

MODELLING THE EFFECTS OF SUBSTITUTING POLLINATORS IN DECLINE

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Abstract

While pollination is essential for many plant species and ecosystem functions, pollinator populations worldwide are declining. This decline is largely due to abiotic changes in the environment: climate change and other anthropogenic impacts, such as pesticides and land use change. Against this background, I investigate the effects of introducing a non-native pollinator species (substituting invader”) in a pollination network with declining resident pollinators. In particular, I ask 1) whether interspecific competition is a necessary driver for local extinctions of resident pollinator species after environmental changes; and 2) how much the pollination benefits for the resident plants differ between a pollination network including a substituting invader and a network without. To answer this, a standard Lotka-Volterra competition model is extended with terms accounting for mutualism (pollination) and adaptation to the environment. I model a community of two resident plants, as well as two resident pollinators and a substituting invader. I find that interspecific competition is a necessary driver for local pollinator extinction following an abiotic change in the environment. The competitive effect of the substituting invader on resident pollinators is therefore negative, although a minor indirect benefit is observed for one resident pollinator species. However, the resident plants benefit from the introduction of a substituting invader, which leads to a small relative change in the plant population numbers.

Populärvetenskaplig sammanfattning

I denna rapport innebär *pollinering*, eller *pollination*, att ett djur transporterar pollen från en växt till en annan växt. Djuren som utför pollineringen (ofta insekter) kallas *pollinerare*, eller *pollinatörer*, och växterna sägs bli *pollinerade*. Det uppskattas att omkring 90% av alla kända växtarter, och 35% av all odling av grödor, behöver pollinering för att växterna ska kunna sprida sina fröer och föröka sig. Pollineraren får ofta näring i form av nektar från växterna, och gynnas därmed också av pollineringen. Eftersom pollinering fyller en viktig funktion, är många forskare oroad över att pollinerare världen över minskar i antal. Det antas bero till stor del på klimatförändringar och annan mänsklig påverkan, såsom bekämpningsmedel och förändrad markanvändning.

I detta kandidatarbete modelleras effekterna av att introducera ej inhemska pollinerare i ekosystem där de inhemska pollinerarna minskar i antal på grund av förändringar i sin livsmiljö. Det är tänkbart att en ej inhemsk pollinerare med lämpliga egenskaper ("ersättande pollinerare") skulle kunna tillgodose en fortsatt fungerande pollinering av växterna i ekosystemet, när de inhemska pollinerarna har blivit färre. Jag skapar därför en matematisk modell för tillväxten av populationerna för växter och pollinerare. Växter och pollinerare interagerar genom pollinering, och mellan växter respektive pollinerare sker en konkurrens om resurser. Exempel på sådana resurser är lämpliga växtplatser eller pollinatörernas föda och boplatser. Modellen tillämpas på fem arter: två inhemska växter samt två inhemska pollinerare och en ersättande pollinerare. Jag jämför fallet när miljön ändras, men ingen ersättande pollinerare införs, med fallet då miljön ändras **och** en ersättande pollinerare införs. Genom denna jämförelse utreder jag 1) om konkurrens mellan pollinerande arter är nödvändig för att de ska utrotas lokalt i samband med att deras livsmiljö förändrats. Jag undersöker även 2) om de inhemska växterna gynnas olika mycket med eller utan ersättande pollinerare.

Modellen visar att 1) konkurrens mellan pollinerande arter är nödvändig för att pollinerande arter ska utrotas vid miljöförändring. Dessutom visar modellen att 2) en ersättande pollinerare gynnar de inhemska växterna när de två inhemska pollinerarna minskat i antal. En ersättande pollinerare kan alltså påverka inhemska växter positivt, medan inhemska pollinerare påverkas negativt eller till och med utrotas lokalt. För att undersöka om det är gynnsamt att införa en ersättande pollinerare är det därmed viktigt att väga de positiva effekterna för växter mot de negativa effekterna för pollinerare. Ett viktigt steg för en sådan jämförelse är att studera och modellera fler olika nätverk av pollinerare och växter för att besvara hur de positiva och negativa effekterna beror på arternas egenskaper i det nätverk som undersöks. Det bör ha i åtanke att det finns stora risker med att en ej inhemsk art införs av människor, med tanke på att vi inte kan förutse exakt hur det kommer påverka ekosystemet. Därför är det viktigt att en ersättande pollinerare enbart införs om det är väl beforskat och om det förväntas vara mer gynnsamt

än andra alternativ. I första hand bör det undersökas ifall en liknande positiv effekt kan uppnås utan mänskligt ingrepp eller med ingrepp utan att en ej inhemska art införs.

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1 Introduction

1.1 Background

Pollination is a common mutualistic interaction between plants and animals (together constituting a *pollination network*), most of them insects [9], which underpins reproduction and yields of many wild plants and crops [4]. Pollination plays an important role in ecosystem functioning [4]; out of all angiosperm species, 87.5% [9] to 90% [4] depend on pollination for their reproduction. In addition to its importance for wild plant diversity, it is also estimated that 35% of crop production comes from animal-pollinated plant species [4]. Not only the number of pollinators is important for ecosystem functioning, but also the diversity of pollinator species. For example, a decreased diversity has been shown to lead to reduced process rates and stability in ecosystems, which suggests that the presence of different pollinator species underpins many ecosystem functions [2].

Because of the dependence of ecosystem functioning on both the number of pollinator individuals and the number of pollinator species, it is difficult to predict the consequences of lost species richness of pollinating insects [2]. Understanding such consequences is made more urgent by the decline of many pollinators (including insects) and associated plants globally [4]. An example is the bumblebee (*Bombus*) genus, of which many species have decreased in population number in Sweden [2]. The pollinator decline has been attributed mainly to the abiotic factors of climate change and other human-induced changes ("anthropogenic impacts") [4]. However, there are indications that such abiotic changes in the environment are not enough in themselves to drive extinctions. For example, a study modelling eco-evolutionary responses of species to a changing climate found no case where extinctions happened in the absence of competition from other species [8]. This suggests an opportunity for the pollination function to be maintained even in a changed environment, which for example agriculture depends on.

Specifically, the decline of wild pollinators has made agriculture increasingly reliant on managed pollinators for crop yields. Several studies have therefore been made regarding the introduction of the principal managed pollinators globally, the Western honeybee *Apis mellifera* and the buff-tailed bumblebee *Bombus terrestris* [12]. From the managed colonies, escaped individuals have often formed feral populations [12, 1]. Such feral populations can in many cases be considered invasive alien species (IAS), which are defined as species introduced beyond their natural ranges by humans, and then spreading rapidly to impact native species both ecologically and evolutionarily [12]. While IAS often affect their host ecosystems adversely, positive impacts have also been observed [12]. One example is that introduced pollinators can benefit native pollination networks by maintaining pollination function over large distances, especially in cases where pollinator loss mediated by humans has disrupted the ecosystem and indigenous

pollinators [12]. However, this benefit has mainly been observed for small numbers of introduced pollinators [12]. Hence, there is a research gap in quantifying the potential benefits and risks of intentionally introducing non-native pollinator species in pollination networks disrupted by abiotic environmental changes mediated by humans. Such quantification is the purpose of the present thesis.

1.2 Aims of this thesis

I aim to investigate the effects on native ("resident") pollination networks from the introduction of a non-native pollinator species (a "substituting invader") when the resident pollinators are declining due to an abiotic change in their environment. I assume that the substituting invader is introduced into a community of two resident pollinators and two plants to maintain the pollination services that the resident pollinators provided before their decline. I compare the equilibrium populations of the species in the community between two scenarios: one with and one without a substituting invader. I seek to find 1) a mechanism for pollinator extirpations catalyzed by an abiotic change in the environment, and 2) whether a non-native pollinator species can substitute the services provided to the resident plants by the resident pollinators. Specifically, I ask:

1. Does the model support that an abiotic change in the environment leads to the extirpation of **resident pollinator** species only in the presence of interspecific competition?
2. What is the difference in mutualistic benefits to the **resident plants** between the two scenarios?

To answer these questions, I develop a model accounting for competition, mutualism and use of resources in the environment, as well as a framework for quantification of the associated parameters. The model thus developed applies to pollination networks in a changing environment. I then use this model to study the introduction of a substituting invader as a potential way of maintaining the pollination function otherwise lost due to the decline of resident pollinator species.

2 Methods

2.1 Model description

Modelled pollination network

Figure 2.1 shows the pollination network considered in this thesis. Firstly, there is the "environment", which contains all the resources pollinators and plants can use to survive and reproduce except those derived from pollination. There are three pollinators: the resident pollinators, B_1 and B_2 , as well as the substituting invader, B_3 . These compete (red arrows) over resources from the so-called "environment" (green arrows). These resources include food sources and nesting space. In addition, there are plants belonging to the resident community, R_1 and R_2 , which compete over other resources in the environment than the pollinators, such as access to sunlight and the area for them to spread their seeds. Pollination is modeled as a mutualistic interaction between the plants and pollinators (blue arrows), which means that both species interacting are benefited from the pollination.

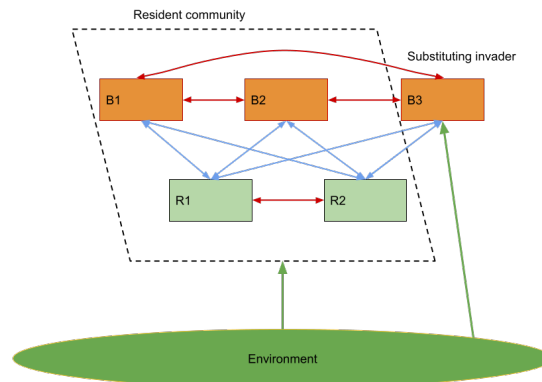


FIGURE 2.1: Illustration of the studied pollination network, including the resident community and the substituting invader. Double-headed arrows represent interactions between species, where red (competition) is mutually negative and blue (mutualism) is mutually positive. The green arrows represent the resources derived from the environment (positive impact).

Each individual of a species has one *environmental trait value* and one *mutualistic trait value*. The environmental trait value determines which resources an individual can use

from the environment. Since the resources derived from the environment are different between plants and pollinators, the environmental trait value for pollinators represents another real-world characteristic of a pollinator individual than the environmental trait value for plants does for a plant individual. Henceforth, the plant environmental trait value will be exemplified by plant height and the pollinator environmental trait value by pollinator body size. The mutualistic trait value determines if a pollinator and a plant individual can interact through pollination, and is exemplified by flower size and *preference* for flower size for plants and pollinators, respectively. Pollination is likely to happen when the mutualistic trait value for the plant individual is close to that of the pollinator individual, and unlikely when the two mutualistic trait values are widely different. A representative (average) individual of each species is given the following characteristics related to these trait values:

- R_1 : A short plant with small flowers
- R_2 : A tall plant with large flowers
- B_1 : A small pollinator with a preference for small flowers
- B_2 : A large pollinator with a preference for large flowers
- B_3 (the substituting invader): A small pollinator with a generalist preference for flowers of a wide range of sizes, although it is given a bias towards smaller flowers, such as R_1

Population equation

In my model, the population number of a plant species R_i is denoted N_{Ri} , and for a pollinator species B_i , the population number is N_{Bi} . The model accounts for all the interactions shown in 2.1 and also the decline of the resident pollinators catalyzed by a changing environment. The following population equations are used to calculate the growth rate of each plant and pollinator population, respectively:

$$\frac{1}{N_{Ri}} \frac{dN_{Ri}}{dt} = g_{Ri} \cdot \left(\exp \left(-\frac{1}{2} \left(\frac{\mu_{r,Ri} - \mu_{r,env}}{\sigma_{r,env}} \right)^2 \right) + \frac{-\sum_j \alpha_{Ri,Rj} N_{Rj} + \sum_k c_{Ri,Bk} N_{Bk}}{K_{m,Ri}} \right), \quad (2.1)$$

and

$$\frac{1}{N_{Bi}} \frac{dN_{Bi}}{dt} = g_{Bi} \cdot \left(\exp \left(-\frac{1}{2} \left(\frac{\mu_{b,Bi} - \mu_{b,env}}{\sigma_{b,env}} \right)^2 \right) + \frac{-\sum_k \alpha_{Bi,Bk} N_{Bk} + \sum_j c_{Bi,Rj} N_{Rj}}{K_{m,Bi}} \right), \quad (2.2)$$

with notation explained in Table 2.1.

Competition

The population equations (2.1) and (2.2) are based on the standard Lotka-Volterra competition model according to Kot [5, Chapter 12]. To account for competition between species (*interspecific competition*), I define an *interspecific competition component* for species B_i :

Explanation of notation	Plant	Pollinator
Population number	N_{Ri}	N_{Bi}
Intrinsic growth rate	g_{Ri}	g_{Bi}
Average environmental trait value	$\mu_{r,Ri}$	$\mu_{b,Bi}$
Optimal environmental trait value	$\mu_{r,env}$	$\mu_{b,env}$
Environment distribution width	$\sigma_{r,env}$	$\sigma_{b,env}$
Competition coefficient	$\alpha_{Ri,Rj}$	$\alpha_{Bi,Bk}$
Mutualistic conversion coefficient	$c_{Ri,Bk}$	$c_{Bi,Rj}$
Ideal carrying capacity	$K_{m,Ri}$	$K_{m,Bi}$

TABLE 2.1: Variables and constants in the population equations (2.1) and (2.2).

$$N_{\text{comp},Bi} = \sum_{k \neq i} \alpha_{Bi,Bk} N_{Bk}, \quad (2.3)$$

where $\alpha_{Bi,Bk}$ is the competition coefficient for a pollinator species B_i competing with a pollinator species B_k . It translates the population number of species B_k into the number of individuals of species B_i which would give the same competitive cost for an individual of species B_i . Therefore, $N_{\text{comp},Bi}$ is the equivalent number of B_i individuals added due to the competition with other pollinator species, B_k . The definition is analogous for $N_{\text{comp},Ri}$, the interspecific competition component for the plant species R_i . The red arrows entering a species in Figure 2.1 correspond to the interspecific competition experienced by this species, and the negative impact is defined to become smaller with an increasing difference between the average environmental trait values of the two competing species.

Mutualism

A *mutualistic component* is defined in line with Kot [5, Chapter 13]. The mutualistic component accounts for the mutualistic benefit derived from the pollination interactions between plants and pollinators in the pollination network. For a pollinator B_i , this is given by:

$$N_{\text{mut},Bi} = \sum_j N_{Bi,Rj} = \sum_j c_{Bi,Rj} R_j, \quad (2.4)$$

where $c_{Bi,Rj}$ is a *mutualistic conversion coefficient*, which is multiplied by the population number of plant species R_j to translate the total mutualistic benefit from pollinating plants of species R_j into how large competitive cost to an individual of pollinator species B_i that it weighs up for. The definition is analogous for $N_{\text{mut},Ri}$, the mutualistic component for a plant R_i . The mutualistic component corresponds to all the blue arrows entering a species in Figure 2.1, and is defined to become smaller with an increasing difference between the average mutualistic trait values of the two interacting species.

Adaptation to the environment

In addition, an *ideal carrying capacity* is defined, K_{m,R_i} for plants and K_{m,B_i} for pollinators. For a given species, this ideal carrying capacity assumes an average environmental trait value equal to the optimal environmental trait value (a situation hereafter called "optimal adaptation to the environment"), for which there is the largest amount of resources to be used by an individual with the optimal environmental trait value. Note that the word "adaptation" does not in this thesis imply the evolution of any species, but rather the suitability of their constant average trait values in the given environment. By assuming that the resources in the environment are normally distributed (see Appendix A for rigorous definition), the *realized carrying capacity* is defined for a pollinator B_i by scaling the ideal carrying capacity, K_{m,B_i} , by a factor accounting for the difference between its average environmental trait value, μ_{b,B_i} , and the optimal environmental trait value for pollinators, $\mu_{b,env}$. This difference in environmental trait values gives a measure of the degree of adaptation to the environment, from no adaptation at large differences to optimal adaptation for zero difference. For B_i , the realized carrying capacity is given by:

$$K_{B_i} = K_{m,B_i} \cdot \exp\left(-\frac{1}{2}\left(\frac{\mu_{b,B_i} - \mu_{b,env}}{\sigma_{b,env}}\right)^2\right), \quad (2.5)$$

where $\sigma_{b,env}$ is the width of the environment (resource) distribution with respect to pollinator environmental trait values. The definition and formula are analogous for K_{m,R_i} , the realized carrying capacity of a plant R_i . The realized carrying capacity corresponds to the green arrows in Figure 2.1 since they represent the total amount of resources available to the different species from the environment. By definition, the realized carrying capacity becomes smaller with an increasing difference between the average environmental trait value and the optimal environmental trait value. Note again that these environmental trait values are defined differently between plants and pollinators. The realized carrying capacity is by definition smaller than or equal to the ideal carrying capacity since the adaptation to the environment is in general not optimal. By letting the species have a (realized) carrying capacity, and thus a maximum equilibrium population number, dependent on their adaptation to the environment, it is possible to model how an abiotic change in the environment affects the different populations by changing their adaptation to the environment.

2.2 Modelled scenarios

Description of scenarios

I consider two different *scenarios*. The first scenario, the "declining residents scenario" (DRS), includes only the resident community. The second scenario, the "substituting invader scenario" (SIS), includes both the resident community and the substituting invader. Both scenarios assume the same abiotic change in the environment which only directly affects pollinators by changing their realized carrying capacities. When the population numbers of the species in these scenarios do not change appreciably on time scales short enough for evolution to be negligible, the populations are said to be at *ecological equilibrium* and are called *equilibrium populations* for the associated scenario.

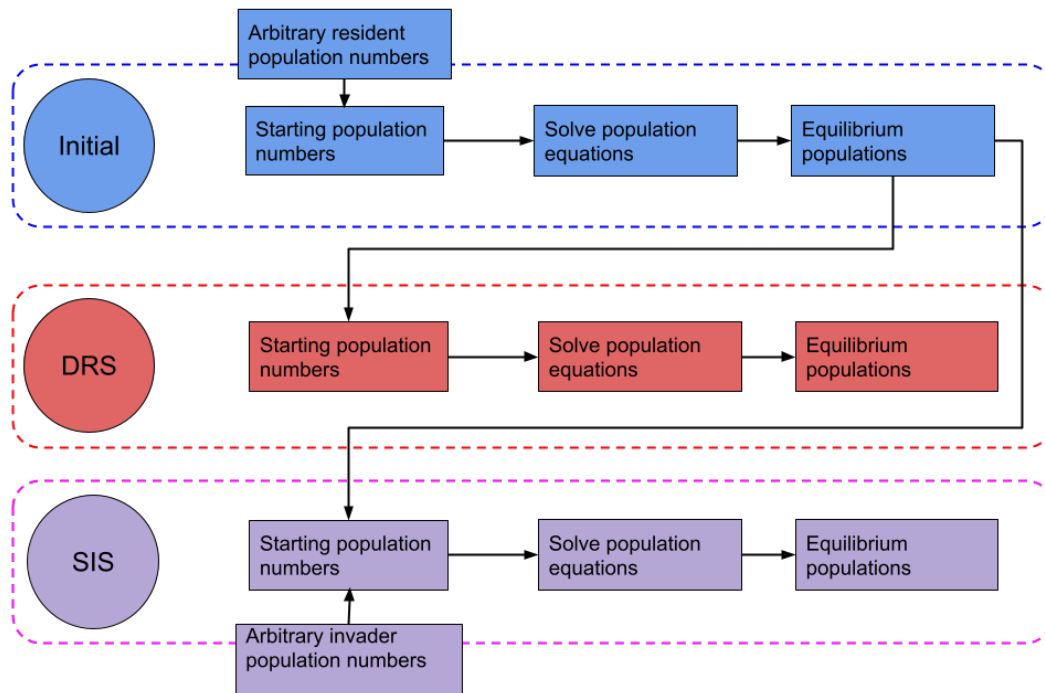


FIGURE 2.2: Schematic diagram of the numerical procedure to calculate the different equilibrium population numbers compared in this thesis. "Initial" refers to the equilibrium population numbers of the resident community before the abiotic change in the environment. "DRS" refers to the declining residents scenario and "SIS" to the substituting invader scenario, both assuming the same abiotic change in the environment. These two scenarios differ in that the pollination network in SIS also includes a substituting invader, whereas DRS includes only the resident community.

Note that this definition of ecological equilibrium is mathematically approximate. Figure 2.2 shows the methodology used for numerically calculating the equilibrium population numbers. The initial equilibrium population numbers are calculated before an abiotic change in the environment, and the equilibrium population numbers in the DRS and SIS are calculated with a change in the environment.

To investigate the effects of the substituting invader, the equilibrium populations in the SIS are compared to the equilibrium populations in the DRS. To obtain the population numbers over time, a numerical solver for ordinary differential equations (ODEs) is used to solve the system of ODEs consisting of the coupled population equations (2.2) and (2.1). The population numbers obtained at the model end time ("final time") of a scenario are chosen as equilibrium population numbers. First, the equilibrium population numbers of the resident community are calculated with $\mu_{b,env}$ held constant. These were the resident community population numbers at the start of the DRS and to which a population of

the substituting invader was added at the start of the SIS. To model the assumed abiotic change in the environment over time in both the SIS and DRS, the optimal environmental trait value for pollinators, $\mu_{b,env}$, changed as a function of time, t , according to:

$$\mu_{b,env}(t) = \mu_{b,env,init} + (1 - \exp(-t/\tau))(\mu_{b,env,fin} - \mu_{b,env,init}), \quad (2.6)$$

where the initial and final values are, respectively:

$$\mu_{b,env,init} = \mu_{b,env}(0) \quad \text{and} \quad \mu_{b,env,fin} = \lim_{t \rightarrow \infty} \mu_{b,env}(t),$$

and τ is a time constant (see Figure 2.3). This function gives a decreased optimal environmental trait value for pollinators (and not for plants), where the abiotic change over time in the environment can be for example temperature rise or increasing pesticide use. The substituting invader is given a smaller average environmental trait value, $\mu_{b,B3}$, than the other two species to make it the pollinator which is best adapted to the changed environment. However, this means that it will be the least adapted to the initial environment. For more details regarding the theory used to model a changing environment as well as the resulting relative advantages and disadvantages of the studied species, see Figures A.4 and A.5, and associated arguments in Appendix A.

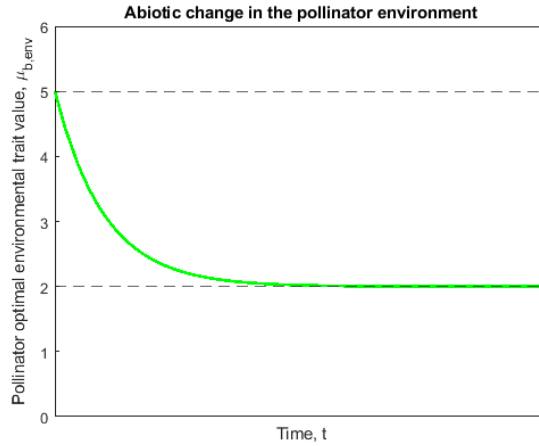


FIGURE 2.3: Change of the optimal environmental trait value, $\mu_{b,env}$, over time according to (2.6).

Components of population numbers

In the implementation of the scenarios, a threshold population number, $N_t = 1$, was defined. As soon as a population number (of either pollinators or plants) decreased below $N = N_t$, the associated population was set to $N = 0$, after which the population equations (2.1) and (2.2) give that for all future times, $N = 0$.

If B_i has a nonzero equilibrium population number, $N_{Bi}^* > 0$, it can be divided into three components: mutualism component ($N_{mut,Bi}^*$), interspecific competition ($N_{comp,Bi}^*$)

and realized carrying capacity (K_{Bi}). Using the equilibrium population sizes of all species in the studied community, the mutualism component is given by (2.4), the interspecific component by (2.3) and the realized carrying capacity by (2.5). This gives the decomposition:

$$N_{Bi}^* = N_{mut,Bi}^* - N_{comp,Bi}^* + K_{Bi}. \quad (2.7)$$

An analogous decomposition can be made for a plant R_i . Since this decomposition depends on the population number being nonzero, (2.7) is not valid for a population number of 0. However, when (2.7) gives the ecological impossibility $N_{Ri}^* < 0$, it should be interpreted as R_i becoming extirpated (locally extinct). This holds even if new individuals of R_i are introduced, because of the persistingly negative growth rate of the population.

2.3 Selected parameter values

The values for the competition coefficients are shown in (2.8) and (2.9), while mutualistic conversion coefficients are shown in (2.10) and (2.11). All remaining parameter values used in the population equations, (2.1) and (2.2), are shown in Tables 2.2, 2.3 and 2.4. The derivation of formulas for $\alpha_{Ri,Rj}$, $\alpha_{Bi,Bk}$, $c_{Ri,Bk}$, $c_{Bi,Rj}$, $K_{m,Ri}$ and $K_{m,Bi}$, is described in Appendix A, and the internal model parameter values to calculate these in Appendix B.

$$\begin{pmatrix} \alpha_{R1,R1} & \alpha_{R1,R2} \\ \alpha_{R2,R1} & \alpha_{R2,R2} \end{pmatrix} = \begin{pmatrix} 1.00 & 0.82 \\ 0.20 & 1.00 \end{pmatrix} \quad (2.8)$$

$$\begin{pmatrix} \alpha_{B1,B1} & \alpha_{B1,B2} & \alpha_{B1,B3} \\ \alpha_{B2,B1} & \alpha_{B2,B2} & \alpha_{B2,B3} \\ \alpha_{B3,B1} & \alpha_{B3,B2} & \alpha_{B3,B3} \end{pmatrix} = \begin{pmatrix} 1.00 & 1.11 & 0.79 \\ 0.28 & 1.00 & 0.14 \\ 0.79 & 0.54 & 1.00 \end{pmatrix} \quad (2.9)$$

$$\begin{pmatrix} c_{R1,B1} & c_{R1,B2} & c_{R1,B3} \\ c_{R2,B1} & c_{R2,B2} & c_{R2,B3} \end{pmatrix} = \begin{pmatrix} 0.092 & 0.0092 & 0.14 \\ 0.027 & 0.021 & 0.054 \end{pmatrix} \quad (2.10)$$

$$\begin{pmatrix} c_{B1,R1} & c_{B1,R2} \\ c_{B2,R1} & c_{B2,R2} \\ c_{B3,R1} & c_{B3,R2} \end{pmatrix} = \begin{pmatrix} 0.046 & 0.053 \\ 0.0046 & 0.042 \\ 0.048 & 0.071 \end{pmatrix} \quad (2.11)$$

Parameter	For all plants, R_j	For all pollinators, B_k
$\mu_{z,env}$	3	5 \rightarrow 2 *
$\sigma_{z,env}$	2	2

TABLE 2.2: Parameter values for the environment. The trait "z" stands for either "r" or "b" when the parameter applies to the plant or pollinator environment, respectively. * The value of $\mu_{b,env}$ starts at 5 and asymptotically approaches 2 (see Figure 2.3).

Parameter	R_1	R_2
g_{R_i}	1.51	1.10
μ_{r,R_i}	2	4
K_{m,R_i}	3500	3250

TABLE 2.3: Parameter values for every plant species, R_i .

Parameter	B_1	B_2	B_3 (substituting invader)
g_{B_i}	1.51	1.10	1.51
μ_{b,B_i}	4	6	3
K_{m,B_i}	1500	1125	1500

TABLE 2.4: Parameter values for every pollinator species, B_i .

3 Results

In the DRS, it is apparent that the population number of B_2 is zero, meaning that this species is extirpated in the DRS (see Figure 3.1). Similarly, B_1 becomes extirpated in the SIS. In contrast, the plants, R_1 and R_2 , are relatively unaffected by the changes between the scenarios, as seen by the relatively small differences between their respective population numbers at the different equilibria.

As intended in the SIS, the substituting invader, B_3 , had an equilibrium population number comparable to those of B_1 and B_2 initially (see Figure 3.1). The method used to achieve this was setting the environmental trait value of the invader, $\mu_{b,B_3} = 3$, closer to the optimal value in the changed environment, $\mu_{b,env,fin} = 2$, than the other two pollinator species, B_1 and B_2 , with $\mu_{b,B_1} = 4$ and $\mu_{b,B_2} = 6$, respectively. Even if the optimal environmental trait value, $\mu_{b,env}$, is not the only determinant of the population numbers, changing it has a large impact on the realized carrying capacities and thus the equilibrium population numbers, as implied in comparing Figures A.5 and A.4 in Appendix A.

Figure 3.2 shows the population numbers in Figure 3.1 divided into components according to (2.7): mutualism, interspecific competition and realized carrying capacity. The mutualism and realized carrying capacity components are positive for all species at all equilibria, in contrast to the negative (or zero) interspecific competition components. Although the realized carrying capacities of the pollinators change when the environment changes, they never reach below the threshold population number, $N_i = 1$. Therefore, it would not be possible in the present model for any of the pollinator species to be extirpated from the assumed abiotic change in the environment, in the absence of interspecific competition. I conclude that interspecific competition is required in the scenarios studied for the environmental change to catalyze the extirpation of any species. Since the mutualism component is much smaller than the realized carrying capacity for almost all species in all equilibria, the mutualism is *facultative*, as defined by Kot [5], since the plants can survive independently of the pollinators and vice versa.

Figure 3.3 shows the difference in population numbers between the SIS and the DRS. From the increase in population numbers for both plants, the benefit of introducing an invader was positive for the plants. This represents that the substituting invader would ensure more pollination for the plants when the environment has changed than the scenario without a substituting invader (DRS). The introduction of a substituting invader also benefited B_2 by outcompeting B_1 , the main competitor for both B_2 and B_3 . This is seen by the large decrease in population number for B_1 and the slight increase for B_1 , shown in Figure 3.3. B_3 and B_2 don't compete strongly with each other, as defined by the small values of their competition coefficients, $\alpha_{B_2,B_3} = 0.14$ and $\alpha_{B_3,B_2} = 0.54$, compared to the other coefficients in (2.9). This leads to the small interspecific competition

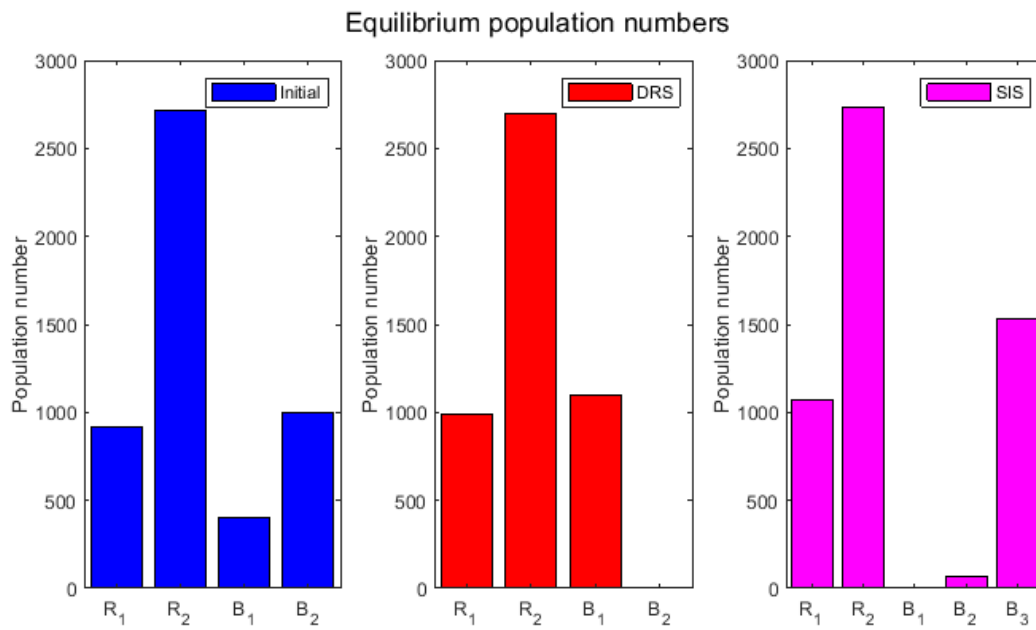


FIGURE 3.1: Equilibrium population numbers in the different scenarios of the honeybee case. "Initial" refers to the initial equilibrium, "DRS" to the declining residents scenario, and "SIS" to the substituting invader scenario.

components when these are the only pollinators in the SIS compared to the DRS, where B_2 has a substantially larger interspecific competition component. Because of the weak competition between them, B_2 and B_3 can coexist in the SIS, even if B_3 vastly outnumbers B_2 .

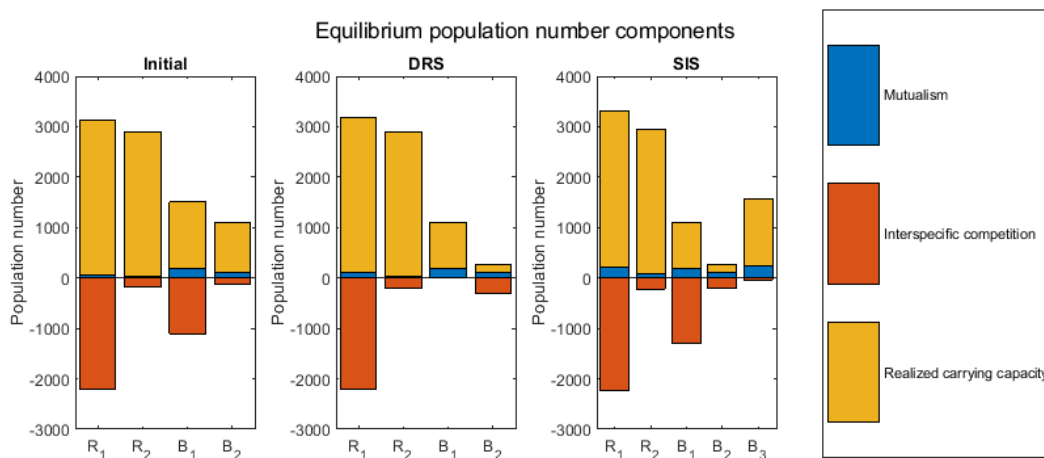


FIGURE 3.2: Equilibrium population number components in the different scenarios of the honeybee case. "Initial" refers to the initial equilibrium, "DRS" to the declining residents scenario, and "SIS" to the substituting invader scenario. Note that the sum of all three components gives the equilibrium population numbers seen in Figure 3.1, whenever these are non-zero, according to (2.7).

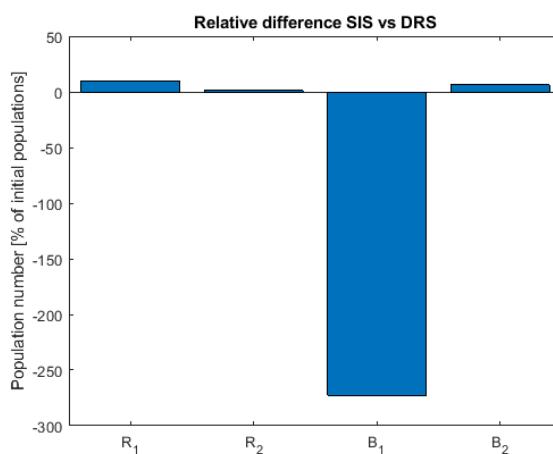


FIGURE 3.3: Difference in equilibrium population number between the substituting invader scenario (SIS) and the declining residents scenario (DRS) relative to the initial equilibrium population numbers.

4 Discussion

The results support that interspecific competition is a necessary driver for the loss of any pollinator species following an abiotic change in the environment. This is expected, since a species has a negative growth rate when the interspecific competition that a species faces is larger than the sum of its mutualism and realized carrying capacity components, according to the model used. In reality, a negative growth rate means that the species can't survive and reproduce sufficiently well to maintain its population number, which decreases. If the negative growth rate persists over time, extirpation occurs. This gives an approximate mechanism for how an abiotic change in the environment can contribute to the loss of pollinator species: by reducing the realized carrying capacity of a pollinator species to the extent that it becomes smaller than the magnitude of the interspecific competition. By identifying the negative impact of competition as a mechanism for species extirpations, it might seem as if the introduction of a substituting invader cannot benefit the resident pollinators. However, it was also found that the introduction of a substituting invader can outcompete competitively dominant resident pollinators and thus have an indirect positive effect on other resident pollinators. The results of modeling suggest that this happens when the competition between the substituting invader and the previously disadvantaged resident pollinators is weak compared to their competition with the previously dominant pollinators.

In addition, the plant population numbers increase with the introduction of a substituting invader in the model community, which is a positive effect of substituting pollinators in decline. Such a benefit is expected, considering that the substituting invader is chosen to be well adapted to the changed environment and to the two plant species compared to the two resident pollinators. However, the contribution of the mutualistic benefit to the entire population number of a species was small in both scenarios, with and without a substituting invader. The difference in the mutualistic benefit between these two scenarios will likely be larger if plants that are more dependent on mutualism are considered. Within the present model, such a situation can be modeled with larger mutualistic conversion coefficients for the plants. Since the mutualistic benefit of introducing a substituting invader is strongly dependent on the mutualistic conversion coefficients, it is important to choose empirically supported values for these coefficients before drawing conclusions about the potential effects of substituting pollinators in decline in real pollination networks. Such validation of the positive effect on resident plants is particularly relevant when the substituting invader is a bee species because it would support the finding that some pollination networks experience several positive effects from introduced managed bees, even if the impacts are mainly negative for a majority of studied bee invasions.

To better understand the effects of substituting pollinators in decline, the model

allows for several extensions. For example, it is possible to use another function for the changing environment or change another parameter than the optimal environmental trait value for pollinators. For example, dynamic effects arising from a periodically or very slowly changing environment might be studied. Importantly, empirical observations and measurements might make it possible to determine parameter values corresponding to a real pollination network. This enables using the model to generate testable predictions about the effects of substituting pollinators in decline. It has been suggested by Parra-Tabla et al [10] that testable predictions are crucial for understanding the effects of invasive species, even if it was mainly stated for invasive plant species. Empirical studies are needed to confirm or refute such predictions. Even if the idea of substituting pollinators in decline were found to be untenable after further study, the understanding of how the resident community would respond to this intervention is likely beneficial to other areas of study. For example, such understanding can contribute to better mapping of how invasive species affect pollination networks as well as contributing to guidelines for responsible human interventions to preserve declining pollination functions. Because of the potentially negative effects of introducing non-native pollinator species, it is important to not deploy this intervention to ensure continued pollination if more certain measures are feasible or if the risks of this intervention have not been extensively studied. Therefore, I make no judgment of whether substituting pollinators in decline is a desirable intervention in any real pollination network.

5 Conclusion

The results are in line with my expected answers to the two questions posed. Firstly, I show that the model requires interspecific competition for an abiotic change in the environment to catalyze the extirpation of pollinator species. Secondly, I find larger mutualistic benefits for the resident plants with the introduction of a non-native pollinator species than without, when the resident pollinators are declining in number. These two findings clarify a mechanism for the extirpation of pollinator species and suggest that a non-native pollinator species can benefit the resident plants by substituting lost resident pollinators. The impact of the non-native pollinator species is mainly negative for the resident pollinators, while mainly positive for the resident plants. Therefore, it is not possible to conclude whether it is beneficial to the resident pollination network as a whole, without specifying how to evaluate the trade-off between resident pollinator population numbers and resident plant population numbers.

To better understand the effects of substituting pollinators in decline, it would be beneficial to model a wide variety of pollination networks, with respect to the degree of dependence between plants and pollinators, as well as considering the magnitude of the resident pollinator decline. At a later stage, such modeling might be followed by empirical studies to investigate whether the model results are in line with the effects observed in field studies or controlled experiments. Crucially, before trying this method in a real pollination network, it is necessary to as extensively as possible confirm that it can ensure a substantial positive difference in maintained pollination function compared to without a substituting invader and that it is more suitable for the given pollination network than other methods to mitigate the negative consequences from the loss of pollinators. Since a diversity of pollinators is crucial for crop production and many ecosystem functions, it is important to be cautious in applying this method because of the risks it poses to the resident pollinators.

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A Derivation of the model

All figures in this appendix are made using the parameter values for the modeled community in the main text, found in their entirety in Appendix B.

A.1 Probability theory

A stochastic variable X can be defined as a variable for which each possible value is taken on by X with a given probability. If it can only take on discrete values, this probability is given by the function $p_X(k)$ and in the case of a continuous variable X , it takes on a value in the open interval $x \in (x_1, x_2)$ with a probability

$$P(x_1 < X < x_2) = \int_{x_1}^{x_2} f_X(x) dx, \quad (\text{A.1})$$

where $p_X(k)$ and $f_X(x)$ are respectively called a probability mass function and a probability density function (PDF) for the variable X . An example of a PDF is given by the normal distribution, $N(\mu, \sigma)$, which for $X \in N(\mu, \sigma)$, gives the PDF

$$f_X(x) = \frac{1}{\sqrt{2\pi} \cdot \sigma} \exp\left(-\frac{1}{2}\left(\frac{x - \mu}{\sigma}\right)^2\right). \quad (\text{A.2})$$

Often, quantitative physical traits are assumed to be normally distributed, for example the weight of individuals of a given animal species or the height of plants of the same species in the same geographical area, although many such traits are only approximately normally distributed [6, 7]. Since there are many mechanisms impacting the expression of such a trait, often divided into genetic and environmental factors, they can be considered stochastic variables for each individual [6]. For the species as a whole, the PDF for a trait of an individual in the species can define one dimension of the ecological niche of that species, since it shows the interval(s) in which the majority of the individuals of that species have their trait value [6, 11].

Natural selection operates on the principle that individuals with certain traits have a better ability to survive and reproduce than those who do not have the same trait [3]. This drives evolution of the species as a whole towards a larger proportion of the population having that trait [3]. In particular, this applies to quantitative traits, which means that the niche as described by a PDF is likely to move along the trait value axis and change its width when subjected to selection pressure [3]. Assuming no evolution or rapid disturbance directly to the population, the PDF representing the niche of a given species will therefore be considered constant in this thesis. This is likely accurate, since this thesis considers ecological, but not evolutionary, population effects.

Many of the arguments below are made for pollinators, B_k , but all of them also apply analogously to plants, R_j , if not explicitly stated otherwise.

A.2 Environment

Each species is assumed to have an associated "environmental trait PDF" (ETPDF) describing the distribution of an "environmental trait" in the species population (see Figure A.1). Such a trait indicates what resources in the environment that an individual of the species can use for its survival and reproduction. For plants, this is r , and for pollinators, b . They are assumed to be normally distributed, with peak trait values denoted by $\mu_{r,Rj}$ and $\mu_{b,Bk}$, respectively, as well as standard deviations, $\sigma_{r,Rj}$ and $\sigma_{b,Bk}$, respectively. The ETPDF for a pollinator B_i is given by:

$$f_{B_i}(b) = \frac{1}{\sqrt{2\pi} \cdot \sigma_{b,B_i}} \exp\left(-\frac{1}{2}\left(\frac{b - \mu_{b,B_i}}{\sigma_{b,B_i}}\right)^2\right). \quad (\text{A.3})$$

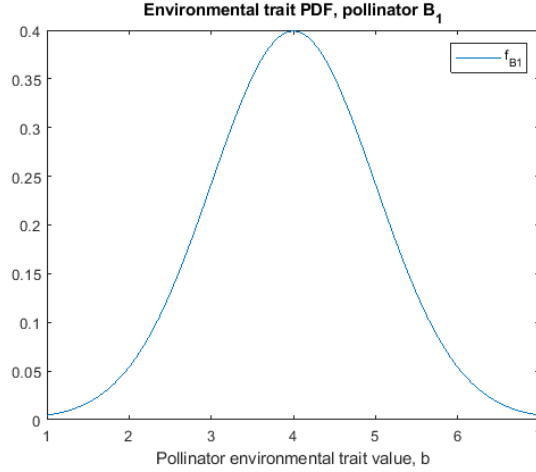


FIGURE A.1: Environmental trait PDF (ETPDF), $f_{B_1}(b)$, for species B_1 .

Furthermore, the pollinator species are assumed to have a common "environment distribution function" (EDF), dK/db , giving a distribution of resources in the environment, necessary for pollinator survival and reproduction (see Figure A.2). This EDF is assumed to be a scaled normal PDF with its peak at $b = \mu_{b,env}$ and the standard deviation $\sigma_{b,env}$:

$$\frac{dK}{db} = \frac{K_{\max,b}}{\sqrt{2\pi} \cdot \sigma_{b,env}} \exp\left(-\frac{1}{2}\left(\frac{b - \mu_{b,env}}{\sigma_{b,env}}\right)^2\right). \quad (\text{A.4})$$

The coefficient $K_{\max,b}$ represents the maximal carrying capacity of the environment. It is determined so that, when integrated between two trait values, b_1 and b_2 , this distribution gives the amount of resources in the environment that are possible to consume for individuals with traits in the range $b \in (b_1, b_2)$. In line with its definition as the maximal

carrying capacity of the environment, $K_{\max,b}$ is obtained by integrating the EDF over the entire real axis.

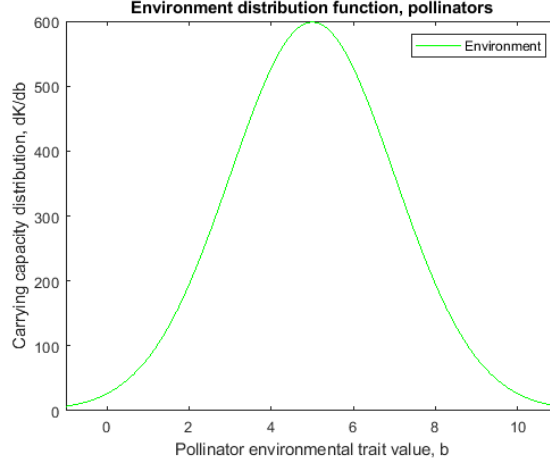


FIGURE A.2: Environment distribution function (EDF), dK/db , for all pollinators, B_k .

Using the ETPDF and the EDF, it is possible to define an ideal carrying capacity, $K_{m,Bi}$, for each pollinator species. It represents the carrying capacity a species would have if it were optimally suited to the environment, i.e. $\mu_{b,Bi} = \mu_{b,env}$. To calculate $K_{m,Bi}$, the ETPDF is translated along the b axis to be centered at $b = \mu_{b,env}$ and then scaled to have its peak at the same environmental trait value as the EDF (see Figure A.3):

$$\left. \frac{dK}{db} \right|_{b=\mu_{b,env}} = \frac{K_{\max,b}}{\sqrt{2\pi} \cdot \sigma_{b,env}}.$$

After dividing by the individual resource use, k_{Bi} , the integral of the resulting distribution (no longer a PDF) over the real axis gives $K_{m,Bi}$. This simplifies to

$$K_{m,Bi} = \frac{\sigma_{b,Bi}}{\sigma_{b,env}} \frac{K_{\max,b}}{k_{Bi}}.$$

Based on the ideal carrying capacity, B_i has a so-called "realized carrying capacity", K_{Bi} . It stems from the fact that B_i is not optimally adapted to the environment and thus has to have its ETPDF scaled to have its peak at the function value of the EDF at $\mu_{b,Bi}$ (see Figure A.4), rather than the peak value of the EDF (see Figure A.3).

The scaling of the ETPDFs shown in Figure A.4 gives the following relation:

$$K_{Bi} = K_{m,Bi} \cdot \exp\left(-\frac{1}{2}\left(\frac{\mu_{b,Bi} - \mu_{b,env}}{\sigma_{b,env}}\right)^2\right). \quad (\text{A.5})$$

We define an effective population for B_i , with consideration of both competition and mutualism:

$$N_{Bi,eff} = \sum_j \alpha_{Bi,Bk} N_{Bk} - \sum_k c_{Bi,Rj} R_j. \quad (\text{A.6})$$

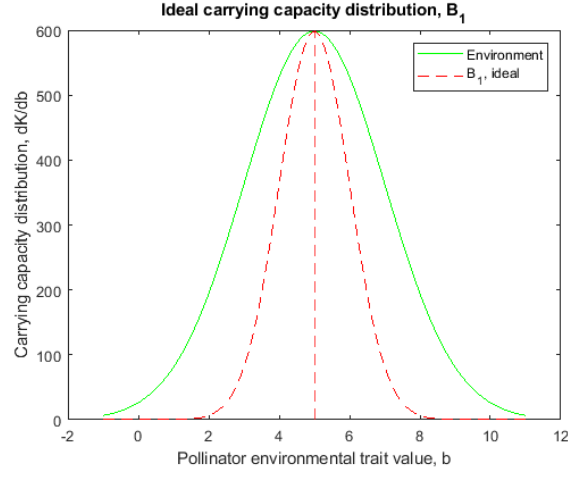


FIGURE A.3: Visualization of the ideal carrying capacity. Environment distribution function (EDF), dK/db , together with a translated and scaled ETPDF for pollinator species B_1 .

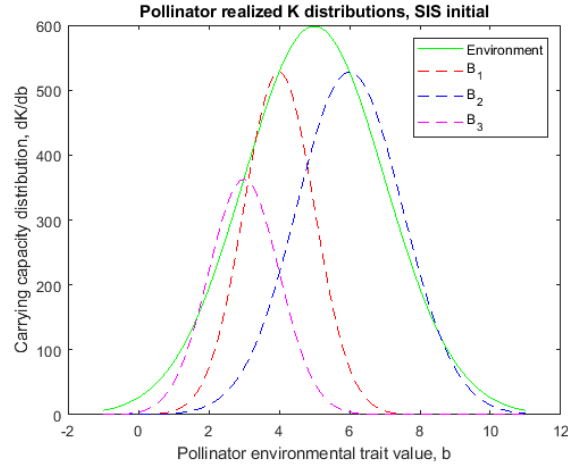


FIGURE A.4: Visualization of realized carrying capacities at the beginning of the SIS. Environment distribution function (EDF), dK/db , together with scaled ETPDFs for pollinator species B_1 , B_2 and B_3 .

By the definition of K_{Bi} as a carrying capacity, equilibrium should be reached when $N_{Bi,eff} = K_{Bi}$, which is shown using the pollinator population equation (2.2):

$$\frac{1}{N_{Bi}} \frac{dN_{Bi}}{dt} = \frac{g_{Bi}}{K_{m,Bi}} (K_{Bi} - N_{Bi,eff}). \quad (\text{A.7})$$

By analogous arguments and definitions (see Table B.1), for a plant species, R_i , the realized carrying capacity is given by

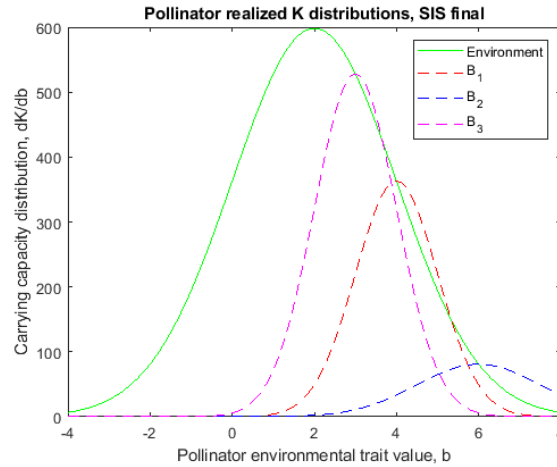


FIGURE A.5: Visualization of realized carrying capacities at final time of the SIS (compare with Figure A.4). Environment distribution function (EDF), dK/db , together with scaled ETPDFs for pollinator species B_1 , B_2 and B_3 .

$$K_{Ri} = K_{m,Ri} \cdot \exp\left(-\frac{1}{2}\left(\frac{\mu_{r,Ri} - \mu_{r,env}}{\sigma_{r,env}}\right)^2\right),$$

where

$$K_{m,Ri} = \frac{\sigma_{r,Ri}}{\sigma_{r,env}} \frac{K_{max,r}}{k_{Ri}}.$$

To model a changing environment, the optimal environmental trait value for pollinators is changed over time. This is equivalent to translating the EDF along the b -axis without changing its shape (compare Figures A.5 and A.4). The resulting change in species adaptation to the environment is illustrated by the decreased peak heights of the scaled ETPDFs for B_1 and B_2 in Figure A.5 compared to Figure A.4, which correspond to smaller realized carrying capacities, K_{B1} and K_{B2} , according to (A.5). The increased peak height of B_3 corresponds to an increased realized carrying capacity, K_{B3} . However, B_3 was less adapted to the environment initially, seen by the lower peak of its scaled ETPDF compared to B_1 and B_2 initially (compare Figures A.4 and A.5).

A.3 Competition

The competition effect in the model is based on the interaction between two individuals of the same type (plant or pollinator). They can be of either the same species or two different species. These two individuals have a certain probability of trying to consume the same resource and thus competing. Exactly what constitutes "consuming the same resource" depends on the resource. If the resource is a nesting space, for example, consuming the resource can mean that a pollinator has already claimed it, so that it becomes unavailable for the competitor. Furthermore, the relative resource needs for

survival and reproduction of the two individuals determine how large the per capita impact of this competition is. The method described below to calculate the competition coefficients, α_{R_i,R_j} , uses the ETPDFs of the respective species. It is slightly similar to a method of calculating niche overlap briefly mentioned in [11].

The two individuals competing are denoted X_1 and X_2 , of species B_i and B_k , respectively. First, assume that X_1 has the fixed environmental trait value b . Assume that X_2 has a stochastically determined trait value b' with a probability determined by its ETPDF. We define the probability to compete for two individuals with a difference in trait value $\Delta b = x$ as a scaled normal PDF:

$$h_{B_i,B_k}(x) = \exp\left(-\frac{1}{2}\left(\frac{x}{\sigma_{B_i,B_k}}\right)^2\right), \quad \sigma_{B_i,B_k} = \frac{\sigma_{b,B_i} + \sigma_{b,B_k}}{5} \quad (\text{A.8})$$

The scaling in (A.8) compared to the associated normal PDF means that two different individuals with exactly the same trait would compete with a probability $h(0) = 1$, which declines proportionally to a normal PDF as the difference x in their trait values is increased. The ETPDFs and $h(b - b')$ are shown in Figure A.6.

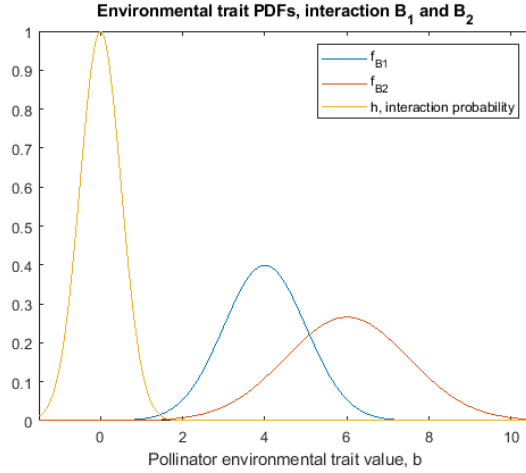


FIGURE A.6: ETPDFs for B_1 and B_2 , respectively $f_{B_1}(b)$ and $f_{B_2}(b)$, as well as the associated interaction probability, $h(b)$.

We further define the convolution operation for two functions, f and g :

$$(f * g)(x) = \int_{-\infty}^{\infty} f(x - y)g(y) dy. \quad (\text{A.9})$$

X_2 will compete with X_1 with a probability $h(b - b')$ given by (A.8). Thus, the probability of X_1 to experience competition from X_2 is given by $(f_{B_k} * h)(b)$, since the trait b' is determined stochastically according to the ETPDF $f_{B_k}(b')$. With also the trait b being stochastic, distributed according to $f_{B_i}(b)$, one can define the so called "competition PDF":

$$f_{B_i,B_k}(b) = f_{B_i}(b) \cdot (f_{B_k} * h)(b), \quad (\text{A.10})$$

which gives the probability of competing:

$$p_{B_i, B_k} = \int_{-\infty}^{\infty} f_{B_i, B_k}(b) db. \quad (\text{A.11})$$

The way that the pollinator population equation (2.2) is defined, the competition coefficient α_{B_i, B_k} needs to translate N_{B_k} , the population size of species B_k , into the equivalent population size of species B_i giving the same competition effect.

The population equation (2.2) assumes that the competition coefficient, α_{B_i, B_k} , measures the average cost for each pollinator of species B_i from the competition per pollinator of species B_k . By deriving it from their respective ETPDFs, the competition is assumed to be caused by their need for the same resources in the environment. This can for example be food or nesting space.

Thus, I define α_{B_i, B_k} as a measure of the average amount of resources unavailable to a pollinator X_1 of species B_i due to a single individual of species B_k already having consumed them. By multiplying with N_{B_k} , the population size of B_k , I calculate the cost of unavailable resources that X_1 experiences from the competition with the entire population of B_k . This total cost for X_1 is defined as the equivalent number of competing individuals of the species B_i that the competition with B_k adds:

$$N_{B_i, B_k} = \alpha_{B_i, B_k} N_{B_k}. \quad (\text{A.12})$$

Considering the interaction with all pollinator species, including B_i itself, the equivalent number of B_i competitors added is given using (A.12):

$$N_{\text{comp}, B_i} + N_{B_i} = \sum_k N_{B_i, B_k} = \sum_k \alpha_{B_i, B_k} N_{B_k}, \quad (\text{A.13})$$

which is the competition term in the pollinator population equation (2.2). N_{comp, B_i} represents the interspecific competition.

To calculate α_{B_i, B_k} , 1) the probability of competition in (A.11) is put in relation to the probability of intraspecific competition, and 2) the possibly different individual resource needs k_{B_i} and k_{B_k} of species B_i and B_k , respectively, are accounted for. To achieve 1), the probability of intraspecific competition is calculated by replacing B_k with B_i in (A.10) and (A.11):

$$p_{B_i, B_i} = \int_{-\infty}^{\infty} f_{B_i, B_i}(b) db. \quad (\text{A.14})$$

Since an individual of species B_k consumes k_{B_k}/k_{B_i} times the amount of resources as an individual of B_i , 2) is fulfilled if the competition coefficient is multiplied by this factor. With definitions according to (A.11) and (A.14), this gives:

$$\alpha_{B_i, B_k} = \frac{k_{B_k}}{k_{B_i}} \frac{p_{B_i, B_k}}{p_{B_i, B_i}}. \quad (\text{A.15})$$

Note that p_{B_i, B_k} in (A.11) is not very useful by itself, since the "probability of competition" is not well-defined. For example, is it the probability of competing when X_1 and X_2 are foraging for food in the same geographical area, or is it the probability that X_1 would find

a resource missing because it has been consumed by X_2 ? Because the alleged probability is normalized by p_{B_i, B_i} before feeding into the competition coefficient, according to (A.15), the interpretation of the probability is somewhat arbitrary, as long as it is interpreted consistently for all pollinator species. The definition in (A.15) also has the feature that $\alpha_{B_i i} = \alpha_{B_k k} = 1$, which is to be expected since this refers to intraspecific competition, where the number of competitors is given directly by the population size of B_i . Therefore, it is already translated into the equivalent number of B_i competitors, which is otherwise the purpose of multiplying with $\alpha_{B_i, B_k} \neq 1$.

Also note that in general $\alpha_{B_i, B_k} \neq \alpha_{B_k i}$, for two reasons. The first is that the competition coefficient is dependent on the individual resource need, which is ecologically motivated. Assume that B_k has a larger individual resource need than B_i , i.e. $k_{B_k} > k_{B_i}$. Then it is reasonable that X_1 would face a larger competition from X_2 than vice versa, since the competitive interaction amounts to a larger share of the resource need of X_1 than for X_2 . Secondly, the ETPDFs of B_i and B_k are in general different, meaning that the factor $1/p_{B_i, B_i} \neq 1/p_{B_k, B_k}$, thus leading to different competition coefficients according to (A.15). This can be understood as individuals of B_i having another probability of competing with other individuals of B_i , than for B_k individuals to compete with each other.

Similar arguments can be made with the affected species changed from pollinator B_i to plant R_i , and the competing species changed from pollinator B_k to plant R_j . A key difference is that plants compete over other resources than pollinators, for example access to sunlight and nutrients in the soil. However, the definition of α_{R_i, R_j} is analogous to α_{B_i, B_k} : a measure of the average amount of resources unavailable to a plant of species R_i due to a single individual of species R_j already having consumed them. Paralleling the competition term (A.13) in the pollinator population equation (2.2), the competition term in the plant population equation (2.1) represents the equivalent number of R_i competitors added from competition with all plant species:

$$N_{\text{comp}, R_i} + N_{R_i} = \sum_j \alpha_{R_i, R_j} R_j. \quad (\text{A.16})$$

Analogously to α_{B_i, B_k} in (A.15), with similar definitions, the competition coefficient for plant R_i competing with plant R_j is:

$$\alpha_{R_i, R_j} = \frac{k_{R_j} p_{R_i, R_j}}{k_{R_i} p_{R_i, R_i}}. \quad (\text{A.17})$$

A.4 Mutualism

Similarly to the ETPDF, one can also define a "mutualistic trait PDF" (MTPDF), which differs from the ETPDF by being a function of the mutualistic trait for a pollinator, β , or a plant, γ . These traits give a measure of how well suited the pollinator individual and the plant individual are to each other. The MTPDFs are given for pollinator species B_i and plant species R_j , respectively, by:

$$\phi_{B_i}(\beta) = \frac{1}{\sqrt{2\pi} \cdot \sigma_{\beta, B_i}} \exp\left(-\frac{1}{2}\left(\frac{\beta - \mu_{\beta, B_i}}{\sigma_{\beta, B_i}}\right)^2\right), \quad (\text{A.18})$$

and

$$\phi_{R_j}(\gamma) = \frac{1}{\sqrt{2\pi} \cdot \sigma_{\gamma, R_j}} \exp\left(-\frac{1}{2}\left(\frac{\gamma - \mu_{\gamma, R_j}}{\sigma_{\gamma, R_j}}\right)^2\right). \quad (\text{A.19})$$

First, assume that a pollinator individual, X_1 , of species B_i has the fixed trait β , while the plant individual, Y_2 , of species R_j , has a stochastic trait value γ' determined by $\phi_{R_j}(\gamma')$. We define the probability to interact mutualistically for two individuals with a difference in mutualistic trait values $\beta - \gamma' = x$ as

$$h_{B_i, R_j}(x) = \exp\left(-\frac{1}{2}\left(\frac{x}{\sigma_{B_i, R_j}}\right)^2\right), \quad \sigma_{B_i, R_j} = \frac{\sigma_{\beta, B_i} + \sigma_{\gamma, R_j}}{5}$$

analogously to (A.8). The MTPDFs and $h(\beta)$ are shown in Figure A.7.

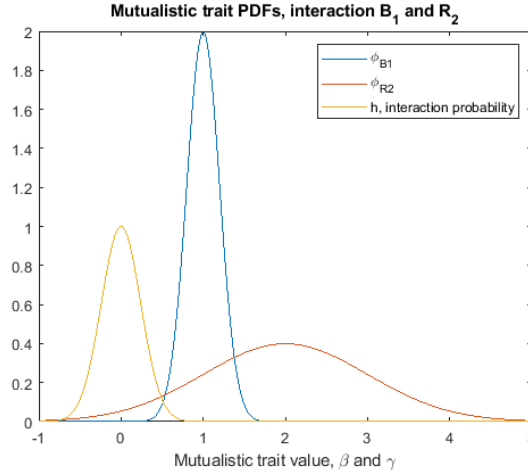


FIGURE A.7: MTPDFs for B_1 and R_2 , respectively $\phi_{B_1}(\beta)$ and $\phi_{R_2}(\gamma)$, as well as the associated interaction probability, $h(\beta)$.

X_1 will interact mutualistically with (i.e. pollinate) Y_2 with a probability $h(\beta - \gamma')$. Thus, the probability of X_1 to experience mutualistic benefits from Y_2 is given by the convolution $(\phi_{R_j} * h)(\beta)$, which integrates over all possible values of γ' and calculates the associated interaction probability at fixed β . Now, let also the trait β be stochastic, distributed according to $\phi_{B_i}(\beta)$. One can then define the so called "mutualism PDF":

$$\phi_{B_i, R_j}(\beta) = \phi_{B_i}(\beta) \cdot (\phi_{R_j} * h)(\beta), \quad (\text{A.20})$$

which gives the probability of mutualistic interaction:

$$p_{B_i, R_j} = \int_{-\infty}^{\infty} \phi_{B_i, R_j}(\beta) d\beta. \quad (\text{A.21})$$

The pollinator population equation (2.2) requires that the mutualistic conversion coefficient, c_{B_i,R_j} , measures the average benefit derived by each pollinator of species B_i from the mutualistic interaction with each plant of species R_j . From pollination, the pollinator receives this benefit mainly in the form of food. Thus, I define c_{B_i,R_j} as a measure of the nutrition a pollinator X_1 of species B_i receives on average from the nectar of a plant of species R_j , taking into account that they may not undergo a pollination interaction. By multiplying with N_{R_j} , the population size of R_j , I calculate the mutualistic benefit that X_1 experiences from the mutualism with the entire population of R_j . This total benefit is defined as the equivalent number of other pollinators of the species B_i whose competition the mutualism with R_j weighs up for:

$$N_{B_i,R_j} = c_{B_i,R_j} N_{R_j}. \quad (\text{A.22})$$

Considering the interaction with all plant species, the equivalent number of B_i competitors removed is given using (A.22):

$$N_{\text{mut},B_i} = \sum_j N_{B_i,R_j} = \sum_j c_{B_i,R_j} R_j, \quad (\text{A.23})$$

which is the mutualism term in the pollinator population equation, (2.2).

To calculate c_{B_i,R_j} , the mutualistic conversion coefficient for B_i benefitting from R_j , 1) the probability of mutualistic interaction, p_{B_i,R_j} in (A.21), is put in relation to that of intraspecific competition, 2) the mutualistic benefit of a mutualistic reference interaction is determined, and 3) the individual resource need, k_{B_i} , of species B_i is accounted for. To achieve 1) and 2), the mutualistic reference interaction is defined to have the same probability as for intraspecific competition, p_{B_i,B_i} according to (A.14). The average benefit to X_1 from this reference interaction with one plant individual is called the "reference mutualistic benefit" and is denoted by c_{m,B,R_j} . The actual interaction between individuals of B_i and R_j is assumed to give an average absolute benefit of:

$$c_{B_i,R_j,\text{abs}} = c_{m,B,R_j} \frac{p_{B_i,R_j}}{p_{B_i,B_i}},$$

measured in absolute resources. To satisfy 3), I divide by k_{B_i} . These steps give:

$$c_{B_i,R_j} = \frac{c_{m,B,R_j}}{k_{B_i}} \frac{p_{B_i,R_j}}{p_{B_i,\text{Req}}}. \quad (\text{A.24})$$

Analogous arguments can be made with the benefiting species changed from pollinator B_i to plant R_i , and the benefit-providing species changed from plant R_j to pollinator B_k . A key difference is that a plant benefits from pollination mainly through increased dispersion of its seeds and thus a higher reproductive success, rather than the additional food source that a pollinator receives. Therefore, c_{R_i,B_k} represents the average increase in reproductive success for a plant of species R_i per pollinator of species B_k . Paralleling the mutualism term (A.23) in the pollinator population equation (2.2), the mutualism term in the plant population equation (2.1) represents the equivalent number of R_i competitors removed from mutualistic interaction considering all pollinators:

$$N_{\text{mut},R_i} = \sum_k c_{R_i,B_k} B_k, \quad (\text{A.25})$$

Analogously to c_{B_i,R_j} in (A.24), with similar definitions, the mutualistic conversion coefficient for plant R_i benefiting from pollinator B_k is:

$$c_{R_i,B_k} = \frac{c_{m,R,B_k}}{k_{R_i}} \frac{p_{R_i,B_k}}{p_{R_i,R_i}}. \quad (\text{A.26})$$

B Values to calculate parameters in population equations

Table B.1 labels the parameters not used directly in the population equations, (2.1) and (2.2), which are used to calculate α_{R_i,R_j} , α_{B_i,B_k} , c_{R_i,B_k} , c_{B_i,R_j} , K_{m,R_i} and K_{m,B_i} . The other parameters present in the population equations are labelled in Table 2.1. The values for all parameters, whether directly used in the population equations or not, are shown in Tables B.2, B.3 and B.4.

Parameter description	Plant, R_i	Pollinator, B_i
Individual resource need	k_{R_i}	k_{B_i}
Environmental niche width	σ_{r,R_i}	σ_{b,B_i}
Reference mutualistic benefit	c_{m,B,R_j}	c_{m,R,B_k}
Peak mutualistic trait value	μ_{γ,R_i}	μ_{β,B_i}
Mutualistic niche width	σ_{γ,R_i}	σ_{β,B_i}

TABLE B.1: Description of parameters used in the model, which the population equations, (2.1) and (2.2), indirectly depend on. See Appendix A for detailed definitions.

Parameter	R_1	R_2
g_{R_i}	$\ln 5 \approx 1.51$	$\ln 3 \approx 1.10$
k_{R_i}	1	2
μ_{r,R_i}	2	4
σ_{r,R_i}	0.7	1.3
c_{m,B,R_j}	0.05	0.1
μ_{γ,R_i}	1	2
σ_{γ,R_i}	0.5	1

TABLE B.2: Parameter values for every plant species, R_i .

As a general consideration, it is intended that the ETPDFs and MTPDFs should have standard deviations rising in rough proportion to their respective peak trait values, also considering whether a species might be generalist or specialist in a given aspect. Notably, the standard deviations for the substituting invader, assumed to be a honeybee, are chosen to be in line with a very generalist species.

It was judged that reasonable bounds for the parameters varied were:

Parameter	B_1	B_2	B_3 (substituting invader)
g_{Bi}	$\ln 5 \approx 1.51$	$\ln 3 \approx 1.10$	$\ln 5 \approx 1.51$
k_{Bi}	1	2	1
$\mu_{b,Bi}$	4	6	3
$\sigma_{b,Bi}$	1	1.5	1
$c_{m,R,Bk}$	0.1	0.05	0.15
$\mu_{\beta,Bi}$	1	2	1.2
$\sigma_{\beta,Bi}$	0.2	0.2	0.4

TABLE B.3: Parameter values for every pollinator species, B_i .

Parameter	For all plants, R_j	For all pollinators, B_k
$\mu_{z,env}$	3	$5 \rightarrow 2^*$
$\sigma_{z,env}$	2	2
$K_{max,z}$	10,000	3,000

TABLE B.4: Parameter values for the environment. The trait "z" stands for either "r" or "b" when the parameter applies to the plant or pollinator environment, respectively. * The value of $\mu_{b,env}$ starts at 5 and asymptotically approaches 2 (see Figure 2.3).

$$\begin{aligned} \mu_{\beta,B3} &\in (0, 3), \\ \sigma_{\beta,B3} &\in (0.1, 0.6), \text{ and} \\ c_{m,R,B3} &\in (0, 1). \end{aligned}$$

For the substituting invader to be relevant in providing benefits to the plants, it was judged suitable for $\mu_{\beta,B3}$ to be close to $\mu_{\gamma,R1}$ and $\mu_{\gamma,R2}$. Since it was judged hard to biologically interpret negative trait values, it was judged reasonable that $\sigma_{\beta,B3} < 0.5\mu_{\beta,B3}$, since there would otherwise be an appreciable fraction of the B_3 population with a negative trait value. Considering that the species in the pollination network are assumed to be dependent mainly on the resources from the environment, and less so on the mutualism, it is reasonable that $c_{m,R,B3} > 0$, corresponding to a non-negligible mutualistic benefit from the invader, and $c_{m,R,B3} < 1$ corresponding to a mutualistic benefit which is smaller than the competition cost for the plants.

The values for g_{Ri} and g_{Bi} were chosen to correspond to either a 5-fold or 3-fold increase in population number per model time unit in the absence of any competition or mutualism (i.e. intrinsic growth, hence the name "intrinsic growth rate" for these parameters).

For each scenario, each species (denoted by "S" below) were given initial populations

$$N_{0,S} = 0.1K_{m,S},$$

which corresponds to 10% of their ideal carrying capacity, $K_{m,S}$. The time period for the model runs of each scenario was 100 model time units, with a time constant for the environmental change, $\tau = 10$ model time units, in the DRS and SIS.

Other than the above considerations, the choice of parameter values is largely based on reasonable relations between species, so that a large species would also have a large resource need, for example. The absolute values of the parameters are not considered in detail in this thesis. When time units are given, it is done mainly to give an indication of how the model might be applied to real ecosystems. However, the time scale used has not been subjected to rigorous scrutiny in this thesis.

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