

The effects of the exploiters (non-pollinating insects) on mutualistic interactions between the plant and its pollinator

Master's Thesis
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Abstract

Mutualistic interactions between, for example, plants and pollinators play a crucial role in maintaining the biodiversity of ecosystems, while non-pollinating insects (exploiters) that exploit plants are commonly thought to have destabilizing effects. The long-term, i.e., evolutionary time scale, effects of such potential destabilization is however largely unknown. The eco-evolutionary implications of exploiters on plants and their pollinator community thus need to be studied in more detail. In this project, I formulate a functional trait-based model of interacting species to explore the effects of exploiters on the trait evolution of plants and pollinators. I use an abstract model that allows for the generalization of important functional traits such as the proboscis length of the pollinator and the exploiter, and corolla tube depth of plant flowers. I simulate a system of plants and pollinators that interact mutually and I use it as a reference point to analyze the effect of an introduction of exploiters in the system. More specifically, I simulate the introduction of different types of exploiters, i.e., different proboscis's lengths and their effect on the reference plant-pollinator system. My results suggest that exploiters will reduce both plant and pollinator population abundance in an ecosystem but they do not necessarily destabilize the mutualistic interactions. Instead, exploiters induce selective pressure on both plant and pollinator trait co-evolution. The exploiters, for example, reduce the fitness of plants, leading to the selection of the functional traits of the plants to evolve avoidance of the exploitation. Furthermore, the pollinator will co-evolve with the plants to improve their fitness because of the mutualistic relationship between them. These results improve our understanding of the mechanism of the exploiters' stressor driving the co-evolution of plants and pollinators. Understanding that may inform human interventions for biodiversity protection and ecosystem stability in the natural plant-pollinator-exploiter network.

Keywords: Mutualisms; Exploiters; Trait-based Approach

1. Introduction

Mutualism, defined as cooperative interactions between species, is a well-studied concept (Ringel et al., 1996). However, insects that exploit the rewards offered by plants without providing pollination services, have received less attention. With this thesis, I aim to investigate the ecological and evolutionary implications of exploiters in a plant-insect community context. More specifically, I aim to study short (ecological

time scale) and long-term (evolutionary time scale) effects on plant-insect communities that include both pollination and plant exploitation by insects. This is a theoretical study, a functional trait-based model is used to study which exploiters are likely to co-exist with the plant and its pollinator and quantify their direct or indirect effects on plant population abundance and their trait evolution after the co-existence. First, I formulate a model of the plant-pollinator interactions and I use it as a reference for further analyses of exploiter effects. Second, I extend the model to include three species interactions including plants, pollinators, and exploiters. By comparing population dynamics, fitness landscapes, and evolution in functional traits between the reference community and the plant-pollinator-exploiter community I isolate exploiter effects.

1.1 Mutualisms

Four types of mutualisms have been proposed: seed-dispersal mutualisms, pollination mutualisms, digestive mutualisms, and protection mutualisms (Janzen, 1985). In this thesis, I will focus on pollination as mutualistic interactions between plants and their pollinators play an essential role in many ecosystems (Bascompte & Jordano, 2007). Specifically, the flowering plants receive pollination service from their pollinators, and at the same time, nectar or nutrients are provided to pollinators in return (Van Der Kooi et al., 2021). This intricate relationship underpins the reproductive success and genetic diversity of numerous plant species. Several papers have contributed to our understanding of such pollination mutualism. For example, one seminal study in the field of pollination mutualism is Charles Darwin's work (Darwin, 1862), which discussed adaptations of orchids and their coevolution with pollinators. Moreover, a study conducted by Weiss (1992) explored the role of flower color in attracting specific pollinators, which explained the coevolutionary dynamics of plants and their pollinators. In recent years, "Global Pollinator Decline: Trends, Impacts, and Drivers" by (Potts et al., 2010) serves as a reminder of the contemporary challenges facing pollination mutualism, highlighting the critical importance of protecting pollinators and their habitats.

1.2 The exploiters

Several studies show that exploiters are ubiquitous and have been associated with mutualisms throughout evolutionary history (Pellmyr et al., 1996). Exploiters can be generally categorized into two types: nectar(pollen) thefts and nectar(pollen) robbers which forage these rewards offered by plants without providing pollination services (Inouye, 1980). Usually, robbers access nectar by using a perforation on the base of the flower without contacting anthers or stigmas or pollinating (Bronstein et al., 2017). Theft, on the other hand, commonly includes nectar consumption or pollen by insects

entering flowers and precluding pollination. More specifically, Sakhalkar and her colleagues (Sakhalkar et al., 2022) video-recorded 14,391 flower visitors, of which about 4.3% were from robbers (mostly bees and birds), and about 2.1% were from thieves (mostly flies, bees, and moths). Such exploitation can obviously have negative ecological time-scale impacts on plant reproductive success by reducing pollination efficiency (Irwin & Brody, 1998). Also, evolutionary effects are expected as mutualistic relationships between a plant and its pollinator often include coevolution where plants evolve traits to attract pollinators and pollinators evolve traits that allow them to utilize the plant resources. However, if a non-pollinator or an exploiter threatens the plant, the plant may evolve defenses that could inadvertently deter pollinators. Along these lines, existing studies also indicate that both pollinators and exploiters can induce substantial selective pressure on flora evolution (Strauss & Whittall, 2006), partly because pollinators and exploiter share similar preference for flowering plants. Pollinators of *Fragaria virginica*, for example, prefer larger flowers and more flowers per plant. The corresponding weevil exploiter shares similar preferences by also being attracted to larger flowers (Ashman et al., 2004). This said exploiters are generally less known for their ecological or evolutionary implications for both plants and the mutualism that plants and pollinators engage in (Bronstein, 2001). The theory of mutualism under exploitation is not well explored compared to the well-developed theory of predator-prey interactions. Thus, a comprehensive understanding of the ecological and evolutionary mechanisms underlying mutualistic interactions in the context of non-pollinating insects' exploitation is needed.

1.3 Research goal

This project aims to investigate the impacts of exploiters on plant and pollinator traits evolution, and understand the short- and long-term effects of exploiters on plant and pollinator interactions.

In this study, I aim to address three specific research questions:

- RQ1: Under what conditions can exploiters co-exist with the plant and its pollinator network?
- RQ2: What are the short-term effects of exploiters on the mutualistic relationship between plant and pollinator and their subsequent population abundances?
- RQ3: What are the long-term effects of exploiters, i.e., what happens to mutualism if the plant adapts to the introduction of the exploiters?

1.4 Results and Contribution

In summary, my results show that exploiters can co-exist with the plant-pollinator under

moderate exploitation. Population abundance of the plant and pollinator decreased after the introduction of the exploiter. At the evolutionary time scale, the exploiter can drive the co-evolution of the plant and its pollinator. Destabilization of the mutualistic relationship seems to be less of an issue, according to my modeling results. These results contribute to the theoretical understanding of how exploiters affect the growth of plant-pollinator and their trait evolution, which can help empiricists formulate hypotheses that need testing in the future. Also, it may help to develop conservation strategies for plant species and the maintenance of ecosystem diversity. By addressing these research questions, the thesis provides valuable insights into the intricate dynamics of mutualistic relationships, with a particular focus on exploiters.

2. Methods

2.1 Ecology models description

I model the growth rate of populations being dependent on the intrinsic growth rate, carrying capacity, and the benefits or detriments from interacting species. For the modeling of interactions, I use a trait-based approach and I simulate the response of the plant and its pollinator in the presence/absence of the exploiter. I simulate different scenarios. First, I start with two species interactions, i.e., plant-pollinator. Then, I introduce an exploiter to the system. These scenarios are essentially formulated as two different models, which include plant-pollinator interactions, and plant-pollinator-exploiter interactions. In the latter model, we distinguish two types of exploiters, i.e., with direct or indirect competition with the pollinator in this system. Below I will describe the model components in more detail focusing first on trait-based interactions and how such trait-based modeling can be included in population dynamical models of both plant-pollinator systems and plant-pollinator-exploiter systems. Thereafter a description of the simulated scenarios and model analyses will follow.

2.1.1 Trait-based approach

My trait-based approach functionally links individual traits to community structure and dynamics, ultimately addressing complex interactions among species. More specifically, I use a trait-based approach to model the ecological dynamics of plants, pollinators, and exploiters. Functional traits are measurable morphological and phenological characteristics of species, and they are key determinants of interaction preferences that can be linked to their ecological strategies (Neu et al., 2022). A Gaussian function, as shown in Eq.1, is used to quantify the effects between interacting

species. The effects can be maximized by having the traits values of interacting species being similar (Loeuille & Loreau, 2005).

$$\mu(\gamma, \beta) = e^{(-\frac{1}{2} * (\frac{\gamma - \beta}{\sigma})^2)} \quad (1)$$

Here, $\mu(\gamma, \beta)$ denotes the per capita mutualistic interaction μ as a function of the plant trait γ and pollinator trait β . The Gaussian form makes interactions strong if the difference is small and less strong as traits are mismatching. This formulation aligns well with empirical observation where the strength of a plant and its pollinator is dependent on how similar they are, i.e., how similar the proboscis's length of pollinator and corolla tube depth of flowers are. For example, *Calathea crotalifera*, its deep-tubed flowers have adapted to long-tongued legitimate pollinators, *euglossine* bees. At the same time, exploiter, *Eurybia lycisac* butterflies would consume nectar on flowers of its preferred plant, *Calathea crotalifera* (Bauder et al., 2015). Another example is Ollerton, who studied the wildflower communities in an English churchyard (Ollerton, 2007). The authors found that some plant species, such as red campion (*Silene dioica*), had evolved specialized floral traits that were tailored to the feeding morphology of their primary pollinators, such as long-tongued bumblebees (Moquet et al., 2020). In exchange for pollination services, the bumblebees received a rich nectar source. Those insects with long proboscis would also exploit red campion. This abstract model can thus be viewed as a general representation of ecological interactions being dependent on the length of the proboscis of insects and the corolla tube depth of the flower.

2.1.2 Plant and Pollinator Interactions Model

The trait-based interactions described above ultimately affect ecological dynamics for plant and pollinator species. We thus plug the formulation from equation 1 into a population dynamical model where the dynamics of a species i are given by Eq.2a and 2b. N denotes to the population size of the plant, and P denotes to the population size of the pollinator. This is a logistic model with saturating effect for the mutualistic interactions. The first term of equation 2a and 2b describes intrinsic growth rate limited by carrying capacity, and the second term is the benefits from interacting species. This being said, if mutualistic interactions are included in a population dynamical model, without any limiting factors such as death rate or pathogens then this can lead to unrealistic infinite growth of the interacting species. To avoid such problems, I therefore use a Holling type II (Holling et al., 2002) a saturating function shown in the second term of Eq.2a and 2b. Other parameters used are listed in Table 2 Appendix.

$$\frac{dN_i}{N_i dt} = r_{N_i} * \left(1 - \frac{\sum_{j=1}^n \alpha_{N_{ij}} * N_j}{K_{N_i}}\right) + \sum_{j=1}^n \frac{\mu(\gamma_i, \beta_j) * P_j}{1 + C_N * \mu(\gamma_i, \beta_j) * P_j} \quad (2a)$$

$$\frac{dP_i}{P_i dt} = r_{P_i} * \left(1 - \frac{\sum_{j=1}^n \alpha_{P_{ij}} * P_j}{K_{P_i}}\right) + \sum_{j=1}^n \frac{\mu(\beta_i, \gamma_j) * N_j}{1 + C_P * \mu(\beta_i, \gamma_j) * N_j} \quad (2b)$$

In the general form of my model (as described above) subscript i denotes the number of species in this model, and N_i and P_i represent plant species i , and pollinator species i , respectively. Since one plant and one pollinator are considered in this study, I assume that the intra-specific competition coefficient equals 1. The model thus simplifies to Eq.3a, 3b.

$$\frac{dN}{Ndt} = r_N * \left(1 - \frac{N}{K_N}\right) + \frac{C_N * e^{\left(-\frac{1}{2} * \left(\frac{\gamma - \beta}{\sigma}\right)^2\right)} * P}{1 + C_N * e^{\left(-\frac{1}{2} * \left(\frac{\gamma - \beta}{\sigma}\right)^2\right)} * P} \quad (3a)$$

$$\frac{dP}{Pdt} = r_P * \left(1 - \frac{P}{K_P}\right) + \frac{e^{\left(-\frac{1}{2} * \left(\frac{\beta - \gamma}{\sigma}\right)^2\right)} * N}{1 + C_P * e^{\left(-\frac{1}{2} * \left(\frac{\beta - \gamma}{\sigma}\right)^2\right)} * N} \quad (3b)$$

Here, the first term of the two equations describes logistic growth limited by carrying capacity of plant and pollinator, respectively. The second term of Eq. 3a represents a saturating effect aiming to limit the benefits that plant N receives from interacting with pollinator P as the density of P increases, which is governed by the per capita interaction strength $\mu(\gamma, \beta)$. In other words, as the density of P increases, the per capita benefit N receives from interacting with P decreases and eventually reaches a maximum value. This saturating effect is a common feature of mutualistic interactions, where the benefits one partner receives from the other eventually level off as the density of the partner increases (Holland et al., 2002; Okuyama & Holland, 2008). C_P , C_N denotes to the conversion coefficient for pollinator and plant, respectively.

2.1.3 Plant, pollinator, and Exploiter Interactions Model

First, I present a general model (i.e., Eq. 4a – 4c) for these three species, I extend the plant-pollinator model described above by including one exploiter in the network. The dynamics of the three species are given by the following per capita growth rate equations:

$$\frac{dN_i}{N_i dt} = r_{N_i} * \left(1 - \frac{\sum_{j=1}^n \alpha_{N_{ij}} * N_j}{K_{N_i}}\right) + \sum_{j=1}^n \frac{C_N * \mu(\gamma_i, \beta_j) * P_j}{1 + C_N * \mu(\gamma_i, \beta_j) * P_j} - \sum_{j=1}^n \frac{C_E * \mu(\lambda_i, \gamma_j) * E_j}{1 + C_E * \mu(\lambda_i, \gamma_j) * E_j} \quad (4a)$$

$$\frac{dP_i}{P_i dt} = r_{P_i} * \left(1 - \frac{\sum_{j=1}^n \alpha_{P_{ij}} * P_j}{K_{P_i}}\right) + \sum_{j=1}^n \frac{C_P * \mu(\beta_i, \gamma_j) * N_j}{1 + C_P * \mu(\beta_i, \gamma_j) * N_j} \quad (4b)$$

$$\frac{dE_i}{E_i dt} = r_{E_i} * \left(1 - \frac{\sum_{j=1}^n \alpha_{E_{ij}} * E_j}{K_{E_i}}\right) + \sum_{j=1}^n \frac{C_E * \mu(\lambda_i, \gamma_j) * N_j}{1 + C_E * \mu(\lambda_i, \gamma_j) * N_j} \quad (4c)$$

Here, N denotes to the population size of plant and P for pollinator, E denotes to the population size exploiter. The first term of the three equations describes logistic growth

limited by intrinsic growth rate and carrying capacity of plant and pollinator, respectively. The second term of Eq. 4a-4c represents a saturating effect aiming to limit the benefits between interacting species. The third term of 4a equation represents the negative effect from the exploiter on the plant growth.

Based on the general model above (i.e., Eq.4a-4c), I introduce an exploiter that would directly compete with the legitimate pollinator, for example, they have an overlap nesting place. The competition coefficient is denoted as α_{EP} , α_{PE} , respectively, as shown in Eq.5b and 5c. Other parameters used are listed in Table 2 Appendix.

$$\frac{dN}{Ndt} = r_N * \left(1 - \frac{N}{K_N}\right) + \frac{C_N * \mu(\gamma, \beta) * P}{1 + C_N * \mu(\gamma, \beta) * P} - \frac{C_E * \mu(\lambda, \gamma) * E}{1 + C_E * \mu(\lambda, \gamma) * E} \quad (5a)$$

$$\frac{dP}{Pdt} = r_P * \left(1 - \frac{P + \alpha_{PE} * E}{K_P}\right) + \frac{C_P * \mu(\beta, \gamma) * N}{1 + C_P * \mu(\beta, \gamma) * N} \quad (5b)$$

$$\frac{dE}{Edt} = r_E * \left(1 - \frac{E + \alpha_{EP} * P}{K_E}\right) + \frac{C_E * \mu(\lambda, \gamma) * N}{1 + C_E * \mu(\lambda, \gamma) * N} \quad (5c)$$

To explore which exploiters can coexist with the plant-pollinator network, I construct a model based on general model (4a-4c) without competition between exploiters and pollinators. Adverse effects on plant growth are shown as the last term of Eq. 6a. In this case, as there is one plant, one pollinator, and one exploiter, the equations can be simplified as Eq.6a, 6b, 6c.

$$\frac{dN}{Ndt} = r_N * \left(1 - \frac{N}{K_N}\right) + \frac{C_N * \mu(\gamma, \beta) * P}{1 + C_N * \mu(\gamma, \beta) * P} - \frac{C_E * \mu(\lambda, \gamma) * E}{1 + C_E * \mu(\lambda, \gamma) * E} \quad (6a)$$

$$\frac{dP}{Pdt} = r_P * \left(1 - \frac{P}{K_P}\right) + \frac{C_P * \mu(\beta, \gamma) * N}{1 + C_P * \mu(\beta, \gamma) * N} \quad (6b)$$

$$\frac{dE}{Edt} = r_E * \left(1 - \frac{E}{K_E}\right) + \frac{C_E * \mu(\lambda, \gamma) * N}{1 + C_E * \mu(\lambda, \gamma) * N} \quad (6c)$$

2.2 Evolutionary models description

2.2.1 Mutation fitness in the absence of exploiter

The evolutionary time scale analysis assumes that the community is at its ecological equilibrium population size based on adaptive dynamics theory (Brännström et al., 2013; Geritz et al., 1998). Mutation fitness of plants and pollinators in the absence of exploiter is written as W_{N_1} and W_{P_1} in Eq.7a and 7b, which represent the fitness of a given mutant.

In this case, the fitness function describes the per capita growth rate of an initially rare mutant in the environment set by the resident population (Brännström et al., 2013). The mutant trait γ' is a variant of the plant resident population. β' denotes the mutant trait of the pollinator resident population in this system.

$$W_{N_1}(\gamma', N^*, \beta, P^*) = r_{N_m} * \left(1 - \frac{N^*}{K_N}\right) + \frac{C_N * \mu(\gamma', \beta) * P^*}{1 + C_N * \mu(\gamma', \beta) * P^*} \quad (7a)$$

$$W_{P_1}(\beta', N^*, \gamma, P^*) = r_{P_m} * \left(1 - \frac{P^*}{K_P}\right) + \frac{C_P * \mu(\beta', \gamma) * N^*}{1 + C_P * \mu(\beta', \gamma) * N^*} \quad (7b)$$

Here, N^* , P^* values are given by the ecological Eq. 3a and 3b, respectively, by solving these two equations equal to zero. r_{N_m} , r_{P_m} are intrinsic growth rates of mutant populations of plants and pollinators. In this study, I assume that the mutant plant is rare, and its birth rate can be regarded as equal to the resident plant's birth rate by neglecting competition between mutants and resident.

2.2.2 Mutation fitness in the presence of exploiter

Mutation fitness of plants and pollinators in the presence of exploiter are written as W_{N_2} , W_{P_2} in Eq. 8a and 8b, which represent the fitness as experienced by a rare mutant.

$$W_{N_2}(\gamma', N^*, \beta, P^*, \lambda, E^*) = r_{N_m} * \left(1 - \frac{N^*}{K_N}\right) + \frac{C_N * \mu(\gamma', \beta) * P^*}{1 + C_N * \mu(\gamma', \beta) * P^*} - \frac{C_E * \mu(\lambda, \gamma') * E^*}{1 + C_E * \mu(\lambda, \gamma') * E^*} \quad (8a)$$

$$W_{P_2}(\beta', N^*, \gamma, P^*) = r_{P_m} * \left(1 - \frac{P^*}{K_P}\right) + \frac{C_P * \mu(\beta', \gamma) * N^*}{1 + C_P * \mu(\beta', \gamma) * N^*} \quad (8b)$$

Here, γ' and β' represent the trait value of the potential mutant plant and pollinator, respectively. N^* , P^* , E^* represent the population size at their equilibrium states, by solving Eq. 6a, 6b, 6c equal to zero. Other parameters can be found in Table 2 in the Appendix. These two evolutionary models aim to explore the long-term effects of exploiters on the system of the plant-pollinator, which is research question 3.

2.3 Simulation scenarios and analyses

This section will present simulation scenarios and analyses for plant-pollinator interactions and plant-pollinator-exploiter interactions, respectively, which includes ecological dynamics and evolutionary dynamics. Ecological dynamics include population dynamics and model stability analysis with different parameters. The purposes of ecological analysis are to check how the reference system works, and also the short-term effects of exploiters. The long-term effects of exploiters can be found by doing evolutionary analysis including fitness landscape, PIPs, trait evolution plot based on theory of adaptive dynamics.

2.3.1 Simulation scenarios

I consider one plant and one pollinator interaction, assuming that these two species are well adapted to the environment and the resource availability is adequate. Equations 3a and 3b are used to simulate the population dynamics of plant-pollinator interactions. In this simulation, the parameters $\gamma=1$, $\beta=1$ is used, which means the traits of the plant and its pollinator match perfectly. The `deSolve`, a R package, is used for the population dynamics simulations. For the other parameters see Table 2 in the appendix. For evolutionary dynamics, I simulate the fitness landscape and PIP based on the equation sets of 7a, and 7b. The `pracma`-package is used for the fitness landscape and PIP simulations. The initial conditions for fitness landscape and PIPs are both trait values $\gamma=1$, $\beta=1$.

I simulate population dynamics for the plant, pollinator and exploiter with different parameters, details shown in Table 1. In this model, I assume that there is no direct competition between pollinators and exploiters, see equations 6a – 6c. Based on this model, I have simulated three scenarios for population dynamics, as shown in Table 1 below. I use three different trait values of exploiter (referred as λ) for numerical simulations, including 1, 3, and 4, which means a full match of the proboscis's length and the depth of the corolla tube as the pollinator does, and intermediate match, and less match, respectively. There is another model that there is direct competition between the pollinators and the exploiters, with the competition coefficients ($\alpha_{EP}=0.5$, $\alpha_{PE}=0.6$), see equations 5a – 5c. The purpose of doing this is to check what type of exploiters can coexist with the plant-pollinator system.

Table 1 Simulation scenarios for the plant, its pollinator and the exploiter

Plant, its pollinator and exploiter interactions		
Simulation	Parameters	Comments
Population dynamics	$\gamma=1, \beta=1, \lambda=1$	See Fig.3. The purpose of these simulations is to check how the different trait values of exploiter affect the population dynamics of the plant and pollinator
	$\gamma=1, \beta=1, \lambda=3$	
	$\gamma=1, \beta=1, \lambda=4$	
	$\gamma=1, \beta=1, \lambda=4, \alpha_{EP}=0.5, \alpha_{PE}=0.6$	
Fitness landscape	$\gamma=1, \beta=1, \lambda=3$	See left plot in Fig. 7
	$\gamma=0,48, \beta=1, \lambda=3$	$\gamma=0,48$ is the trait value after the plant first evolution because of introduction of exploiter, see the right plot in Fig,7
PIP	$\gamma=1, \beta=1, \lambda=3$	See Fig. 8
Trait evolution plot	$\gamma=1, \beta=1, \lambda=3$	See Fig. 9

Trait evolution simulation implemented in R (see Appendix – Trait evolution implementation), the code models the coevolution of traits in a tri-trophic system, encompassing plants, pollinators, and exploiters. Utilizing the deSolve library, the simulation employs ordinary differential equations (ODEs) to capture population dynamics. Evolution is about the fitness-maximizing process. The first step of simulation is initializing the parameters for the evolutionary dynamics, like the starting trait values are 1,1,3 for the plant, pollinator and exploiter respectively, then calculating equilibrium population size for the plant, pollinator and the exploiter based on specified equations (Eq. 6a-6c). Then evaluating the fitness landscape for these three species, finding the trait values for the plant and pollinator at their peak fitness. The last step aims to save the trait values in the process of the trait evolution over multiple generations, incorporating mutations and selecting traits yielding positive population sizes. The method concludes with a visual representation of the evolving plant (γ) and pollinator (β) traits over generations. This simulation framework provides insights into the dynamic interplay of traits in ecological systems influenced by exploitation.

2.3.2 Analyses

First, I do the analysis of stability of the plant-pollinator model, by solving partial derivatives with respect to state variables N and P, which is written as $\frac{\partial f_1}{\partial N}$, $\frac{\partial f_1}{\partial P}$ for Eq. 3a, and $\frac{\partial f_2}{\partial N}$, $\frac{\partial f_2}{\partial P}$, for Eq. 3b. To derive the partial derivative with respect to variable N, then P is treated as a constant, and vice versa. See Appendix for more details of these partial derivatives expressions. I compute the Jacobian matrix of that equilibrium to determine if it is stable or not. Then, all derivatives are evaluated at the equilibrium point.

$$J = \begin{pmatrix} \frac{\partial f_1}{\partial N} & \frac{\partial f_1}{\partial P} & \frac{\partial f_2}{\partial N} & \frac{\partial f_2}{\partial P} \end{pmatrix} = (-0.2 \ 0.025 \ 0.027 \ -0.2) \quad (9)$$

Moreover, the stability of this community has been fulfilled by using saturated functional responses in Eq. 3a and 3b. To get the zero-growth isoclines for each species, I solved the differential Eq. 3a, 3b by setting them to zero in the R studio.

3. Results

3.1 Ecological dynamics

3.1.1 Plant and pollinator interactions

3.1.1.1 Population dynamics

Based on the simulation as described in section 2.3.1, the results reveal that the population size of the plant at its equilibrium state is 8.5, and the pollinator size is 8.2 (Fig.1).

The trajectory of plant-pollinator interactions begins with population size one and ends with the corresponding equilibrium population size for each species (i.e., the plant and its pollinator). In this plant-pollinator interaction, the model has an equilibrium point, i.e., the intersection of the plant isocline, pollinator isocline, and the trajectory, as shown in the lower plot of Fig.1. Eventually, two populations have reached an equilibrium state.

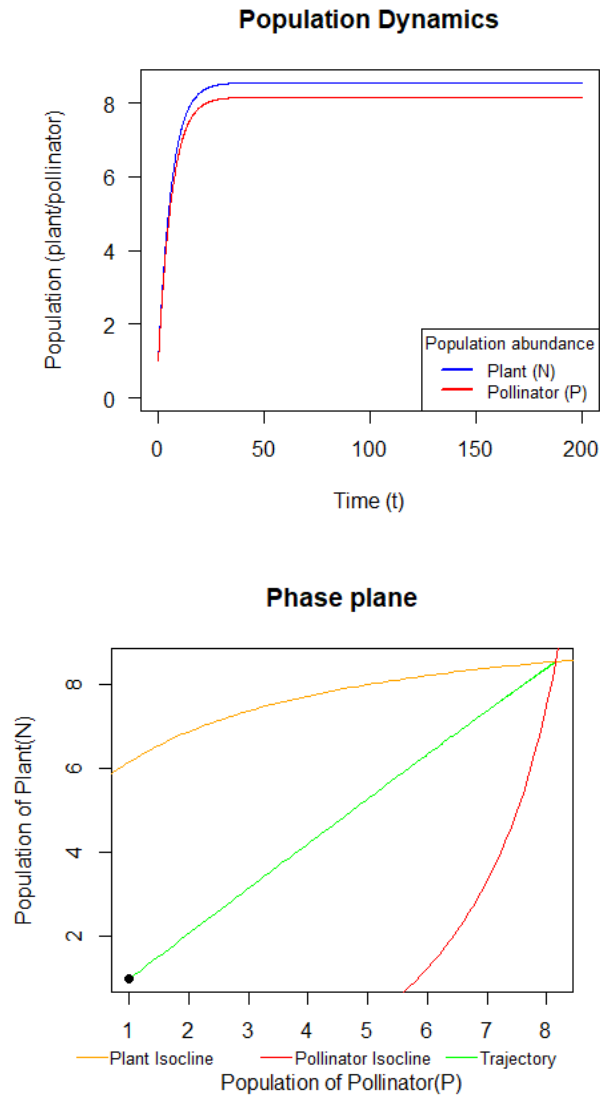


Figure 1 Population dynamics of plant-pollinator interactions in the absence of the exploiter. The upper plot illustrates the population abundance of plants and pollinators over time. The lower plot illustrates the phase plane of the plant-pollinator network. The black dot in Phase plane indicates the starting population size of the plant and the pollinator, i.e., 1. The intersection of the yellow, green, and red curve indicates the equilibrium point of this system.

The results in population dynamics indicate that the ecological equilibrium is indeed stable, that is the population abundance of the plant and its pollinator is level off after a certain generation. I also find this stability in a more formal way to evaluate the stability, which is by computing Eigenvalues as described in Method 2.3.2. Eigenvalues of the J matrix is -0.2259808 , -0.1740192 , as solved by Eq.9. Therefore, the equilibrium is stable as all eigenvalues of the Jacobian matrix have a negative real part.

3.1.2 Plant, pollinator, and exploiter interactions

3.1.2.1 RQ1 In which conditions can the exploiter co-exist with the plant-pollinator community

Eq.5a, 5b, and 5c represent the interactions between three species. In this model, I assume that there is no direct competition between pollinators and exploiters. Based on this model, I have simulated three scenarios, as shown in Table 1-Population dynamics. I use three different trait values of exploiter (referred to as λ) for numerical simulations, including 1, 3, and 4, which means a full match between the trait values of the plant and exploiter, an intermediate match, and less match, respectively.

As shown in Fig.2 A), when the exploiter trait λ is 1, the exploiter becomes the dominant population in this community. The intermediate abundance species is the pollinator. The exploitation from the exploiter on plants leads to the smallest abundance of the plant, which is significantly smaller compared to the system in the absence of the exploiter (as shown in Fig.1).

The population abundance of the exploiter at ecological equilibrium decreases when the trait value of λ increase to 3 and 4, which can be seen in Fig.2 B) and C), respectively. In contrast, plant abundance increases as the trait value of the exploiter increases, which is as shown in Fig.2 B) and C).

Lastly, the exploiter cannot co-exist with the plant-pollinator community when it competes for resources or nest places with the pollinator, and the plant exploitation is low with trait value 4. As shown in Fig.2 D) exploiter population abundance is steadily approaching zero, but still larger than 0; thus, indicating it cannot co-exist with the plant-pollinator community in this situation.

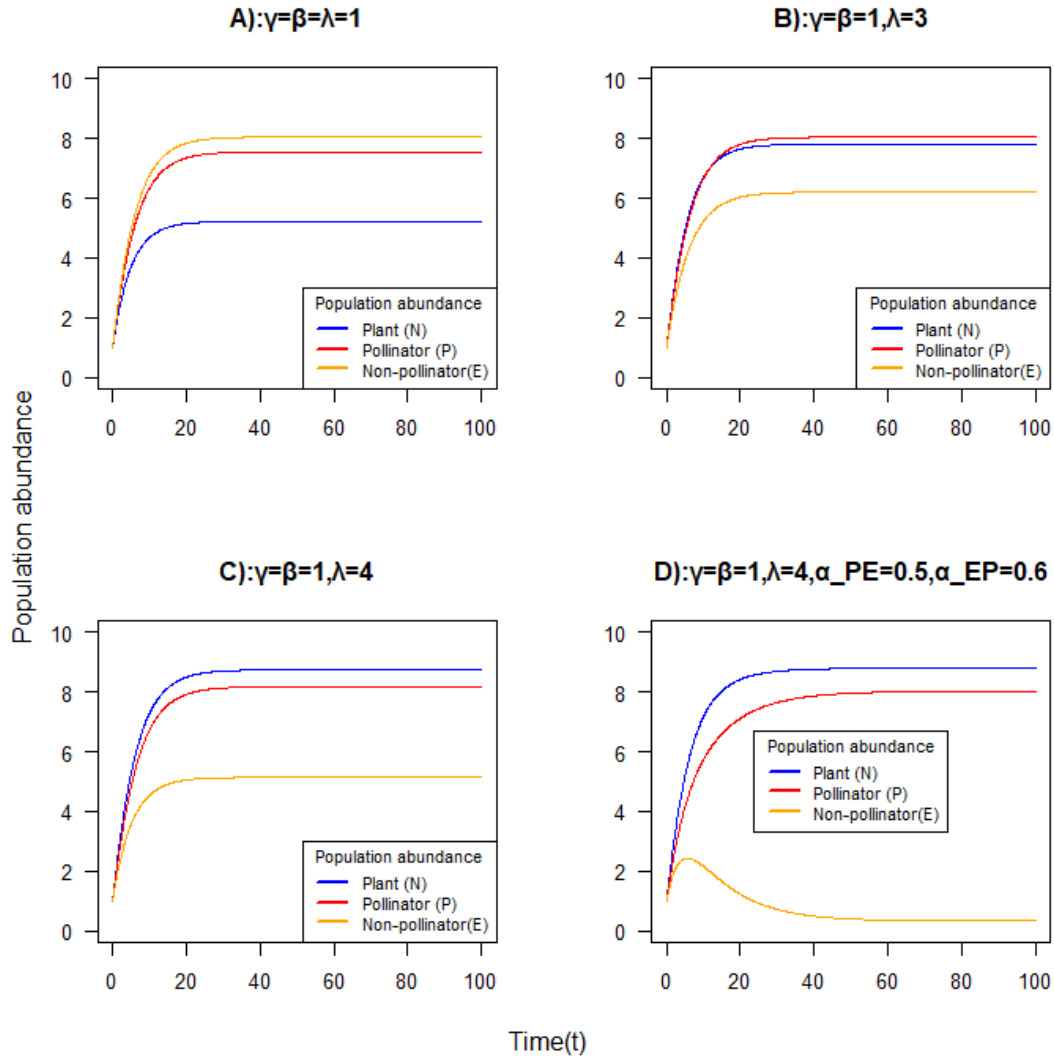


Figure 2 Numerical simulation with different trait values of exploiter. γ denotes the plant trait, i.e., flower size, and is set to 1. β denotes the pollinator trait, i.e., proboscis length, and is set to 1. λ denotes the exploiter trait, proboscis length, and is set to 1 in A), 3 in B), and 4 in C) and D). Each sub-plot illustrates the population sizes changing over time with the specified values. Particularly, D) illustrates the population size change with competition coefficient α_{PE} 0.5 and α_{EP} 0.6.

3.1.2.2 RQ2-3 The effect of exploiter on the plant-pollinator interactions

The population sizes of the plant and its pollinator at their equilibrium states in Fig.1 and Fig.2A are extracted to quantify the effects of the exploiter in a histogram plot. As shown in Fig.3, the population size of the plant and the pollinator is 8.55 and 8.15 (Fig.1), respectively in the absence of an exploiter and reduced to 5.46 for plants and 7.6 for pollinators after the exploiter is introduced. Obviously, the population size reduction of the plant is more significant, mainly because the effects of the exploiter on the plant are direct, while the effect on the pollinator is indirect.

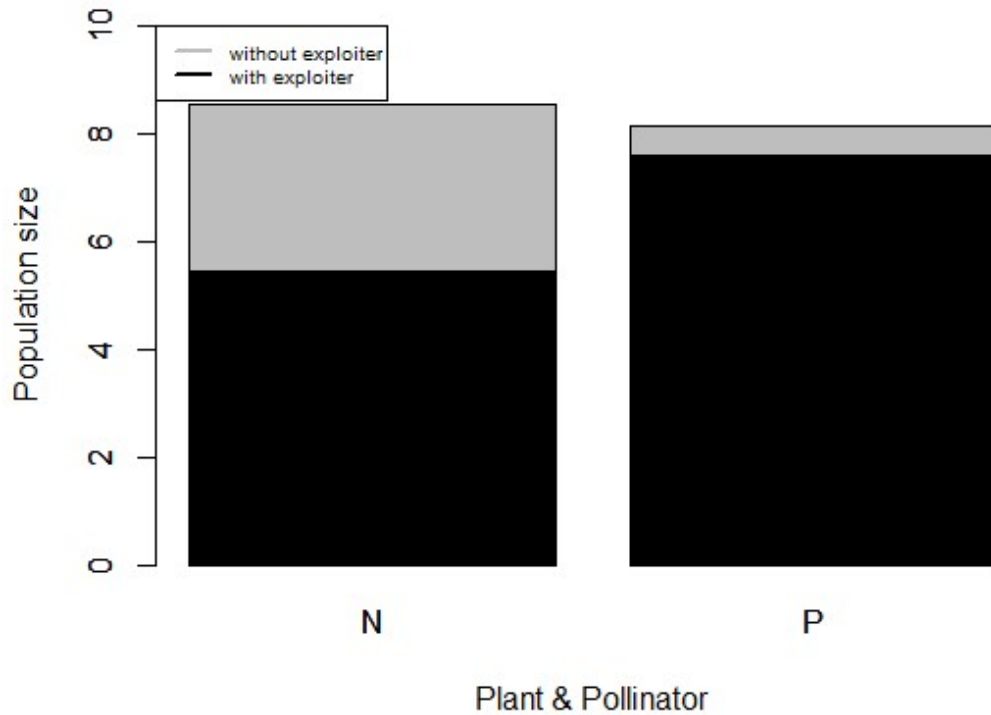


Figure 3 Population size changes after the introduction of exploiter into plant-pollinator interactions. N and P represent the plant and the pollinator, respectively. The gray histogram represents plant and pollinator population abundance in the absence of exploiter. The black histogram represents the population abundance of plants and pollinators in the presence of exploiter.

3.2 Evolutionary dynamics

3.2.1 Plant and pollinator interactions

In the model of plant-pollinator (i.e., Eq. 3a and 3b), the initial conditions are set to the optimal adaptation in traits for the two interacting species, which is shown in Fig.4. The fitness is maximized for plants and pollinators when the trait values (trait β and γ) are 1. Thus, there are no mutants of plants or pollinators that can invade this community. The system reaches an evolutionary stable state (ESS) when the mutualistic interactions are maximized.

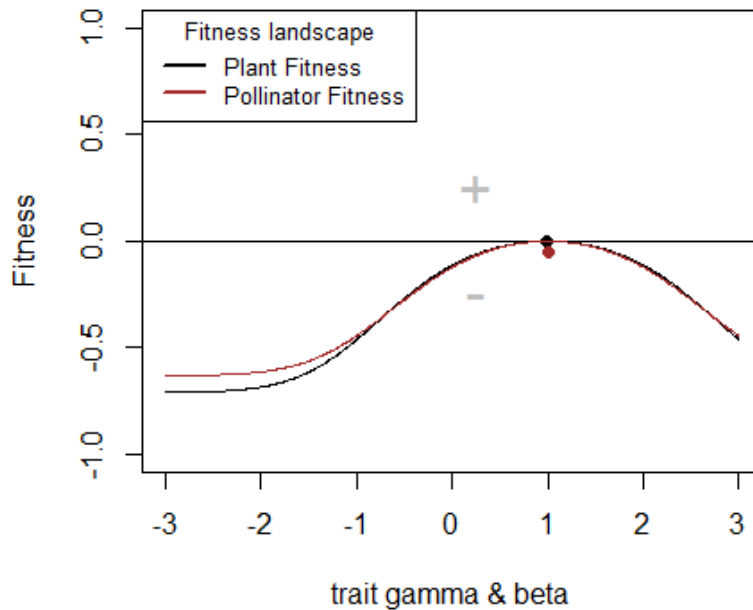


Figure 4 Fitness landscape of plants and pollinators in the absence of exploiter. The black dot implies the corresponding trait value of the plant when the system is at its fitness maximum, i.e., trait value equals 1. Analogously, the brown dot means the corresponding trait value of the pollinator when the system is at its fitness maximum, which equals 1. The black and brown dots should be overlapped, shifting down a bit for pollinator clarification. The plus and minus signs simply indicate the fitness values are positive and negative respectively.

I also performed a Pairwise invasibility plot (referred to as PIP) analysis on the plant resident population, as shown in Fig.5, which illustrates a series of invasions in a certain range trait value of the resident population. PIP describes the fitness of all combinations of mutants and residents with certain trait values. When the fitness value is positive, it means the mutant can invade the ecological equilibrium of the resident plant, and vice versa. In Fig.4, all possible pairs of resident plant and mutant plant have trait values ranging from -3 to 3. The intersection of contour lines is at the 0 point of fitness; corresponding trait values for plant and pollinator are 1. Hence this intersection is the ESS for this system. The result is consistent with the fitness landscape, as shown in Fig.4. More specifically, the trait values are 1 for both interacting species. It is an endpoint of evolution if there is no disturbance.

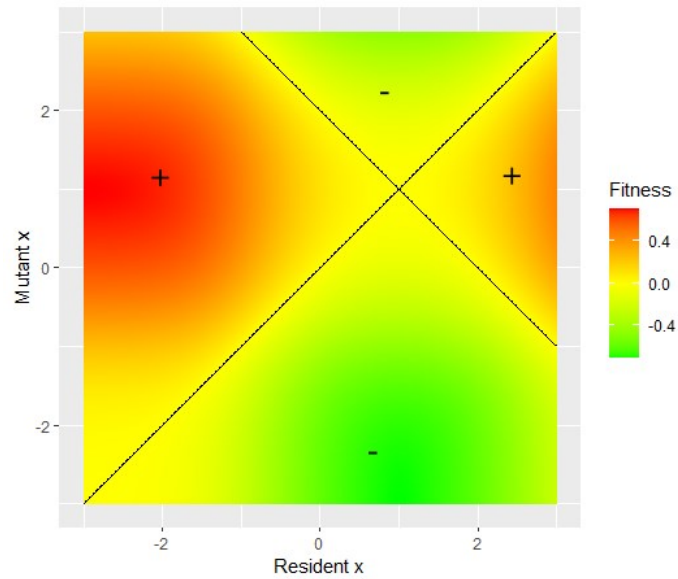


Figure 5 Pairwise invasibility plot (PIP) of the plant in the absence of exploiter. The green areas with minus signs show when the mutant cannot invade the resident community. In contrast, the red regions with plus signs show when the mutant plant can invade the community. The border lines, i.e., contour lines, indicate that fitness equals 0. The intersection of borderlines represents a singular evolutionary point.

As shown in Fig.4 and Fig.5, the trait evolution reveals there is no mutant plant or pollinator that can invade this system based on the assumption the plant and pollinator are well adapted to the environment. Also, there is no disturbance to this system in theory, and the trait values of plant and pollinator could keep the optimal values, i.e., the original trait values, 1 for both of them.

3.2.2 Plant, pollinator, and exploiter interactions

The plant's fitness landscape changed when the exploiter with trait value 3 is introduced into the plant-pollinator system. The initial plant fitness landscape shows an ESS state as Fig.4. It changed after the co-existence with an exploiter, as shown in the left plot in Fig.6. More specifically, the optimal trait value for plants diverges from the exploiter. Also, the fitness maximal corresponding to the optimal trait value of the plant turns to 0.48 from 1, as the black dot shown in left plot of Fig.6. However, the pollinator's fitness landscape does not change to the same extent as the plant, mainly because the exploiter does not directly compete with the pollinator, which is shown as the brown curve in the left plot of Fig.6.

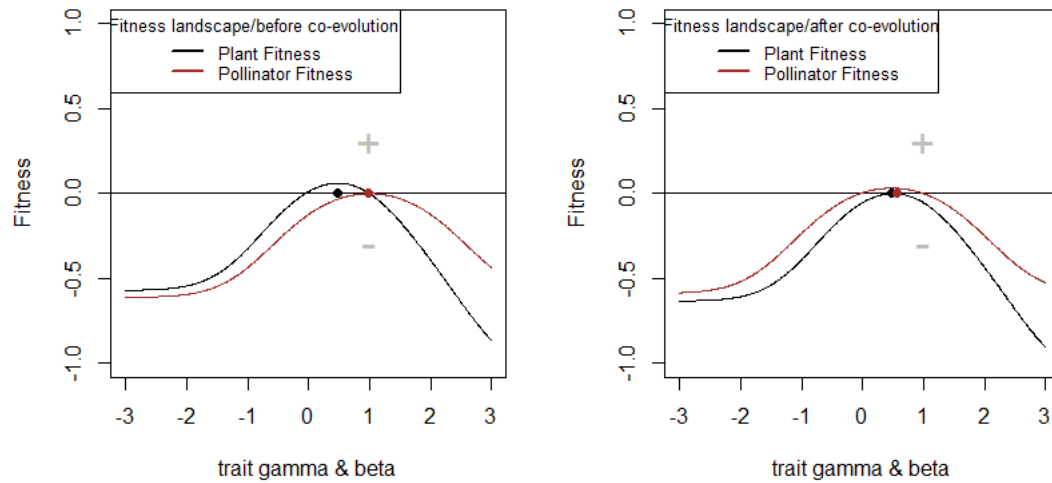


Figure 6 Fitness landscape of the plant and its pollinator in the presence of an exploiter. The left plot indicates the fitness of the plant and its pollinator in the presence of an exploiter with trait value 3. The right plot indicates the first time the plant evolved, after the introduction of the exploiter. The plus sign indicates the fitness value is positive, and the minus sign indicates the fitness value is negative. The black dot shows the corresponding trait value of the plant when the plant is at its fitness maximum. Similarly, the brown dot shows the trait value when the pollinator is at its fitness maximum; these two dots are supposed to be overlapped, shifting for clarification.

Interestingly, when the plant trait evolved, the pollinators' fitness landscape would change along with it. The optimal trait value for the pollinator evolves in line with the plant, as shown in the right plot of Fig.6. In other words, the peak value of the pollinator's fitness has changed in comparison to the fitness of the pollinator in the left plot of Fig.6. Evolution is a fitness maximizing process, evolutionary changes moving upwards in the fitness landscape. Basically, the two plots in Fig.6 indicate the static moments of evolutionary dynamics. And the whole co-evolution process of the plant and its pollinator can be seen in the section on Trait evolution below.

Mutation fitness is defined in Eq. 9a and 9b. Success invasions represent positive fitness values with mutant trait values in the background of the resident population trait value. In the presence of the exploiter, PIP analysis is given in Fig.7. The trait value of the plant is changed after introducing the exploiter with a trait value of 3, and is 0.48 for the plant. This change implies that trait evolution decreases from 1 to 0.48 where the intersection is.

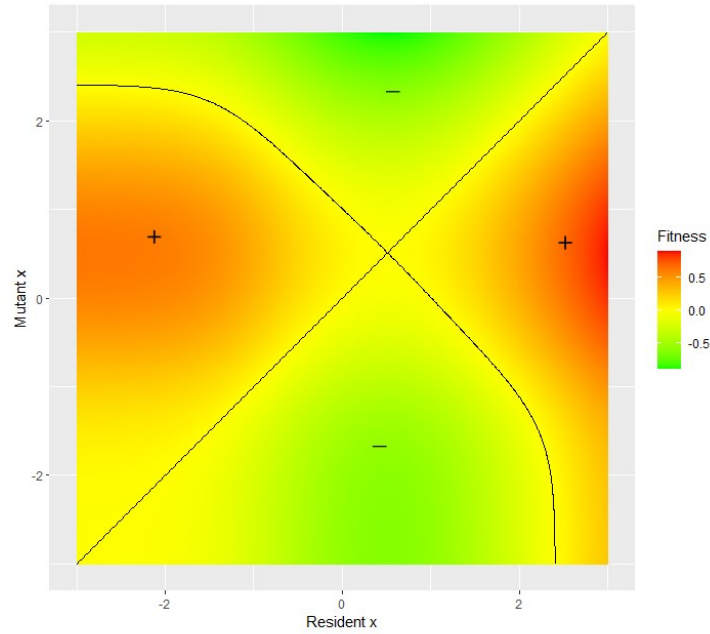


Figure 7 Pairwise invasibility plot of the plant trait in the presence of exploiter with trait value 3. The green areas with a minus sign mean the mutant cannot invade the resident community. In contrast, the red regions with a plus sign mean the mutant plant can invade the community. The border lines, i.e., contour lines, indicate that the fitness equals zero.

I present the trait evolution for plants and pollinators in the presence of an exploiter in Fig.8. The starting values for both plant and pollinator are set to 1, evolving away from the trait value of exploiter, i.e., 3, until community ESS. More specifically, the plant evolves to deter the exploiter. As we can see from the black curve in Fig.8, it declines from 1 to approximately -2. The pollinator evolves in the same way as the plant. That shows a co-evolution pattern for plants and pollinators, and the trait values evolve to a specific value (about -2) where the exploitation from the exploiter is weak enough. Therefore, the exploiter could not destabilize the mutualistic interactions between plants and pollinators. In this case, the exploiter plays a selective pressure in trait evolution.

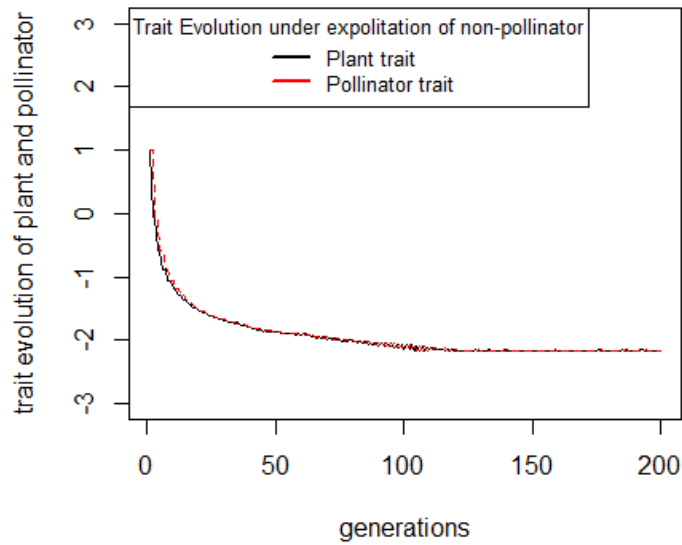


Figure 8 Trait evolution of plant and pollinator in the presence of exploiter. The starting point of the traits is 1 for both the plant and the pollinator. The trait value of the exploiter is always 3 in this system.

4. Discussion

4.1 Coexistence of exploiters with plant and pollinator interactions (RQ1)

In this study, I focus on species interactions based on the matching traits of plant and pollinator, and I model a positive feedback loop between plant and pollinator. The results reveal that the fitness of plants and pollinators is maximized by the mutual benefits from interacting partners, assuming a perfect match between the trait of the plant and pollinator, for example, the trait like the probosci's length of the pollinator and the corolla tube depth of the flower, they are matching well in space and size. Also, the high benefits flow between plant and pollinator maintains the system reaching evolutionary stability if there are no disturbances or resource availability problems. The research conducted by Holland supports these results when the mutualistic benefits are high with low cost for receiving pollination service (Holland et al., 2004). Moreover, the results of this study reveal that exploiters can indeed coexist with the plant-pollinator network under exploitation when there is no direct competition between the pollinator and exploiter. The finding aligns with ecological suggesting that in scenarios of balanced resource utilization and heterogeneous niches, exploiters might find their place within the ecosystem without causing complete disruption (Chesson, 2000). The observed coexistence sheds light on the adaptability of ecological network to the presence of exploiters. Similarly, one more paper also reveals that the stable

coexistence of plant, pollinator, and exploiter would exploit plants and can be obtained with balanced mutualism between plant and pollinator and antagonistic interactions between plant and exploiter (Yacine & Loeuille, 2022).

4.2 *The effects of exploiters (RQ2&RQ3)*

I discover that the abundance of plants and pollinators decreases as the exploiter matches well enough to the plant trait, which mirrors the findings from Yacine and Loeuille (Yacine & Loeuille, 2022). The consumption of exploiter has reduced the reproductive success of the plant. The direct exploitation of plants leads to the fitness of plants decreasing. Empirical research showed that legitimate pollinators could detect the reduced volume of nectar in the fresh flowers by UV reflection from flower spurs, or the scents linger in the chamber of flowers by the nectar thieves affect the behavior of pollinators (Weiss, 1991; Zhang et al., 2014). Thereby, fewer visitations of pollinators would reduce reproductive success, and the effect on the pollinator after introducing exploiter into this community is linked to the population abundance reduction of plants, showing the indirect impacts on the growth of the pollinator.

In the long run, the exploiter would not destabilize the mutual relationship between plant-pollinator. Specifically, the exploiter acts like a selective pressure to drive the traits co-evolution of plant and pollinator. A concrete example is the co-evolution of long proboscides and deep corolla tubes, which explains the evolutionary process is driven by resource competition and pollination limitation (Rodríguez-Gironés & Llandres, 2008). Moreover, Fenster et al. found that some plant species had evolved floral traits that were not only tailored to their primary pollinators (Fenster et al., 2004) but also deterred the exploiter from visiting. For example, the plant species ragged robin (*Lychnis flos-cuculi*) had evolved a highly curved flower shape that was difficult for non-pollinating insects to enter (Baenziger et al., 2008).

Interestingly, a concept of partner manipulation, wherein one partner influences the behavior or traits of the other, often to optimize the mutualistic interaction, was mentioned in research of Nepi and colleagues (Nepi et al., 2018). Similarly, the pollinator would co-evolve with the plant, aiming to maximize the benefits of mutualism in this study. A fundamental aspect of obligate mutualism is the co-evolutionary process. The research conducted by Bronstein (Bronstein, 2009) provides insights into the evolutionary dynamics of mutualistic relationships and the mechanisms that underpin their stability. It discusses how mutualisms can become evolutionarily stabilized over time, which corroborates my findings of the co-evolution of the plant and its pollinator.

5. Conclusion

The eco-evolutionary implications of exploiters on mutualistic interactions between plants and pollinators are significant. I mainly focused on the effects of exploiters on the mutualistic interactions between plants and pollinators. Results include fitness landscape, PIPs, and trait evolution. The principal findings of this study showed that exploiters can co-exist with the plant-pollinator when there is no direct competition between the pollinator and exploiter, and exploiters decrease the population abundances of both plants and pollinators in the short term, further revealing the plant and pollinator coevolution is driven by the exploitation of exploiter based on the constructed models and adaptive dynamics framework. This work improves the understanding of how mutualistic interactions have been maintained in the context of exploitation of exploiters.

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I would also like to thank my husband, Qunying, for his constant support and encouragement. His love and belief in me motivated and inspired me throughout my studies. I am also grateful for the joy and inspiration my daughter Elina has brought to my life during this time. Her innocent smiles, laughter, and the precious moments we shared together provided me with the motivation and happiness to overcome the challenges and complete this thesis. Thank you both for being my pillars of strength and for enriching my journey.

Thank you all for being a part of this journey with me.

Appendix

Parameters description

Table 2 List all model parameters and variables with their biological meaning and values used in the simulations.

Variables and parameters		Biological meaning	Default Value
Variables	P	Pollinator population abundance	1
	N	Plant population abundance	1
	E	Exploiter population abundance	1
Interaction strength	$\mu(\gamma, \beta)$	benefits of Pollinators on plant population growth	
	$\mu(\beta, \gamma)$	benefits of plant on pollinator population growth	
	$\mu(\lambda, \gamma)$	benefits of plant on exploiter population growth	
Other ecological parameters	K_N	Carrying capacity of plant	5
	K_P	Carrying capacity of pollinator	5
	K_E	Carrying capacity of exploiter	5
	r_N	Plant intrinsic growth rate	1
	r_P	Pollinator intrinsic growth rate	1
	r_E	Exploiter intrinsic growth rate	1
	C_N	Plant conversion coefficient	0.4
	C_P	Pollinator conversion coefficient	0.3
	C_E	exploiter conversion coefficient	0.2
	γ	Plant trait value	1

β	Pollinator trait value	1
λ	Exploiter value	3
σ	Niche width	1
α_{PE}	competition coefficient of the pollinator on exploiter	0,5
α_{EP}	competition coefficient of exploiter on pollinator	0,6

Trait evolution implementation

```

###evolutionary dynamics
###Parameter setting###
rm(list = ls())
#Library used to solve ode
library(deSolve)
require("pracma")

rN <- 1 #intrinsic growth rate
rP <- 1
rE <- 1
KN <- 5 #carrying capacity
KP <- 5
KE <- 5
###Initial conditions###
N0 <- 1 #initial population size
P0 <- 1
E0 <- 1
gamma <- 1 # traits values, plant 0.34 optimal trait
beta <- 1 # traits values, pollinator
zee <- 2# traits values, exploiter default 5, test with 3 4
CE <- 0.2 # conversion coefficient
CN <- 0.3
CP <- 0.2
sigma <- 1

###Simulation options###
#Simulation running time
time_end <- 200
# vector containing simulation time
time_vect <- c(0,1e+10)

```

```

####Population dynamics inputs for ODE solver to calculate the eq pop sizes####
Params <- list(rN = rN, rP = rP, rE = rE, KE = KE, KN = KN, KP = KP,
              CN = CN, CP = CP, CE = CE, sigma = sigma, zee = zee)
R_vect <- c(N = N0, P = P0, E = E0) #list of population abundances

per_capita_growth <- function(t, R_vect, Params) {
  N <- R_vect[1] # extracting populations size from vector
  P <- R_vect[2]
  E <- R_vect[3]
  dNdtN <- rN *(1 - N / KN) + exp(-1/2*((gamma-beta)/sigma)^2)*P*CN /
(1+CN*P*exp(-1/2*((gamma-beta)/sigma)^2)) - CE*exp(-1/2*((zee-
gamma)/sigma)^2)*E / (1+CE*exp(-1/2*((zee-gamma)/sigma)^2)*E) #Growth rate
calculation
  dPdtP <- rP *(1 - P / KP) + CP*exp(-1/2*((beta-gamma)/sigma)^2)*N / (1+ CP*exp(-
1/2*((beta-gamma)/sigma)^2)*N)#Growth rate calculation
  dEdtE <- rE *(1 - E / KE) + CE*exp(-1/2*((zee-gamma)/sigma)^2)*N / (1+CE*exp(-
1/2*((zee-gamma)/sigma)^2)*N)
  list(c(dNdtN, dPdtP, dEdtE)) # output the resulting vectors in a list
}

rootfun <- function(t, R_vect, Params) {
  dstate <- unlist(per_capita_growth(t, R_vect, Params))
  return(sum(abs(dstate)) - 1e-10)
}

##### above Neq Peq Eeq
# compute fitness,plant

Xresmut_N <- meshgrid(seq(-3, 3, by = 0.01))
Xres_N <- Xresmut_N$X
Xmut_N <- Xresmut_N$Y

##compute fitness curve for pollinator
Xresmut_P <- meshgrid(seq(-3, 3, by = 0.01))
Xres_P <- Xresmut_P$X
Xmut_P <- Xresmut_P$Y

save_update_gamma_beta <- function(n_loop) {
  v_gamma = rep(NA, n_loop)
  v_beta = rep(NA, n_loop)
  v_gamma[1] <- 1
  v_beta[1] <- 1
}

```

```

gamma_mutation <- NA
beta_mutation <- NA
for(i in 2:n_loop){
  #calculate the equilibrium pop sizes for interacting species, N, P, E
  out <- ode(y=R_vect,times=time_vect, func=per_capita_growth, parms = Params,
rootfun = rootfun,
  method = "lsodar")
  Neq <- out[2,2]
  Peq <- out[2,3]
  Eeq <- out[2,4]

  # Calculate fitness N, P
  fitness_landscape_N <- rN *(1 -Neq / KN) + exp(-1/2*((Xmut_N-
beta)/sigma)^2)*Peq*CN / (1+CN*Peq*exp(-1/2*((Xmut_N-beta)/sigma)^2)) -
CE*Eeq*exp(-1/2*((zee-Xmut_N)/sigma)^2) / (1+CE*Eeq*exp(-1/2*((zee-
Xmut_N)/sigma)^2))
  fitness_landscape_P <- rP *(1 - Peq / KP) + CP*exp(-1/2*((Xmut_P-
gamma)/sigma)^2)*Neq / (1+CP*exp(-1/2*((Xmut_P-gamma)/sigma)^2)*Neq)

  max_index_g <- which.max(fitness_landscape_N)
  gamma_optimal <- Xmut_N[max_index_g]# Ess point # gamma_optimal = 0.34
  gamma_mutation <- rnorm(1,gamma_optimal,0.005)
  N <- rN *(1 -Neq / KN) + exp(-1/2*((gamma_mutation-beta)/sigma)^2)*Peq*CN /
(1+CN*Peq*exp(-1/2*((gamma_mutation-beta)/sigma)^2)) - CE*Eeq*exp(-1/2*((zee-
gamma_mutation)/sigma)^2) / (1+CE*Eeq*exp(-1/2*((zee-
gamma_mutation)/sigma)^2))
  if (N >0){
    v_gamma[i] = gamma_mutation
    gamma <- gamma_mutation
  }else{
    v_gamma[i] = gamma_optimal
    gamma <- gamma_optimal
  }
}

### Find optimal beta from fitness P
max_index_b <- which.max(fitness_landscape_P)
beta_optimal <- Xmut_P[max_index_b]# Ess point beta optimal will evolve to
gamma optimal
beta_mutation <- rnorm(1,beta_optimal,0.005)
P <- rP *(1 - Peq / KP) + CP*exp(-1/2*((beta_mutation-gamma)/sigma)^2)*Neq /
(1+CP*exp(-1/2*((beta_mutation-gamma)/sigma)^2)*Neq)
if (P >0){

```

```

    v_beta[i] = beta_mutation
    beta <- beta_mutation
  }else{
    v_beta[i] = beta_optimal
    beta <- beta_optimal
  }
}

list(v_gamma, v_beta)
}

output <- save_update_gamma_beta(200)

gamma_v <- unlist(output[1])

beta_v <- unlist(output[2])
par(mfrow = c(1,1))

plot(gamma_v[1:200], type = "l", col= "black",ylim = c(-3,3), xlab = "generations",
ylab="trait evolution of plant and pollinator")
lines(beta_v[1:200],lty = 2,col="red")
legend("topleft", legend = c("Plant trait", "Pollinator trait"),
col = c("black", "red"), cex = 0.8, lwd = 2,
title = "Trait Evolution under exploitation of non-pollinator")

```

Partial derivative

The partial derivative with respect to N, P for Eq.3a is written as $\frac{\partial f_1}{\partial N} \frac{\partial f_1}{\partial P}$, respectively. Similarly, the partial derivatives with respect to N and P for Eq.3b are written as $\frac{\partial f_2}{\partial N} \frac{\partial f_2}{\partial P}$, respectively, as shown below. N and P values are the equilibrium population size for plants and pollinator in these equations

$$\frac{\partial f_1}{\partial N} = -(rN * (1/KN))$$

$$\frac{\partial f_1}{\partial P} = \frac{\exp(-1/2 * ((\gamma - \beta)/\sigma)^2) * CN / (1 + CN * P * \exp(-1/2 * ((\gamma - \beta)/\sigma)^2)) - \exp(-1/2 * ((\gamma - \beta)/\sigma)^2) * P * CN * (CN * \exp(-1/2 * ((\gamma - \beta)/\sigma)^2)) / (1 + CN * P * \exp(-1/2 * ((\gamma - \beta)/\sigma)^2))^2}$$

$$\frac{\partial f_2}{\partial N} = \frac{\exp(-1/2 * ((\beta - \gamma)/\sigma)^2) * CP / (1 + N * CP * \exp(-1/2 * ((\beta - \gamma)/\sigma)^2)) - \exp(-1/2 * ((\beta - \gamma)/\sigma)^2) * N * CP * (CP * \exp(-1/2 * ((\beta - \gamma)/\sigma)^2)) / (1 + N * CP * \exp(-1/2 * ((\beta - \gamma)/\sigma)^2))^2}$$

$$\frac{\partial f_2}{\partial P} = -(rP * (1/KP))$$

```

dndtn <- -(rN * (1/KN))
dndtp <- exp(-1/2 * ((gamma - beta)/sigma)^2) * CN/(1 + CN * P * exp(-1/2 * ((gamma -
beta)/sigma)^2)) - exp(-1/2 * ((gamma - beta)/sigma)^2) * P * CN * (CN * exp(-1/2 * ((gamma -
beta)/sigma)^2))/(1 + CN * P * exp(-1/2 * ((gamma - beta)/sigma)^2))^2
dndte <- -(exp(-1/2 * ((zee - gamma)/sigma)^2) * CE/(1 + CE * E * exp(-1/2 * ((zee -
gamma)/sigma)^2)) - exp(-1/2 * ((zee - gamma)/sigma)^2) * E * CE * (CE * exp(-1/2 * ((zee -
gamma)/sigma)^2))/(1 + CE * E * exp(-1/2 * ((zee - gamma)/sigma)^2))^2)
dpdtn <- exp(-1/2 * ((beta - gamma)/sigma)^2) * CP/(1 + N * CP * exp(-1/2 * ((beta -
gamma)/sigma)^2)) - exp(-1/2 * ((beta - gamma)/sigma)^2) * N * CP * (CP * exp(-1/2 * ((beta -
gamma)/sigma)^2))/(1 + N * CP * exp(-1/2 * ((beta - gamma)/sigma)^2))^2
dpdtp <- -(rP * (1/KP))
dpdte <- 0
dedtn <- exp(-1/2 * ((zee - gamma)/sigma)^2) * CE/(1 + N * CE * exp(-1/2 * ((zee -
gamma)/sigma)^2)) - exp(-1/2 * ((zee - gamma)/sigma)^2) * N * CE * (CE * exp(-1/2 * ((zee -
gamma)/sigma)^2))/(1 + N * CE * exp(-1/2 * ((zee - gamma)/sigma)^2))^2
dedtp <- 0
dedte <- -(rE * (1/KE))

```

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