotic environment. These interactions can affect each population's growth and reproductions, and therefore also the dynamics of their future generations. The ecological consequences of these complicated interactions combined with also the possible coevolution and diversification of interactive populations can again make the dynamical system even more complicated (Jones et al., 2009; Hamelin et al., 2017).

The complication in dynamical interactive ecosystems implies the importance of eco-evolutionary processes for dictating the coevolution and diversity patterns (Urban & Skelly, 2006; Cortez & Ellner, 2010; Ellner et al., 2011). In particular, the eco-evolutionary ecological network that generates functional coevolution and diversity when within the trophic level competition is combined with trophic level antagonistic and mutualistic interactions and also environmental interactions acting in concert remains largely unstudied. Some of the previous research, however, provides a theoretical base on which understanding of the interaction and relationship between various ecological interactions, evolutionary and diversification processes.

Adaptation and adaptive radiations are found to be the types of coevolution and diversification processes by which eco-evolutionary processes generate ecological change and stability. Studies show that the coevolution and diversity of various organisms have arisen through adaptive adaptation and radiation and that such dynamical processes can be driven by ecological opportunities (the availability of ecological niches) (Meyer & Kassen, 2007; Losos, 2010; Yoder

et al., 2010; Stroud & Losos, 2016). An important driver of the partitioning of niche space during diversification is competition-driven limiting similarity (Mac Arthur & Levins, 1967, Pontarp et al., 2012, Pontarp et al., 2015, Pontarp et al., 2017; Dieckmann & Doebeli, 1999; Doebeli & Dieckmann, 2000). General theories on ecological and evolutionary adaptation and diversification exist for the link between niche availability (MacArthur & Wilson, 1968; Grant, 1998; Schluter, 2000) and frequency-dependent competition for resources (Geritz et al., 1998; Dieckmann & Doebeli, 1999; Brännström et al., 2013). Character displacement due to competition (Keller & Seehausen, 2012) has also been shown empirically in, for example, Darwin's finches (Schluter et al., 1985).

Other studies have emphasized antagonistic and mutualistic trophic interactions as the driver of adaptation and radiation. Some models exist for the coevolution and adaptive radiations in an antagonistic community context (Loeuille & Loreau, 2005; Ito et al., 2009; Ripa et al., 2009; Brännström et al., 2011; Sauterey et al., 2017; Pontarp & Petchey, 2018, Braga, 2021, Pontarp, 2021). For instance, it has been shown that predation can induce evolution and disruptive selection on prey populations and drive the evolutionary branching of prey (Brown & Vincent, 1992; Ito et al., 2009; Ripa et al., 2009). Furthermore, theories exist for the eco-evolutionary dynamics determined by mutualistic interactions among species. Both empirical and modelling studies show that population abundance (Aguilera et al., 2020), trait evolution (Ramos & Schiestl, 2019) and biodiversity (Aguilera et al., 2020; Häussler, J. et al., 2017) can be affected by mutualistic interactions.

The literature reviewed above provides a theoretical base on which understanding of the interaction and relationship between various ecological interactions, micro-evolutionary processes, diversification, and biodiversity rely. Studies on adaptive radiations have improved our understanding of how both antagonistic and mutualistic ecological interactions (Jones et al., 2009) combine with micro-evolutionary principles (Geritz et al., 1998, Brännström et al., 2013) in generating diversity. However, as mentioned above, different aspects (i.e., ecological opportunities, competitions, antagonism, mutualism) can all affect the ecological system and biodiversity, and since each biological population simultaneously face all these aspects in the ecological community, it is worth taking an overview of all these aspects and see how each population coevolve with each other in a food-web ecological system. (e.g., Brodersen et al., 2018 on radiation cascades).

Therefore, to understand the complicated food-web dynamical ecosystem, we developed a model to investigate the ecological and evolutionary responses to the three main kinds of interactions that each biological population faces (Figure 1), (1) the interaction between the biological population and the abiotic environment; (2) the competitive interaction within the population; (3) the interaction between the population and the other antagonistic and mutualistic populations. We design an eco-evolutionary and trait-based model of three interacting trophic-level populations where the functional traits of species determine their ecological interactions. We specifically apply the model to the three representative trophic-level populations: antagonists (herbivores), mutualists (pollinators) and common resources (plants). Because the model is designed generally, it can be well used in other antagonistic and mutualistic eco-evolutionary dynamical systems (e.g. bad and good bacteria populations inside the human bodies). We use the adaptive dynamics approach (Geritz et al., 1998) to simulate adaptation and diversification in traits as a response to the three interactions.

Methods

We investigate trait coevolution and diversifications in the interactive network system which contains three main interactions that all populations face in nature: (1) biological populations and the abiotic environment interaction, (2) the within-population competitive interaction, and (3) the between-population antagonistic and mutualistic interactions (Figure 1). We developed a trait-based mathematical dynamical system that illustrates the dynamics of three populations here: the plant resource population (R), the antagonistic herbivore population (A), and the beneficiary mutualistic pollinator population (B). The growth and death of the three populations are frequency-dependent with logistic growth rates r, r_A and r_B; and intrinsic death rates d, d_A and d_B (Lotka-Vertera Model, Lotka, 1925; Volterra, 1926). Both the herbivores' and pollinators' evolving traits can affect all three interactions (1) (2) (3) while they are evolving dynamically in the system. The strength of the three interactions follows a normal distribution form, where the strength is highest at the centre values, and tapers off symmetrically towards extremes. Here we focused our study on the evolution of herbivores' and pollinators' traits, which are evolving dynamically across time, but we assume that their common plant resource (e.g., the agricultural plants) trait evolves relatively very slowly, so is considered fixed and not to evolve in this model.

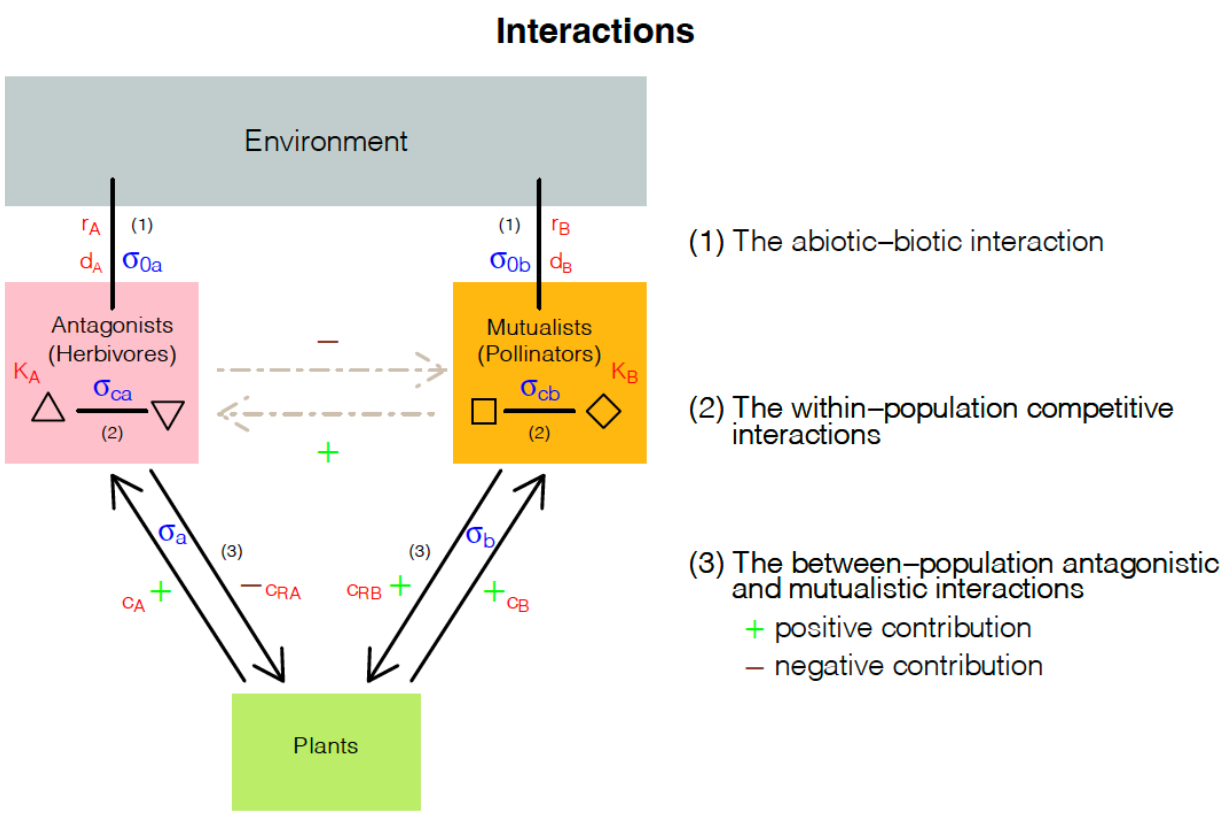

Figure 1. The framework of three interactions in the ecological network. The three interactions are represented by numbers (1) (2) (3) and the black lines/arrows in the figure. The strengths of

the interactions are measured by birth rates (r_A, r_B) and death rates (d_A, d_B) in the interaction (1); carrying capacity (K_A, K_B) in the interaction (2); and interactive convergent coefficient (c_A, c_{RA}, c_B, c_{RB}) in the interaction (3). The strengths of the interactions are found to be influential to the ecological population sizes and trait evolutions mentioned in the Result part. The interactive ranges - adaptive niche width: σ_{0a}, σ_{0b} in (1); competition range: σ_{ca}, σ_{cb} in (2); and antagonistic and mutualistic interactive range: σ_a, σ_b in (3) - are found to be influential to the population diversification mentioned in the Result part.

First, both the herbivore populations and the pollinator populations A and B interact with the environment (Figure 1 interaction (1)). Because of the normal distribution interaction kernel, the interaction with the environment is strongest for the herbivores and pollinators when their trait value equals an optimal adaptive trait value a_0 and b_0. The environmental adaptive niche widths of the herbivores and pollinators are the deviation in the normal distribution, which are σ_{0a} and σ_{0b}. The strength of the interactions with the environment acts on the growth rates of the two populations by the factor of $\left(\exp\left(-\frac{1}{2}\left(\frac{a_i-a_0}{\sigma_{0a}}\right)^2\right)\right)$ for the herbivores and $\exp\left(-\frac{1}{2}\left(\frac{b_l-b_0}{\sigma_{0b}}\right)^2\right)$ for the pollinators, shown in the eq. (I). The intrinsic death rates are constant to the population sizes and not affected by traits.

Second, both the herbivore and pollinator populations have competitive interactions within their own type of populations (Figure 1 interaction (2)). The interaction is strongest when the traits of the two competitive populations are the same, whereas weaker when the traits of the competitive populations are farther away, following the normal distribution form. The strength of the competition interactions acts on the size of the corresponding population by the factor of $\exp\left(-\frac{1}{2}\left(\frac{a_j-a_i}{\sigma_{ca}}\right)^2\right)$ and $\exp\left(-\frac{1}{2}\left(\frac{b_k-b_l}{\sigma_{cb}}\right)^2\right)$ shown in the eq. (I). The competitive distance within the herbivore and pollinator populations are σ_{ca} and σ_{cb}. The total herbivore populations and the pollinator populations compete correspondingly for their own common carrying capacity K_A and K_B.

Third, the plant population is the resource population that both the pollinators and the herbivores can feed on, so the plant population has positive contributions to both the herbivores and the pollinators (Figure 1 interaction (3)). Meanwhile, the response from the herbivore on the plant is negative since the herbivores feed on the plants, but the response from the pollinator on the plant is positive since the pollinators benefit the plants (Figure 1 interaction (3)). The strengths of the interaction between the plant and the herbivore populations are depended on the interactive range σ_a, the conversion coefficient c_A, c_{RA} between the two populations, and herbivore population trait (a_i) with the optimal interactive trait with the plant population (a_m). The strength of the interaction is highest when the herbivore population trait equals the optimal interactive values a_m, and is lower when the herbivore trait value is further away from the optimal interactive values a_m, following the normal distribution pattern ($\exp\left(-\frac{1}{2}\left(\frac{a_i-a_m}{\sigma_{0a}}\right)^2\right)$ in the eq. (I). Similarly to the pollinators, the strength of the positive interaction between the plants and pollinators follows the normal distribution pattern $\exp\left(-\frac{1}{2}\left(\frac{b_l-b_m}{\sigma_{0b}}\right)^2\right)$, with the conversion coefficient c_B, c_{RB} between the two populations. It is worth noting that the pollinators and the herbivores also have indirect interaction

with each other through their own direct interaction with the plants respectively (dashed arrows in Figure 1).

$$\frac{dA_i}{dt}\frac{1}{A_i} = r_A \exp\left(-\frac{1}{2}\left(\frac{a_i - a_0}{\sigma_{0a}}\right)^2\right) - d_A - \frac{1}{K_A}\sum_j A_j \exp\left(-\frac{1}{2}\left(\frac{a_j - a_i}{\sigma_{ca}}\right)^2\right) + c_A \exp\left(-\frac{1}{2}\left(\frac{a_i - a_m}{\sigma_a}\right)^2\right) R$$

$$\frac{dB_l}{dt}\frac{1}{B_l} = r_B \exp\left(-\frac{1}{2}\left(\frac{b_l - b_0}{\sigma_{0b}}\right)^2\right) - d_B - \frac{1}{K_B}\sum_k B_k \exp\left(-\frac{1}{2}\left(\frac{b_k - b_l}{\sigma_{cb}}\right)^2\right) + c_B \exp\left(-\frac{1}{2}\left(\frac{b_l - b_m}{\sigma_b}\right)^2\right) R \quad (I)$$

$$\frac{dR}{dt}\frac{1}{R} = r - d - \frac{1}{K} rR - c_{RA}\sum_j \exp\left(-\frac{1}{2}\left(\frac{a_j - a_m}{\sigma_a}\right)^2\right) A_j + c_{RB}\sum_k \exp\left(-\frac{1}{2}\left(\frac{b_k - b_m}{\sigma_b}\right)^2\right) B_k$$

Table 1 The mathematical terms in the model

	Resources (plants)	Antagonists (herbivores)	Mutualists (pollinators)
Population sizes	R	A_i	B_l
Trait values		a_i	b_l
Growth rates	r	r_A	r_B
Death rates	d	d_A	d_B
Carrying capacities	K	K_A	K_B
Optimal adaptive trait values		a_0	b_0
Optimal interactive trait values		a_m	b_m
Adaptive niche widths		σ_{0a}	σ_{0b}
Competition distances		σ_{ca}	σ_{cb}
Interactive distances		σ_a	σ_b
Interactive conversion coefficients	c_{RA}, c_{RB}	c_A	c_B

To investigate the above frequency-dependent ecological and evolutionary interactive population dynamics, we applied the adaptive dynamics scheme (Dieckmann & Law., 1996; Doebeli & Dieckmann., 2000; Geritz et al., 1998) focusing on the dynamics of ecological population size and the evolution and diversification of the interactive traits. In this approach, the evolutionary mutation is assumed to be sufficiently rare so that the ecological interactive dynamics are much faster than the evolutionary process and can reach the equilibria before any mutations happen. The evolution of traits is treated based on the idea similar to the invasion fitness (Metz et al., 1992), where a population with a mutant trait will replace the resident population given that the mutant population have a positive fitness at the equilibrium. The mutation trait value is assumed to be nearby the resident mutant values and is determined by the Canonical equation (Dieckmann & Law., 1996). The new mutation trait continues to replace the resident trait until the resident fitness reaches the local maximum in the fitness landscape. However, when the resident trait evolves to the local minimum in the fitness landscape, the finesses of mutating traits on both sides of the resident trait are higher than the fitness of the residence trait, and this is when disruptive selection

(diversification) emerges. In this case, the population diverges into two populations with two new mutation traits, and the evolutionary dynamics continue in these two populations. For example, the herbivore population or the pollinator population can diverge from the original population A or B into two and later into several more population A_i ($i=1,\ldots,n_1$) or B_l ($l=1,\ldots,n2$) with their corresponding traits a_i ($i=1,\ldots,n_1$) or b_l ($l=1,\ldots,n2$). Competition happens among populations A_i ($i=1,\ldots,n_1$) and among B_l ($l=1,\ldots,n2$) respectively. The newly generated population will coevolve with the other existing populations. It is also possible that during this coevolutionary process, one or more population sizes drop down to zero, and therefore those populations go extinct and so are removed from the system. Meanwhile, all the population, even though diverge, are constrained by their limited carrying capacities K, K_A and K_B.

All the populations continue to coevolve with the new diverged populations as well as adapt to new extinctions until all the population trait values reach their local maxima in the fitness landscapes. This is when the evolution process becomes stable and stops, and this stable point is called Evolutionary Stable Strategy (ESS, Geritz et al., 1998) in adaptive dynamics. In this research, the results investigated are at the ESS points.

Results

1. The ecological and evolutionary responses to the three interactions

The population size and the coevolving traits can be affected by the interactive coefficient factors of the three interactions, correspondingly; that is (1) the abiotic – biotic interaction related growth and death rates (r_A, r_B, d_A, d_B); (2) the competition interaction related carrying capacities (K_A, K_B); and (3) the herbivory and mutualistic interaction conversion coefficients (c_A, c_{RA}, c_B, c_{RB}). Here we will focus on the responses of ecological population sizes and the evolutionary trait values to the three interactions.

(1) The effect of abiotic–biotic interaction (the related growth and death rates r_A, r_B, d_A, d_B) on population size and trait values.

The growth and death rates measure the rate of change in population sizes of the antagonistic herbivore and mutualistic pollinator populations depending on the biotic trait matching with the abiotic environment. The population size of either population naturally increases with its growth rate and decreases with its death rate (Table 2, Figure A1). The change in population size generated by the change in the growth (or death) rates of the other population is different between herbivores and pollinators. The increase in the growth rate (or the decrease in the death rate) of herbivores decreases the population sizes of the pollinators, due to the herbivores' direct negative interaction with the plants (as the herbivores consume the plants) and so negative indirect contribution to the pollinator population (as the pollinators cooperate with the plants). On the other hand, the increase in the growth rate (or the decrease in the death rate) of the pollinators, increases the population sizes of the herbivores, due to the pollinators' direct positive interaction with the plants, and so positive indirect contribution to the herbivore populations (Table 2, Figure A1).

As for their traits evolution, both the trait values of herbivores and pollinators evolve towards the optimal environmental adaptive traits a_0=0, b_0=0, and away from the optimal interactive traits a_m=1, b_m=2, when the birth rate of the antagonistic herbivores (r_A) increases. This means that the whole system evolves to be less interactive with other biotic populations in the system both for the pollinators and the herbivores. However, when the birth rate of the mutualistic pollinators (r_B) increases, the pollinator traits evolve towards the optimal environmental adaptive traits and away from the optimal interactive traits; but the herbivore traits evolve towards the optimal interactive traits and away from the optimal environmental adaptive trait. This means that the pollinators evolve to rely more on the abiotic environment to survive since they already have a high growth rate, whereas the herbivores evolve to rely more on the interactions in the system to get more benefits by interacting with high-growth-rate pollinators. (Table 2, Figure A2).

As for the death rate, both the trait values of herbivores and pollinators evolve towards the optimal interactive traits a_m=1, b_m=2, and away from the optimal environmental adaptive traits a_0=0, b_0=0, when the death rate of the herbivores (d_A) increases. This means that the whole system evolves to be more interactive with other biotic populations both in the pollinators and in the herbivores, when the antagonistic herbivores suffer from higher death rates. On the other hand, when the death rate of the pollinators (d_B) increases, both traits evolve away from the optimal interactive traits, and towards the optimal environmental adaptive traits. This means that the whole system evolves to be less interactive with other biotic populations when the mututalistic pollinators suffer from higher death rates (Table 2, Figure A2).

Note that detailed results for the responses of populations sizes and trait evolution to different interactive coefficient factors are shown in the Appendix Figure A2, and the corresponding descriptive results are shown in Table 2.

Table 2 The ecological and evolutionary responses to the interactive coefficient factors

parameters		Population sizes		Trait values	
		A	B	a	b
Growth and death rates	r_A	+	-	o	o
	d_A	-	+	×	×
	r_b	+	+	×	o
	d_B	-	-	o	o
Carrying capacity	K_A	+	-	o	o
	K_B	+	+	×	×
Convergent coefficient	c_A, c_{RA}	-	-	o	o
	c_B, c_{RB}	+	+	×	×

+: population size moves in the same direction with the parameters
-: population size moves in the opposite direction with the parameters
×: traits move towards higher interaction with the biotic system when parameters increase
o: traits move towards higher interaction with the abiotic system when parameters increase

(2) The effect of competition interaction (the related carrying capacities K_A, K_B) on population size and trait values.

The carrying capacity measures the level of the antagonistic herbivore population and mutualistic pollinator population size the system can hold, and also the corresponding intensity of competition in the populations. Naturally, the population size of either the herbivores or the pollinators increases with their own corresponding carrying capacities. The change in population size generated by the change in the carrying capacity of the other population is different between herbivores and pollinators. The increase in the carrying capacity of herbivores decreases the population sizes of the pollinators, but the increase in the carrying capacity of the pollinators, increases the population sizes of the herbivores, due to the different responses between the antagonistic herbivores and mutualistic pollinators (Table 2, Figure A1).

Both the trait values of herbivores and pollinators evolve towards the optimal interactive traits a_m=1, b_m=2, and away from the optimal environmental adaptive traits a_0=0, b_0=0, when the carrying capacity of the pollinators (K_B) increases. This means that the whole system evolves to be more interactive with other populations both in the pollinators and in the herbivores, when the positive interaction (mutualism) is high. On the other hand, when the carrying capacity of the herbivores (K_A) is increase, both traits evolve away from the optimal interactive traits, and towards the optimal environmental adaptive traits. This means that the whole system evolves to be less interactive with other populations when the negative interaction (antagonism) is high (Table 2, Figure A2).

(3) The effect of herbivory and mutualistic interaction (the related conversion coefficients c_A, c_{RA}, c_B, c_{RB}) on population size and trait values.

The conversion coefficients measure the levels of interaction between two populations either antagonistically (c_A, c_{RA}) or mutualistically (c_B, c_{RB}). In figure A1, we only show the results for c_A and c_B (not for c_{RA} and c_{RB}), since we assume that c_A and c_{RA} are related (c_A=0.5c_{RA}) and c_B and c_{RB} are related (c_A=0.5c_{RA}). When the conversion coefficients of the antagonistic herbivory interaction (c_A, c_{RA}) increase, both the herbivore and the pollinator population sizes decrease, because the negative interaction in the system is higher. However, when the conversion coefficients of the mutualistic pollination interaction (c_B, c_{RB}) increase, both the herbivores and the pollinators population sizes increase, since the positive interaction in the system is higher (Table 2, Figure A1).

Similarly, when the conversion coefficients of the herbivores (c_A, c_{RA}) increase, both the trait values in the herbivores and pollinators evolve away from the optimal interactive traits (which means less interaction with other populations in the system), since the level of negative interaction in the system is higher. However, when the conversion coefficients of the pollinators (c_B, c_{RB}), both the trait values in the herbivores and pollinators evolve towards the optimal interactive traits (which means more interaction with other populations in the system), since the level of positive interaction in the system is higher (Table 2, Figure A2).

2. The trait diversification responses to the three interactions.

The interactive niche widths in the three interactions are the main reasons for population diversification. When the adaptive niche width of herbivores (σ_{0a}) or the pollinators (σ_{0b}) is wider, which means the population can adapt to a wider environment (temperature, geographic district, external food resource, etc.) range, the corresponding population will have higher diversification at the ESS (Figure 2). When the competition range of herbivores (σ_{ca}) or the pollinators (σ_{cb}) is narrower, which means that the competition is less intense inside the populations, the corresponding population will have higher diversification at the ESS (Figure 2). Finally, when the interactive range of herbivores (σ_a) or the pollinators (σ_b) is wider, which means that the interactive opportunity is higher with the plants, the corresponding population will have higher diversification at the ESS (Figure 2). Note that all these changes do not affect the diversification in the other population (not shown in Figure 2).

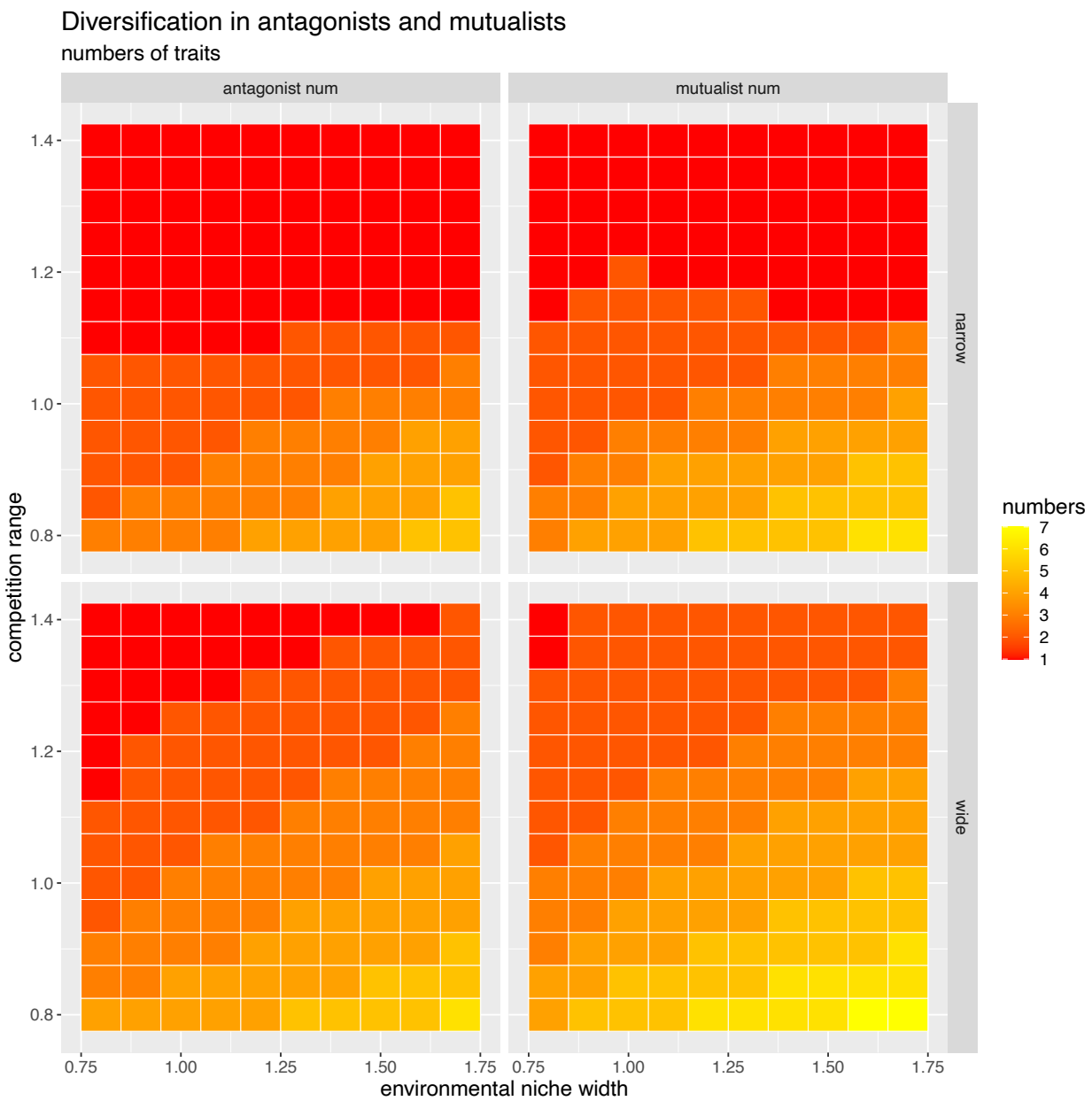

Figure 2. The patterns that the interactive range affect the diversification (the number of populations with different traits) of antagonists and mutualists. The vertical axis of each panel shows the gradient of the competition range. All four panels show that the lower the competition range the higher the diversification in traits. The horizontal axis of each panel shows the gradient of the environmental niche width. All four panels show that the higher the environmental niche width, the higher the diversification in traits. The upper two panels show the narrow antagonistic interactive range (between the antagonists and plants) and the narrow mutualistic interactive range (between the mutualists and plants). The lower two panels show the corresponding wide range for the antagonistic and mutualistic interactive ranges. Comparing the upper two with lower two panels, the wider interactive ranges lead to higher diversification for both antagonists and mutualists. The parameter values: a_0=0, b_0=0, a_m=1, b_m=2, r_A=0.5, r_B=0.5, r=1, d_A=0.1, d_B=0.1, d=0, K=10, K_A=3, K_B=3, c_{RA}=0.2, c_{RB}=0.2, c_A=0.5c_{RA} =0.1, c_B=0.5c_{RB} =0.1, σ_{0a}, σ_{ca}, σ_{0b}, σ_{cb} equal the values shown in the figures, and σ_a=1, σ_b=1 (upper left, upper right), σ_a=1.3, σ_b=1 (lower left), σ_a=1, σ_b=1.3 (lower right). The parameter terms are explained in Table 1.

Discussion

All populations face both abiotic and biotic interactions. The abiotic interactions can be with the environment (e.g., climate conditions, geographic positions, etc. shown in Figure 1 (1)), and the biotic interactions can be with competitors in their own population (Figure 1 (2)) or with populations of a different species either being antagonistic or mutualistic to them (Figure 1 (3)). In this research, we developed a generally based (not on specific species or traits) framework to analyse both the ecologic, coevolutionary and diversification responses from all these three different interactions (Figure 1), and the general model and results here can be applied to understand different specific eco-evolutionary dynamical systems with antagonistic and mutualistic interactions.

We found that the ecological population sizes are naturally higher when the corresponding growth rate (or death rate) in relation to the external environment (e.g. climate conditions, Memmott., 2007), or the corresponding carrying capacity allowed for this population (in relation to the competition among populations) is higher. This is when the populations are more adaptive in a system where the population can rely much on themselves and the environment. At the same time, since the populations also interact with the other populations either positively (mutualistically) or negatively (antagonistically), the level of interactions in the system can affect all the populations. The population sizes of both mutualists and antagonists are typically higher when the mutualistic interaction (either within themselves or within the other populations) is stronger in the system, whereas lower when the antagonistic interaction (either competing within themselves or with the other trophic level populations) is stronger. This indicates that a higher level of mutualistic interaction might benefit all the populations in the interactive system (Jordano., Bascompte., & Olesen., 2006), whereas a higher level of antagonistic interaction might deteriorate all the populations in the interactive system. For example, when the pollinator match with the plants, not

only do the plants and pollinators thrive, but those herbivores that feed on the plants also thrive (Ne'eman et al., 2010). However, when the antagonistic interactions are higher between the herbivores and the plants, the pollinators might suffer. Similar results were found empirically by Fiegna & Velicer (2005), that the cooperative populations can be negatively affected in their reproduction and can even go extinct when the other antagonistic interactions are high.

Besides population ecological responses, the evolution of functioning traits also relies on abiotic and biotic interactions. Here we find that when the mutualistic interaction is stronger (the mutualistic interactions between trophic level populations is higher, or the carrying capacity of the mutualistic populations is higher, or the death rate of the mutualists is lower), the functioning traits of all the populations evolve towards values that can be more interactive with the other biotic populations in the system, and less interactive with the abiotic environment, whereas this is the opposite to the antagonists. For the growth rates, the higher the growth rates (which is related to the adaptation to the abiotic environment in comparison with the intrinsic death rate) of the mutualists, the mutualists evolve to rely more on the abiotic environment which supports their growth rather than on the interaction with the other biotic populations, but the antagonists, evolve to the more interactive with the other biotic populations due to the higher growth rates of the mutualists. However, when the growth rates of the antagonists are higher, the functioning traits of all the populations evolve towards values that are less interactive with the other biotic populations but more interactive with the abiotic environment. Therefore, the responses of evolution to the strengths of different interactions in mutualists and antagonists are usually in opposite directions due to their different functions in the system.

The diversification in populations is also affected by all the interactions mainly through the interactive range in each interaction. As studied by previous studies (Pontarp., 2021), we also find that when lower competitive interactive range, which means that the competition is less intense among populations, the diversification is higher. Also as suggested by other studies (Wellborn & Langerhans, 2015; Petanidou., &Potts., 2006), we find that when the environmental adaptive niche is higher, which means that the populations can be adaptive to a wider environment (higher ecological opportunities), the diversification is higher. Furthermore, we find that when the herbivory or the pollination interactive range between populations is wider, the diversification of the herbivores and the pollinators are higher (supported by Vazquez & Aizen., 2006).

In general, we find that a better condition of one population in the positive interaction or a higher level of positive interaction between populations in the system (mutualism here, but can be positive cooperation) promotes the increase of population sizes in all the positive interaction populations. It also induces an evolution towards higher interaction with the other positively interacted biotic populations. The results are the opposite for a higher level of negative interactions in the system. This can give us insights into why certain populations flourish more than other populations and in helping with rescuing and increasing the sizes of certain populations. Therefore, in order to save certain target populations, we could control the population sizes of their antagonistic populations by changing the abiotic environment, increasing antagonistic populations' competition with themselves or with their other competitors, or we could constrain the level of interactions between the target populations and the antagonistic populations, and do the opposite for the related mutualistic populations.

The diversification is generally higher for milder conditions (wider abiotic environmental opportunities, less intense competitions, higher benefits from other interactive biotic populations) and lower for corresponding harsh conditions for a target population. To help slow down the loss of biodiversification, we could try to improve the environmental conditions to bring wider ecological opportunities for more diversified populations to survive (Wellborn & Langerhans, 2015). We could also build good internal living conditions by separating them from their internal competitors to avoid the ecological niche overlapping and high level of competition. Moreover, a better chance to interact with a wider range of beneficiary trophic-level populations could also increase the target population's diversification.

There is however a limit in our model we need to mention – we assume that the plant resource trait does not coevolve with the traits of antagonistic herbivore and mutualistic pollinator populations. This is reasonable in the system where the plant resource trait is relatively stable, e.g., in agricultural farmland, where the plants are chosen to have desirable traits that are less likely to evolve naturally. Similarly, in human bodies (or other organisms' bodies) with both good bacteria and bad bacteria populations, the evolution of functional traits in human parts is relatively much slower than the evolution in good and bad bacteria, so we can treat the human functional traits to be stable (or fixed), whereas the traits of the mutualistic good bacteria and the antagonistic bad bacteria can coevolve with each other and form a great level of diversity. Therefore, similar conclusions can also be applied to this eco-evolutionary dynamic system. We can also expect that many results still work while the communal interactive trait (i.e., the plant trait in this research) coevolves with the antagonistic and mutualistic traits, although this needs to be further tested with a modified model. We note, however, that, since in reality, the traits in the communal population that interact with the antagonists and the mutualists are usually of different types of traits (e.g., the plant flora traits interacting with pollinators and defence traits interacting with the herbivores, Strauss., 1997), the computational analyses of the diversification in the two-dimensional traits in one population can be much more complicated and time-consuming.

In this research, we have a general and comprehensive analysis of the ecological and evolutionary responses in the three trophic-level interactive ecosystem with both antagonists and mutualists that are affected by three main abiotic or biotic interactions. We are able to figure out the reasons for different responses in this complicated interactive ecosystem and we can apply this general model to explain mechanisms of a lot of specific dynamical eco-evolutionary systems as well as give predictions and suggestions. For example, we can explain why certain species go extinct or their population size is shrinking substantially due to their specific abiotic and biotic interactions; and why certain population traits evolve to be more adaptive to abiotic environmental changes (e.g. climate or geographic changes), whereas some other population traits evolve to be more interactive with the other biotic populations. We can also find the specific reasons for the rapid loss of biodiversity in many species. We hope and encourage the experts who study these crucial questions could use and test our model to explain the dynamic mechanisms, predict future ecological and evolutionary trends and potentially find out suggestions and interventions for ecosystem and biodiversity maintenance.

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Appendix

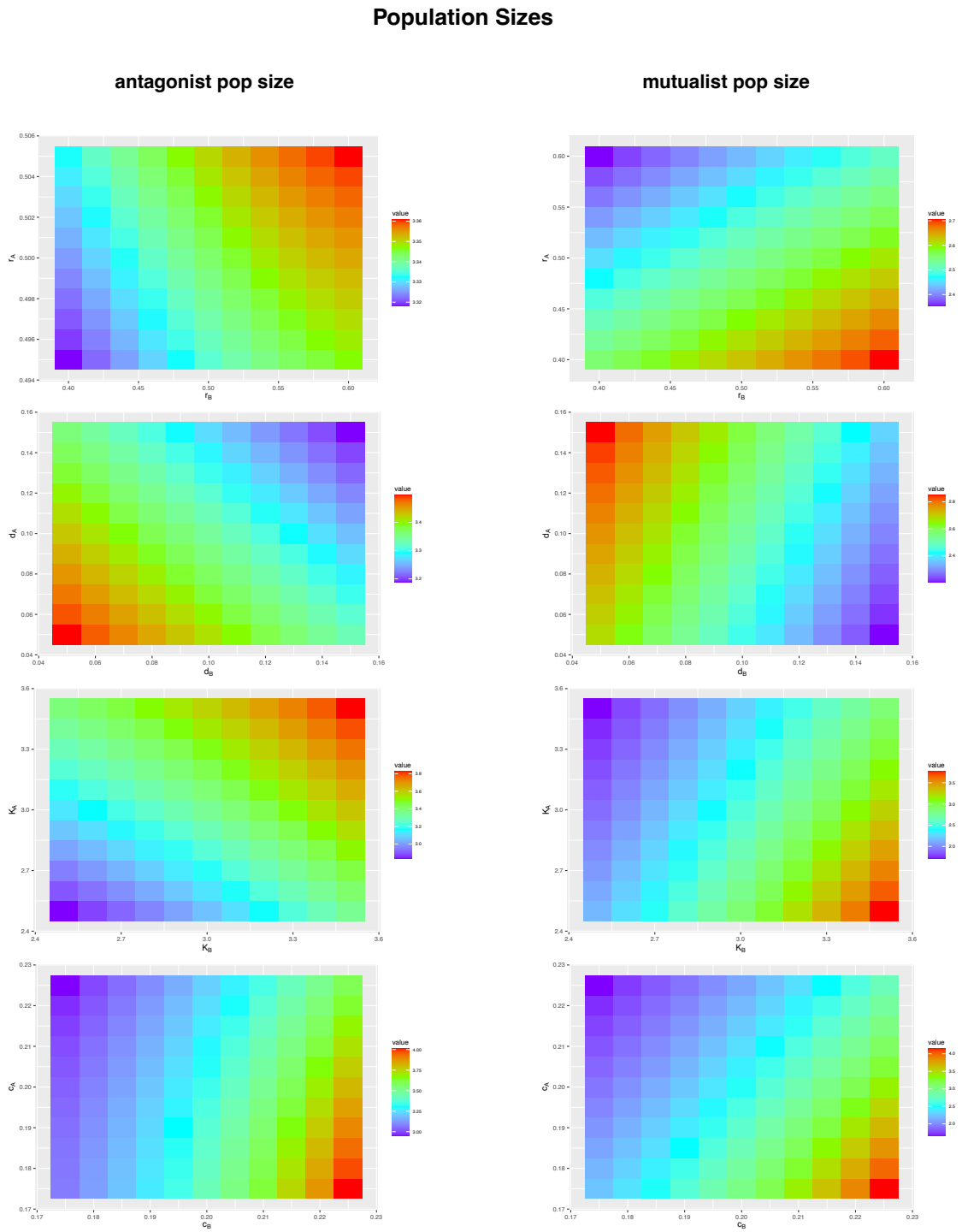

Figure A1 The responses of population sizes of antagonists (left) and mutualists (right) to the interactive coefficient factors (grow rates, death rates, carrying capacity, convergent

coefficients in the 1st, 2nd, 3rd, 4th rows correspondingly). The parameter values: a_0=0, b_0=0, a_m=1, b_m=2, r=1, d=0, K=10, $\sigma_{0a}=\sigma_{ca}=\sigma_a=1$, $\sigma_{0b}=\sigma_{cb}=\sigma_b=1$, r_A, r_B, d_A, d_B, K_A, K_B, c_{RA}, c_{RB}, $c_A=0.5c_{RA}$, $c_B=0.5c_{RB}$ equal the values shown in the figures. The parameter terms are explained in Table 1.

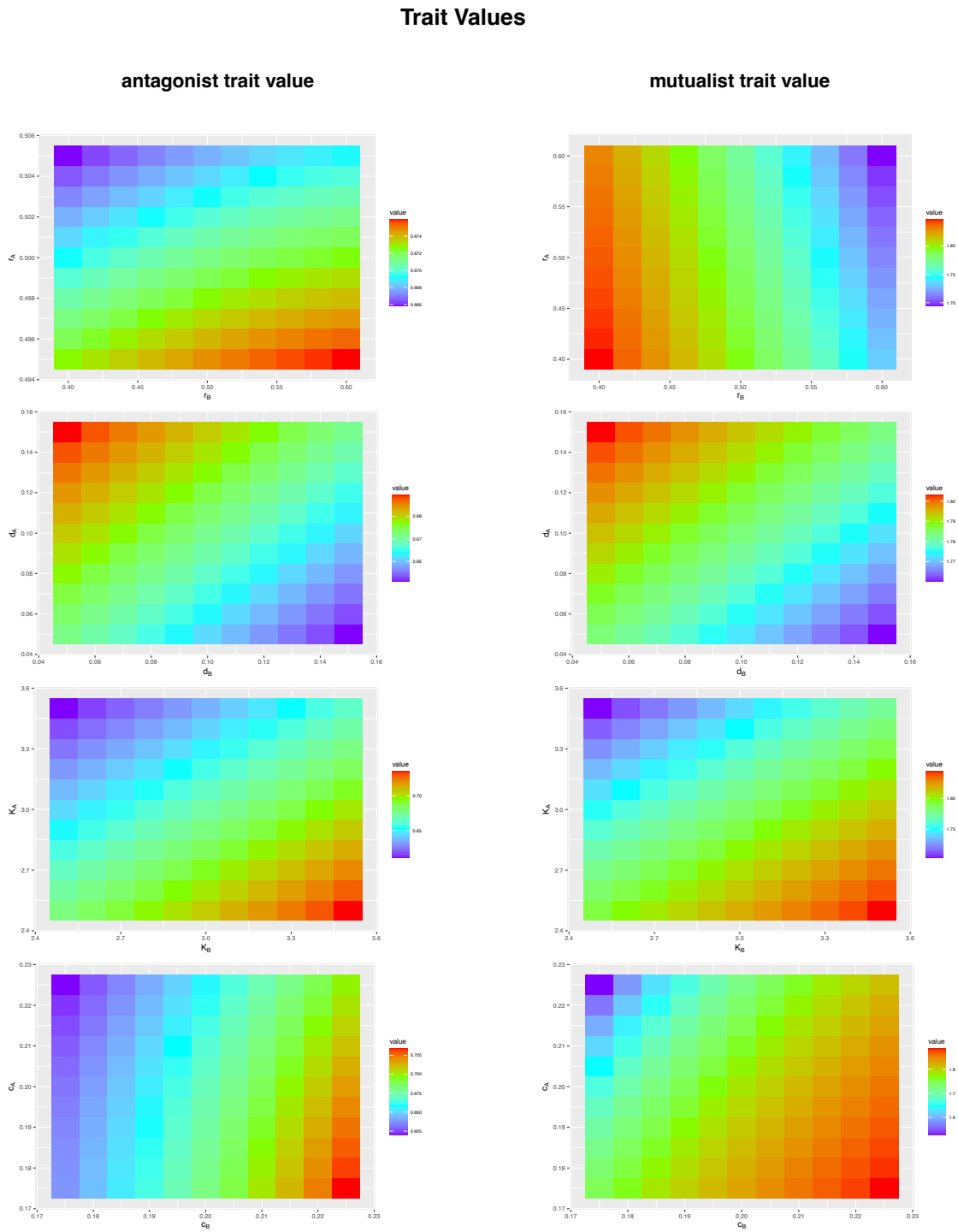

Figure A2 The responses of trait evolution of antagonists (left) and mutualists (right) to the interactive coefficient factors (growth rates, death rates, carrying capacity, and convergent coefficients in the 1st, 2nd, 3rd, 4th rows correspondingly). The parameter values: a_0=0, b_0=0, a_m=1, b_m=2, r=1, d=0, K=10, $\sigma_{0a}=\sigma_{ca}=\sigma_a=1$, $\sigma_{0b}=\sigma_{cb}=\sigma_b=1$, r_A, r_B, d_A, d_B, K_A, K_B, c_{RA}, c_{RB}, $c_A=0.5c_{RA}$, $c_B=0.5c_{RB}$ equal the values shown in the figures. The parameter terms are explained in Table 1.