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

Lingzi Wang[1,3], Mikael Pontarp[2]

Abstract

Understanding the underpinnings of ecosystem dynamics and function is critical as we are currently experiencing restructuring and loss of function in many ecosystems across the globe. Such understanding is however limited due to the complexity in which combined ecological interactions among species and coevolution within and across trophic levels affect ecosystem structure, dynamics, and function. Here, we embrace the complexity of ecosystems in our aims to investigate the eco-evolutionary dynamics that generate plant-insect coevolution and diversification mediated by competitive interactions, antagonistic and mutualistic interactions, and biotic-abiotic interactions. We use an eco-evolutionary and functional-trait-based model of three interacting trophic levels to simulate adaptation and diversification in traits as a response to eco-evolutionary feedback. Our findings reveal a mechanistic link between mutualistic interactions and population size, positively affecting evolvability and trait evolution. Adaptive functional trait matching between species engaging in biotic mutualistic interactions is promoted, while adaptation to the abiotic environment becomes less pronounced. Negative interactions, such as antagonism-related

[1]Centre for Environmental and Climate Science, Lund University, Sweden
[2]Department of Biology, Lund University, Sweden
[3]Department of Physics, University of York, United Kingdom

abiotic or biotic interactions, have the opposite effect. We also find that high ecological opportunities, low within-trophic-level competition, and high adaptive interactions between plants and antagonistic herbivores or mutualistic pollinators can generate a higher level of diversification in both herbivores and pollinators. Benign abiotic and biotic conditions thus promote diversification, while harsh conditions impede diversification. Such results disentangle some of the indirect complexity in which basic and fundamental processes in ecology and evolution affect complex ecosystems. Findings can contribute to our understanding of urgent issues associated with changing environmental conditions, such as climate change and loss of natural habitats. This theoretical approach can be applied and tested in specific ecosystems, furthering our knowledge of eco-evolutionary dynamics and supporting ecosystem management and conservation efforts.

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

Introduction

The societal and economic benefits associated with ecosystems and several of the ecosystems services within are undisputable (Potts *et al.* 2016; Alexandridis *et al.* 2021). We are at the same time changing the environment, the ecology, and biodiversity that have been gradually formed over long evolutionary time scales (Miller., 2005). For example, genes are engineered for higher agricultural plant production and better tastes (Akter., 2016). Pesticides or herbicides are used to reduce pests and unwanted competitive plants (Popp., 2013). Anthropogenic changes toward certain specific short-term outcomes including intensifying certain agricultural species rather than promoting diversified natural plant species also generate unprecedented change in the ecosystem and loss of biodiversity (Díaz et al., 2006, Hilderbrand et al., 2010). The long-term maintenance of a good-functioning and healthy environmental or ecological dynamical system may be threatened as a result (Cardinale., 2012, Naeem., 2002; Loreau et al., 2022).

Although understanding the maintenance of ecological systems is vital, progress in understanding the processes that underlie ecosystem structure (e.g. biodiversity) and function has however been slow. One reason for the slow progress is arguably the complexity with which ecological interactions and evolutionary processes interact while generating diverse ecosystems. Organisms not only interact with the abiotic environment, but they also interact within their own populations (i.e. intra-specific interactions) and with other populations within or across trophic levels (i.e. inter-specific interactions). The ecological consequences of such interactions combined with plausible coevolution imply the importance of eco-evolutionary processes for the diversification of important ecosystems (Urban & Skelly, 2006; Cortez & Ellner, 2010; Ellner et al., 2011). However,

the eco-evolutionary processes that generate functional coevolution and diversity in ecosystems that include a complex mix of environmental effects, as well as antagonistic and mutualistic interactions, remain elusive. Much remains to be learned about how these different factors interact to drive the coevolution and diversity of species within ecosystems.

With the above being said, previous research provides a theoretical base on which understanding of the maintenance and diversification of complex ecosystems may rely. Adaptation in functional traits and adaptive radiations are, for example, considered to reflect 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 can be driven by ecological opportunities (i.e. 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). Others emphasize antagonistic and mutualistic trophic interactions as the driver of adaptation and radiation. More specifically, 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). 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 above provides a theoretical base on which understanding of the interaction and relationship between various ecological interactions, micro-evolutionary processes, diversification, and biodiversity rely. However, different aspects (i.e., ecological opportunities, competitions, antagonism, mutualism) can all affect the ecological system and biodiversity simultaneously, and since each biological population commonly face all these aspects in concert. For instance, the characteristics of an antagonistic herbivore population might have an indirect impact on a mutualist population even though they do not interact directly with each other, but indirectly through a third population (Ohgushi, 2005). Therefore, it is worth adopting a holistic view on ecosystems as a food-web of multiple types of interactions (e.g., Brodersen et al., 2018), since complicated foodweb interactions can have important ecological and evolutionary implications affecting the structure of the ecological communities, and the trait evolution in populations.

With this in mind, we develop a mathematical model to investigate the ecological and evolutionary responses mediated by interactions that biological population commonly faces including (1) the biotic-abiotic interaction; (2) intra-species competitive interaction; (3) inter-species antagonistic and mutualistic interactions (Figure 1). We specifically apply the model to the three representative trophic-level populations: antagonists (herbivores), mutualists (pollinators) and common resources

(plants). We use the adaptive dynamics approach (Geritz et al., 1998) to analyse the eco-evolutionary adaptation and diversification as a response to the three interactions.

Methods

Model overview

We investigate trait coevolution and diversifications in an interacting network of populations that face (1) adaptive environmental interactions, (2) intra-species competitive interactions, and (3) inter-species antagonistic and mutualistic interactions (Figure 1). We develop a trait-based mathematical model to investigate the dynamical eco-evolution and diversification process with these three interactions inside the three types of populations - antagonistic herbivores, mutualistic pollinators and their mutually interacting plant resources. Both the population sizes and the traits of the herbivores and pollinators can change dynamically in the system with their mutually interacting trait-stable size-changing plant resources (e.g. agricultural crops). Furthermore, the herbivory antagonistic and pollination mutualistic interactive traits evolve dynamically and can branch and form new trait-based populations (diversification) during the evolutionary process. The newly emerged population then automatically join the interaction of the existing populations. The dynamics keep going until the whole eco-evolution and diversification process reaches equilibrium. We use the adaptive dynamics approach (Dieckmann & Law., 1996; Doebeli & Dieckmann., 2000; Geritz et al., 1998; Brännström et al., 2013) to analyse this process and the details are described below in "**Eco-evolutionary analyse**".

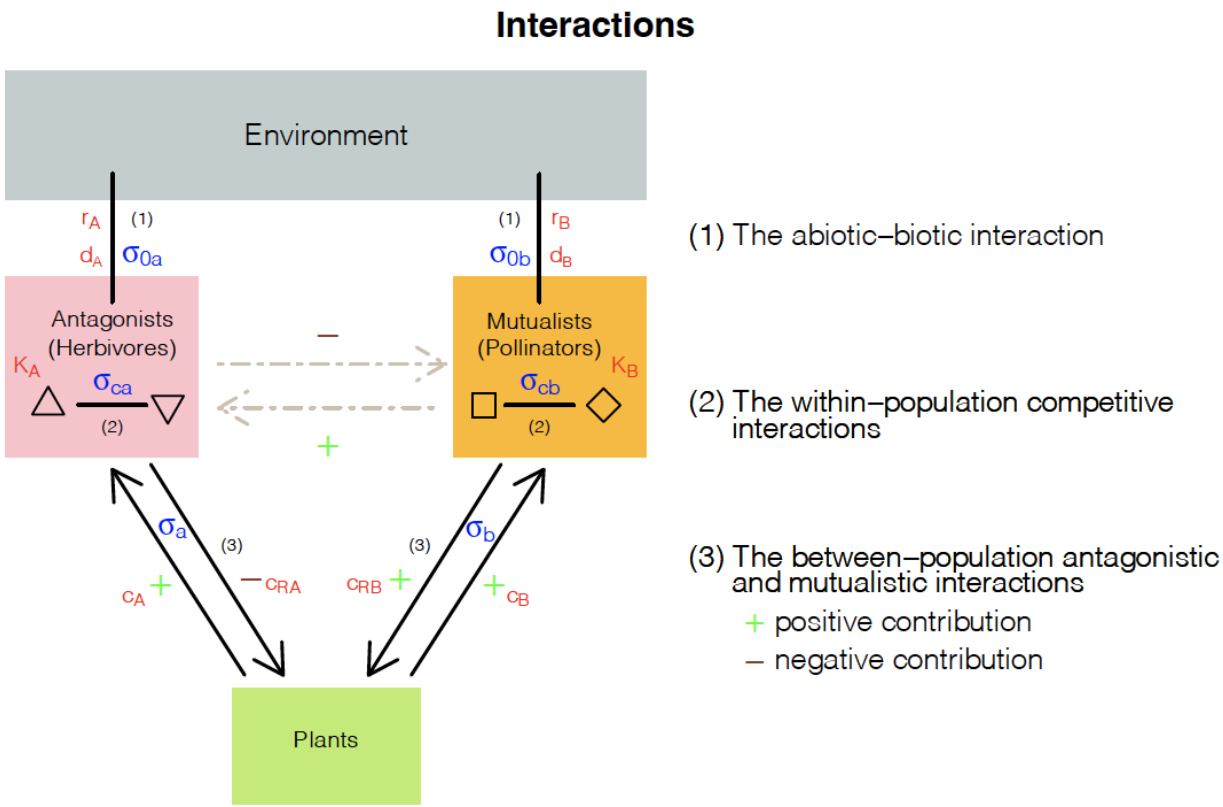


Figure 1. Illustration of the three populations and interactions in the ecological network. Interactions are denoted by numbers 1-3 and represented by black lines/arrows. The strengths of the interactions are measured by birth rates (r_A, r_B) and death rates (d_A, d_B) in the interaction (1); carrying 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 interactive ranges are measured by 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).

Trait based ecological interactions

The three initial populations referred as the plant resource population (R), the antagonistic herbivore population (A), and the beneficiary mutualistic pollinator population (B). The three

initial populations interact and evolve dynamically in the system with each other based on their interactive functioning traits in the three interaction (1) (2) (3) (shown in Figure 1).

First, both the herbivore and the pollinator populations A and B benefit from the adaptation to their environment (Figure 1 interaction (1)). More specifically, the strength of the adaptive interactions with the environment acts on the growth of the populations by the factor of the normal kernel form ($\exp\left(-\frac{1}{2}\left(\frac{a_i-a_0}{\sigma_{0a}}\right)^2\right)$ for the herbivores and $\exp\left(-\frac{1}{2}\left(\frac{b_l-b_0}{\sigma_{0b}}\right)^2\right)$ for the pollinators (eq. I) and their respective growth rates r_A and r_B. It follows that the adaptive interaction with the environment is strongest for the herbivores or pollinators when their trait value equals an optimal adaptive trait value a_0 or b_0 but tapers off symmetrically as the trait value mismatches, with the niche width parameters σ_{0a} and σ_{0b}. The growth rate of plant resource r and the intrinsic death rates of the three populations (d_A, d_B and d) are assumed to be constant and so not affected by the environment (Lotka-Vertera Model, Lotka, 1925; Volterra, 1926).

Second, both the herbivore and pollinator populations engage in their own competitive interactions respectively for the carrying capacity K_A and K_B (Figure 1 interaction (2)). We assume that the competitive interaction among populations is strongest when the two competitive population traits match with each other, but diminish following a normal distribution pattern. More specifically, the strength of the competition acts on population growth by the factor of $\exp\left(-\frac{1}{2}\left(\frac{a_j-a_i}{\sigma_{ca}}\right)^2\right)$ and $\exp\left(-\frac{1}{2}\left(\frac{b_k-b_l}{\sigma_{cb}}\right)^2\right)$ (eq. I), where a and b denotes functional traits and σ_{ca} and σ_{cb} denote the competition interactive niche width.

Third, the plant population represent the resource on which both the pollinators and the herbivores rely. The plant population thus have positive effects on both herbivores and pollinators (Figure 1 interaction (3)). Meanwhile, the effect from the herbivore on the plant is negative since the herbivores feed on the plants, whereas the effect from the pollinator on the plant is positive due to mutualism (Figure 1 interaction (3)). We use a similar model design for the interactions as above where the strengths of the interaction between the plant and the herbivore populations are depended on the matching between herbivore population trait (a_i) the plant population trait (a_m) with a niche width parameter σ_a. It follows that the strength of the interaction is highest when the herbivore population trait equals the optimal interactive values a_m, and tapers off when the herbivore trait value mismatches from the optimal interactive values a_m, following the normal distribution pattern $\exp\left(-\frac{1}{2}\left(\frac{a_i-a_m}{\sigma_{0a}}\right)^2\right)$. We further introduce the conversion coefficients c_A, c_{RA} which measure how much the strength of interaction between the herbivores and the plants are converged into their dynamical population growth respectively (eq. I). Similarly, for the positive interactions between pollinators and plants, the strength of their interaction follows a 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} for 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

Eco-evolutionary analyses

To investigate the above frequency-dependent ecological population dynamics and evolutionary dynamics, we apply the adaptive dynamics theory (Dieckmann & Law., 1996; Doebeli &

Dieckmann., 2000; Geritz et al., 1998; Brännström et al., 2013). In this approach, ecological dynamics are assumed to be much faster than the evolutionary process, i.e., ecological equilibria are reached before any mutation driven trait changes are introduced. When mutations occur we implement the concept of invasion fitness (Metz et al., 1992), i.e. a population with a mutant trait will be able to invade the resident population given that the mutant population have a positive invasion 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). Following the procedure of analyzing ecological equilibrium and mutation invasions, novel traits will continuously replace the resident trait until the resident fitness reaches local maximum or minimum in the fitness landscape. If a maximum is reached evolution will stop as no more mutants can invade. 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 in the fitness landscape are higher than the fitness of the residence trait, and this is when disruptive selection emerges. In this case, the population can diverge into two phenotypically distinct populations, 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 then 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 (eq. I). It is also possible that during this coevolutionary process, one or more population sizes drop to zero and thus go extinct. 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). All results presented below are analyzed at ESS points.

Model analyses

In our study, we investigate how ecological population sizes and evolutionary trait values respond to different factors that influence interactions within and between species in an ecosystem (the coefficients to the three interations eq. I). Specifically, we look at the factors of the three interactions: (1) the abiotic – biotic interaction related growth and death rates (r_A, r_B, d_A, d_B); (2) the competitive interaction related carrying capacities (K_A, K_B); and (3) the herbivory and mutualistic interaction related conversion coefficients (c_A, c_{RA}, c_B, c_{RB}).

We also examine how population diversification is affected by the interactive niche widths in these three interactions. In specific, we look at the adaptive niche width of herbivores (σ_{0a}) or pollinators (σ_{0b}), which includes factors like the range of temperatures, geographic areas, and food resources that they can adapt to. We also investigate the competition ranges of herbivores (σ_{ca}) or pollinators (σ_{cb}), and the interactive ranges of herbivores (σ_a) or pollinators (σ_b) with plant resources.

To understand the patterns in each of these scenarios, we change the parameter values for each of these interactions and explore how they influence ecological population sizes and evolutionary trait values. These parameter values are specified in the figures presented in our study and parameter terms are explained in Table 1. Ultimately, our research provides insights into how different factors and interactions within an ecosystem can impact population sizes, trait evolution, and diversification.

Results

1. Ecological and evolutionary responses 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 trait matching with the abiotic environment. The population size of the focal populations obviously increases with its growth rate and decreases with its death rate (Table 2, Figure A1) but the indirect effects propagating through the network are less obvious. 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 thus subsequent 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 subsequent positive indirect contribution to the herbivore populations (Table 2, Figure A1).

We also see indirect eco-evolutionary effects. 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 population sizes and trait evolution to different interactive coefficient factors are shown in Appendix Figures A1 and 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. As expected, the population size of either the herbivores or the pollinators

increases with their own corresponding carrying capacities. Furthermore, the increase in the carrying capacity of herbivores indirectly decreases the population sizes of the pollinators. An increase in the carrying capacity of the pollinators, however, indirectly increases the population sizes of the herbivores (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}) increase, 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 ranges in the three interactions ((1)(2)(3) in Figure 1) all have major effects on population diversification. Our findings reveals that (1) When the external adaptive range of herbivores (σ_{0a}) or the pollinators (σ_{0b}) is wider, the population can adapt to a broader range of environmental factors, such as temperature, geographic location, external food resource, etc. As a result, the population will more likely to diversify and thrive, as seen in Figure 2. (2) Furthermore, we found that when the intra-species competition range of herbivores (σ_{ca}) or the pollinators (σ_{cb}) is narrower, the competition within the population is less intense, which les to higher diversifction in the ESS (Figure 2). (3) Finally, when inter-species the antagonistic and mutualistic interaction range of the herbivores (σ_a) or the pollinators (σ_b) is wider, which means that the interactive opportunity for either herbivores or pollinators is higher with their mutual plant resources, a higher

diversification is promoted (Figure 2). Note that all these changes do not affect the diversification in the other population (not shown in Figure 2).

Our research provides valuable insights into the complex dynamics of ecosystems and the factors that drive population diversification, highlighting the importance of understanding the interactive ranges within an ecosystem for promoting biodiversity and maintaining a healthy and sustainable environment.

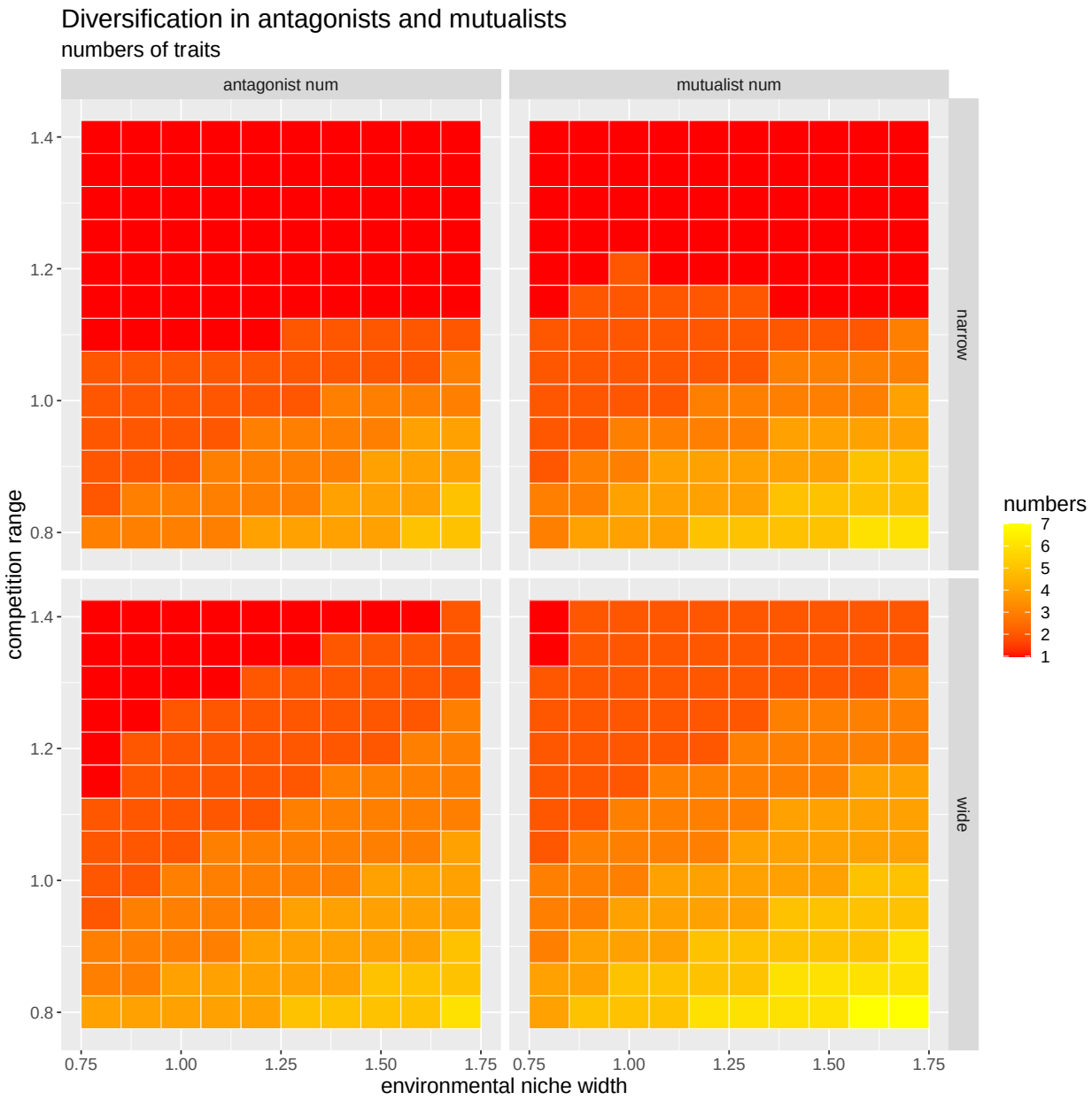


Figure 2. The patterns that the interactive range affect the diversification (the number of populations with different traits) of antagonists and mutualists. The vertical axis of each panel shows the gradient of the competition range. All four panels show that the lower the competition range the higher 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)). Here, we develop a general trait-based and eco-evolutionary model to analyse both the ecologic, coevolutionary and diversification responses to such a diverse range of interactions (Figure 1). The general and somewhat abstract nature of our model allow for a general understanding or different specific eco-evolutionary dynamical systems with antagonistic and mutualistic interactions. More specifically, our model confirms an expected positive relationship between population sizes and growth rate (or death rate) in relation to the external environment (e.g. climate conditions, Memmott., 2007). Similarly a higher carrying capacity allowed for larger population sizes (Del

Monte-Luna et al., 2004). Less obvious results also emerge, since the populations also interact directly or indirectly with the other populations either positively (mutualistically) or negatively (antagonistically). 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 within-trophic level competitions or between-trophic-level interactions) is stronger. This indicates that a higher level of mutualistic interaction might benefit all the populations in the interactive system (Jordano et al., 2006), whereas a higher level of antagonistic interaction might deteriorate all the populations in the interactive system, both directly and indirectly. For example, when pollinators match with 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. Hence in practice, refraining the antagonistic interaction (e.g., by controlling living conditions of the antagonistic populations, increasing their competition, constraining the level of antagonistic relations) and improving the related mutualistic interactions can possibly help to thrive the target populations.

Meanwhich, we find that the evolution of functioning traits also shows similar patterns based on the abiotic and the biotic antagonistic and mutualistic interactions. In general, a better condition of one population in the positive interaction or a higher level of positive interaction between populations in the system (e.g., mutualism or other positive interactions) induces the evolution

towards higher interaction with the other positively interacted biotic populations. This process promotes a higher interactive network inside the ecological system, so every population has a higher impact on other populations. The results are the opposite for a higher level of negative interactions (e.g., antagonism or other negative interactions) in the system. This can give us insights into why populations with certain traits flourish more than other populations and how to help induce higher interaction inside the foodweb ecological system rather than subdue it.

The diversification in populations is also affected by all the interactions mainly through the interactive range in each interaction. Similar to Pontarp., (2021), we find that with lower competitive interactive range, which means that the competition is less intense among populations with their mismatch in functional traits, the diversification is higher. Also as suggested by other studies (Wellborn & Langerhans, 2015; Petanidou & Potts., 2006), we find that when the environmental adaptive range 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 interaction range between populations is wider, the diversification of the herbivores or the pollinators are higher (supported by Vazquez & Aizen., 2006). Therefore, the diversification in biological populations are in general higher for milder conditions (wider abiotic environmental opportunities, less intense competitions, higher benefits from other interactive biotic populations) and lower for relatively harsher conditions. In practice, to slow down the loss of biodiversification, here we suggest improving the environmental conditions to provide milder living conditions and wider ecological opportunities so that more diversified populations can all survive (Wellborn & Langerhans, 2015). Also, it is helpful to separate populations from their internal competitors to avoid the ecological niche overlapping and

intense competition. Moreover, a better chance to interact with a wider range of beneficiary trophic-level populations could also help to keep a higher level of diversification.

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.

References

1.
Aguilera, G., Roslin, T., Miller, K., Tamburini, G., Birkhofer, K., Caballero-Lopez, B., Lindström, S.A.M., Öckinger, E., Rundlöf, M., Rusch, A. and Smith, H.G. (2020). Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. *Journal of Applied Ecology*, 57(11), 2170-2179.

2.
Akter, S., Huq, M. A., Jung, Y. J., Cho, Y. G., & Kang, K. K. (2016). Application of sweet and taste modifying genes for development in plants: current status and prospects. *Journal of Plant Biotechnology*, 43(4), 397-404.

3.
Brännström, Å., Johansson, J. & von Festenberg, N. (2013). The hitchhiker's guide to adaptive dynamics. *Games*, 4, 304-328.

4.
Brännström, A., Loeuille, N., Loreau, M. & Dieckmann, U. (2011). Emergence and maintenance of biodiversity in an evolutionary food-web model. *Theor Ecol-Neth*, 4, 467-478.

5.
Braga, M. P., Janz, N., Nylin, S., Ronquist, F., & Landis, M. J. (2021). Phylogenetic reconstruction of ancestral ecological networks through time for pierid butterflies and their host plants. *Ecology Letters*, 24(10), 2134-2145.

6.
Brodersen, J., Post, D. M., & Seehausen, O. (2018). Upward adaptive radiation cascades: predator diversification induced by prey diversification. *Trends in Ecology & Evolution*, 33(1), 59-70.

7.
Brown, J.S. & Vincent, T.L. (1992). Organization of Predator-Prey Communities as an Evolutionary Game. *Evolution*, 46, 1269-1283.

8.
Cardinale, B. (2012). Impacts of biodiversity loss. *Science*, 336(6081), 552-553.

9.
Cortez, M.H. & Ellner, S.P. (2010). Understanding rapid evolution in predator-prey interactions using the theory of fast-slow dynamical systems. *Am Nat*, 176, E109-E127.

10.
Del Monte-Luna, P., Brook, B. W., Zetina-Rejón, M. J., & Cruz-Escalona, V. H. (2004). The carrying capacity of ecosystems. *Global ecology and biogeography*, 13(6), 485-495.

10.
Díaz, S., Fargione, J., Chapin III, F. S., & Tilman, D. (2006). Biodiversity loss threatens human well-being. *PLoS biology*, 4(8), e277.

11.

Dieckmann, U. & Doebeli, M. (1999). On the origin of species by sympatric speciation. *Nature*, 400, 354-357.

12.

Dieckmann, U., & Law, R. (1996). The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of mathematical biology,* 34(5), 579-612.

13.

Doebeli, M., & Dieckmann, U. (2000). Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *The american naturalist*, 156(S4), S77-S101.

14.

Ellner, S.P., Geber, M.A. & Hairston, N.G. (2011). Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecol Lett*, 14, 603-614.

15.

Fiegna, F., & Velicer, G. J. (2005). Exploitative and hierarchical antagonism in a cooperative bacterium. *PLoS biology*, 3(11), e370.

16.

Geritz, S.A.H., Kisdi, E., Meszena, G. & Metz, J.A.J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol Ecol*, 12, 35-57.

17.

Grant, P.R. (1998). *Evolution on islands*. Oxford University Press, Oxford.

18.

Hamelin, F. M., Hilker, F. M., Sun, T. A., Jeger, M. J., Hajimorad, M. R., Allen, L. J., & Prendeville, H. R. (2017). The evolution of parasitic and mutualistic plant–virus symbioses through transmission-virulence trade-offs. *Virus research*, 241, 77-87.

19.

Häussler, J., Sahlin, U., Baey, C., Smith, H. G., & Clough, Y. (2017). Pollinator population size and pollination ecosystem service responses to enhancing floral and nesting resources. *Ecology and evolution*, *7*(6), 1898-1908.

20.

Hilderbrand, R. H., Utz, R. M., Stranko, S. A., & Raesly, R. L. (2010). Applying thresholds to forecast potential biodiversity loss from human development. *Journal of the North American Benthological Society*, 29(3), 1009-1016.

21.

Hutchings, M. I., Truman, A. W., & Wilkinson, B. (2019). Antibiotics: past, present and future. *Current opinion in microbiology*, 51, 72-80.

22.

Jones, E. I., Ferriere, R., & Bronstein, J. L. (2009). Eco-evolutionary dynamics of mutualists and exploiters. *The American Naturalist*, 174(6), 780-794.

23.

Jordano, P., Bascompte., & Olesen. J. M. (2006) The ecological Consequences of Complex Topology and Nested Structure in Pollination Webs. In Waser & Ollerton., (Eds.) *Plant-Pollinator interactions: from specialization to generalization* (pp. 173-199). University of Chicago Press.

24.

Ito, H., Shimada, M. & Ikegami, T. (2009). Coevolutionary dynamics of adaptive radiation for food-web development. *Popul Ecol*, 51, 65-81.

25.

Keller, I. & Seehausen, O. (2012). Thermal adaptation and ecological speciation. *Mol Ecol*, 21, 782-799.

26.

Loeuille, N. & Loreau, M. (2005). Evolutionary emergence of size-structured food webs. *P Natl Acad Sci USA*, 102, 5761-5766.

27.

Loreau, M., Cardinale, B. J., Isbell, F., Newbold, T., O'Connor, M. I., & de Mazancourt, C. (2022). Do not downplay biodiversity loss. *Nature*, 601(7894), E27-E28.

28.

Losos, J.B. (2010). Adaptive Radiation, Ecological Opportunity, and Evolutionary Determinism. *Am Nat*, 175, 623-639.

29.

MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The american naturalist*, 101(921), 377-385.

30.

MacArthur, H.R. & Wilson, E.O. (1968). *The theory of island biogeography*. Princeton university press, Princeton.

31.

Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the disruption of plant–pollinator interactions. *Ecology letters*, 10(8), 710-717.

32.

Metz, J. A., Nisbet, R. M., & Geritz, S. A. (1992). How should we define 'fitness' for general ecological scenarios?. Trends in ecology & evolution, 7(6), 198-202.

33.

Meyer, J.R. & Kassen, R. (2007). The effects of competition and predation on diversification in a model adaptive radiation. *Nature*, 446, 432-435.

34.

Miller, J. R. (2005). Biodiversity conservation and the extinction of experience. *Trends in ecology & evolution*, 20(8), 430-434.

35.

Naeem, S. (2002). Ecosystem consequences of biodiversity loss: the evolution of a paradigm. *Ecology*, 83(6), 1537-1552.

36.

Ne'eman, G., Jürgens, A., Newstrom-Lloyd, L., Potts, S. G., & Dafni, A. (2010). A framework for comparing pollinator performance: effectiveness and efficiency. *Biological Reviews*, 85(3), 435-451.

37.

Petanidou, T., &Potts, S.G. (2006) Manual Use of Resources in Mediterranean Plant-Pollinator Communities: How specialized Are Pollination Webs? In Waser & Ollerton., (Eds.) *Plant-Pollinator interactions: from specialization to generalization* (pp. 220-244). University of Chicago Press.

38.

Pontarp, M. & Petchey, O.L. (2018). Ecological opportunity and predator–prey interactions: linking eco-evolutionary processes and diversification in adaptive radiations. *Proceedings of the Royal Society B: Biological Sciences*, 285.

39.

Pontarp, M., Ripa, J. & Lundberg, P. (2012). On the origin of phylogenetic structure in competitive metacommunities. *Evol Ecol Res*, 14, 269-284.

40.

Pontarp, M., Ripa, J. & Lundberg, P. (2015). The biogeography of adaptive radiations and the geographic overlap of sister species. *Am Nat*, 186, 565-581.

41.

Pontarp, M. & Wiens, J.J. (2017). The origin of species richness patterns along environmental gradients: uniting explanations based on time, diversification rate and carrying capacity. *J Biogeogr*, 44, 722-735.

42.

Pontarp, M. (2021). Ecological opportunity and adaptive radiations reveal eco-evolutionary perspectives on community structure in competitive communities. *Scientific reports*, 11(1), 1-11.

43.

Popp, J., Pető, K., & Nagy, J. (2013). Pesticide productivity and food security. A review. *Agronomy for sustainable development*, 33(1), 243-255.

44.

Ripa, J., Storlind, L., Lundberg, P. & Brown, J.S. (2009). Niche co-evolution in consumer-resource communities. *Evol Ecol Res*, 11, 305-323.

45.

Ramos, S. E., & Schiestl, F. P. (2019). Rapid plant evolution driven by the interaction of pollination and herbivory. *Science,* 364(6436), 193-196.

46.

Sauterey, B., Ward, B., Rault, J., Bowler, C. & Claessen, D. (2017). The Implications of Eco-Evolutionary Processes for the Emergence of Marine Plankton Community Biogeography. *Am Nat*, 190, 116-130.

47.

Schluter, D. (2000). *The ecology of adative radiations*. Oxford university press, Oxford.

48.

Schluter, D., Price, T.D. & Grant, P.R. (1985). Ecological Character Displacement in Darwin Finches. *Science*, 227, 1056-1059.

49.

Strauss, S. Y. (1997). Floral characters link herbivores, pollinators, and plant fitness. *Ecology*, 78(6), 1640-1645.

50.

Stroud, J.T. & Losos, J.B. (2016). Ecological Opportunity and Adaptive Radiation. *Annual Review of Ecology, Evolution, and Systematics, Vol 47*, 47, 507-532.

51.

Urban, M.C. & Skelly, D.K. (2006). Evolving metacommunities: toward an evolutionary perspective on metacommunities. *Ecology*, 87, 1616-1626.

52.

Vazquez, D.P., & Aizen, M.A., (2006) Community-wide Patterns of Specialization in Plant-Pollinator Interactions Revealed by Null Models. In Waser & Ollerton., (Eds.) *Plant-Pollinator interactions: from specialization to generalization* (pp. 200-219). University of Chicago Press.

53.

Volterra, V. (1926). Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Mem. R. Acad. Naz. dei Lincei* 2, 31–113.

54.

Waser, N. M., & Ollerton, J. (Eds.). (2006). *Plant-pollinator interactions: from specialization to generalization*. University of Chicago Press.

55.

Wellborn, G. A., & Langerhans, R. B. (2015). Ecological opportunity and the adaptive diversification of lineages. *Ecology and evolution*, 5(1), 176-195.

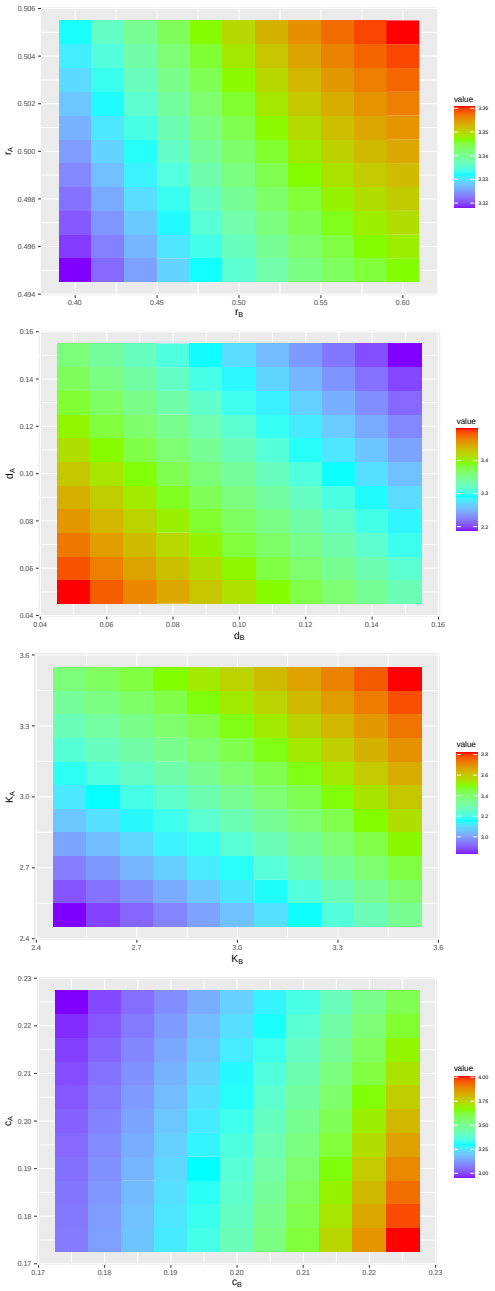
56.

Yoder, J.B., Clancey, E., Des Roches, S., Eastman, J.M., Gentry, L., Godsoe, W. *et al.* (2010). Ecological opportunity and the origin of adaptive radiations. *J Evolution Biol*, 23, 1581-1596.

Appendix

Population Sizes

antagonist pop size



mutualist pop size

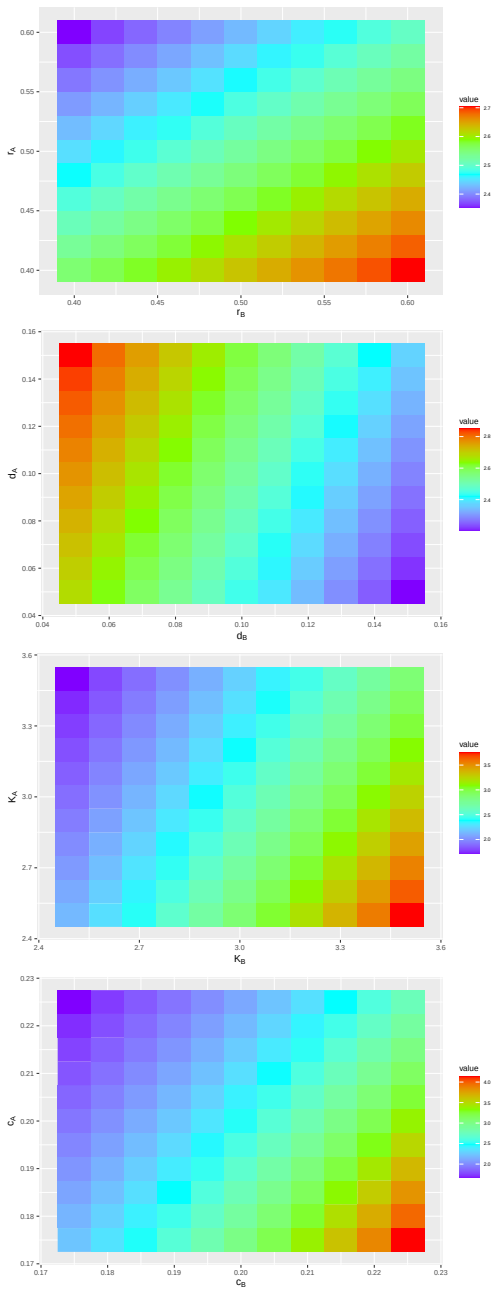


Figure A1 The responses of population sizes of antagonists (left) and mutualists (right) to the interactive coefficient factors (grow rates, death rates, carrying capacity, convergent coefficients in the 1st, 2nd, 3rd, 4th rows correspondingly). The parameter values: a_0=0, b_0=0, a_m=1, b_m=2, r=1, 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.

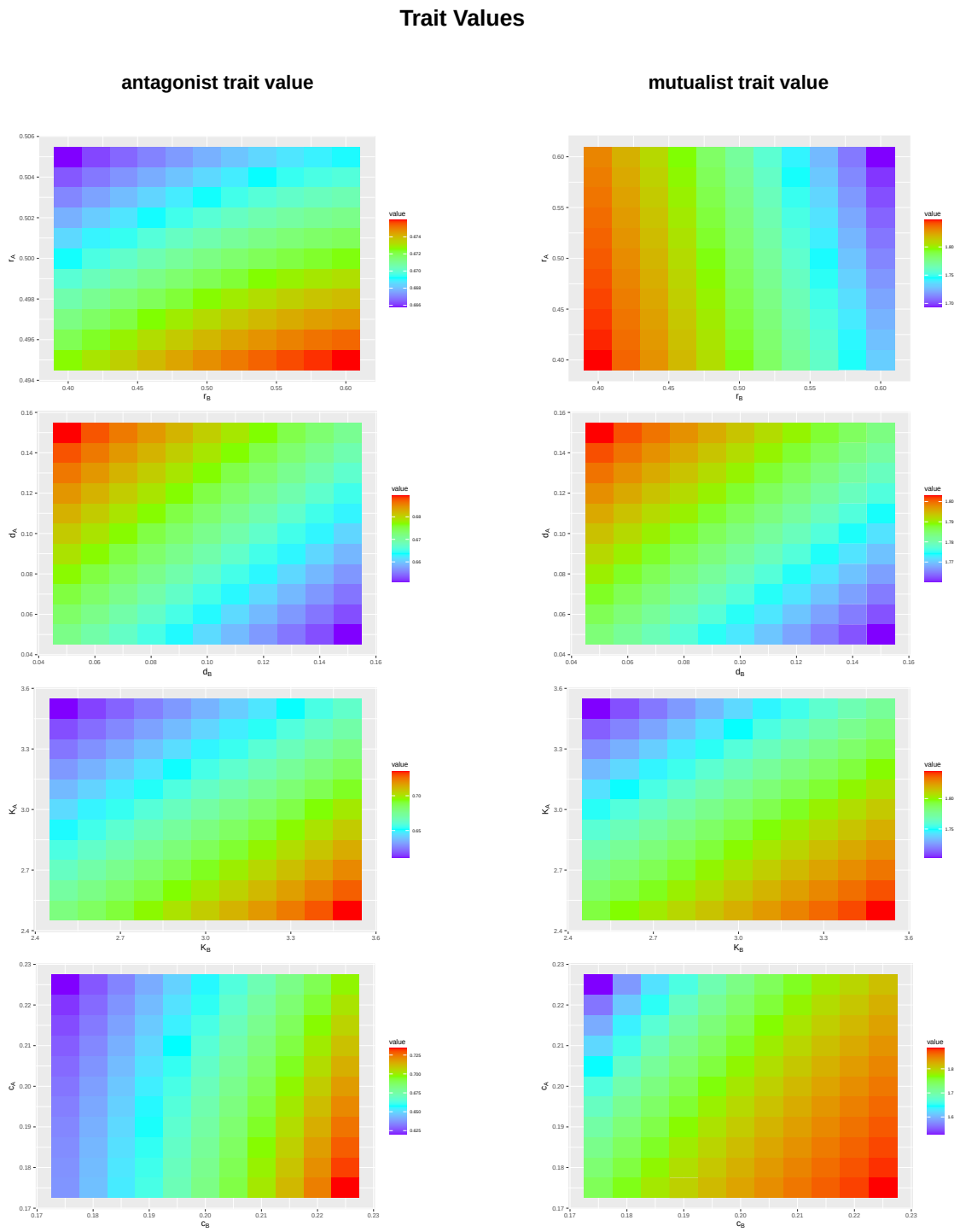


Figure A2 The responses of trait evolution of antagonists (left) and mutualists (right) to the interactive coefficient factors (growth rates, death rates, carrying capacity, and convergent coefficients in the 1st, 2nd, 3rd, 4th rows correspondingly). The parameter values: a_0=0, b_0=0,

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.