



Evolutionary emergence of plant and pollinator polymorphisms in consumer-resource mutualisms

Thomas Marcou^{a,*}, Tomás A. Revilla^{a,b}, Vlastimil Křivan^{a,b}

^a Faculty of Science, University of South Bohemia, Branišovská 1760, 370 05 České Budějovice, Czech Republic

^b Institute of Entomology, Biology Centre, Czech Academy of Science, Branišovská 31, 370 05 České Budějovice, Czech Republic

ARTICLE INFO

Keywords:

Pollination
Trait matching
Darwinian dynamics
Trophic interactions
Resource competition

ABSTRACT

Mutualism is considered a major driver of biodiversity, as it enables extensive codiversification in terrestrial communities. An important case is flowering plants and their pollinators, where convergent selection on plant and pollinator traits is combined with divergent selection to minimize niche overlap within each group. In this article, we study the emergence of polymorphisms in communities structured trophically: plants are the primary producers of resources required by the primary consumers, the servicing pollinators. We model natural selection on traits affecting mutualism between plants and pollinators and competition within these two trophic levels. We show that phenotypic diversification is favored by broad plant niches, suggesting that bottom-up trophic control leads to codiversification. Mutualistic generalism, i.e., tolerance to differences in plant and pollinator traits, promotes a cascade of evolutionary branching favored by bottom-up plant competition dependent on similarity and top-down mutualistic services that broaden plant niches. Our results predict a strong positive correlation between the diversity of plant and pollinator phenotypes, which previous work has partially attributed to the trophic dependence of pollinators on plants.

1. Introduction

Mutualism is known to influence species richness (Chomicki et al., 2019) and is assumed to have played a key role in diversifying life. One example of its influence is the diversification of flowering plants into approximately 300 000 species (Bascompte, 2019), generally attributed to their mutualistic partnership with their pollinators, even though recent studies indicate a mismatch between the diversification of angiosperms and the diversification of their pollinators (Asar et al., 2022). Many underlying mechanisms can lead mutualism to influence biodiversity, whether by increasing or decreasing the speciation or the extinction rate of involved species (Chomicki et al., 2019). Some of them are ecological mechanisms, for example, decreasing the extinction rate of a species by improving its survival rate or reproduction rate (e.g., ant-plant mutualism that decreases herbivory pressure on the plant (Trager et al., 2010), or pollination that increases pollen dispersal). On the other hand, some mechanisms influence the evolution of interacting species, for example, through niche broadening, which promotes adaptive radiation (Litsios et al., 2012), or through host shifts, also known to promote speciation (Breitkopf et al., 2015).

One of these evolutionary mechanisms is coevolution, “a reciprocal evolutionary change among interacting species driven by natural selection” (Thompson, 2013). In the case of antagonistic interactions,

such as competition, predation, or parasitism, coevolution often leads at least one of the interacting species to develop an adaptation to decrease the negative impact of the interaction on its fitness. A good example is the coevolution between crossbills (Aves: *Loxia*) and conifers, where crossbills have evolved large and powerful bills in response to seed defense mechanisms enabled by complex cone geometry (Benkman et al., 2010). On the contrary, in the case of mutualism, interacting species display adaptations that facilitate or strengthen their interaction. The most common pattern of coevolution is the matching of mutualistic traits, such as the matching between the shape and size of the prostomata of some myrmecophytic plants and the shape and size of the ants associated with them (Brouat et al., 2001). A less common coevolution pattern is trait mismatching, which occurs when the interests of both species are not exactly aligned (Anderson, 2015). Coevolution can sometimes lead to cospeciation, where “two or more interacting lineages undergo matched speciation events during their phylogenetic history” (Thompson, 2013). A well-known example of coevolution and cospeciation in pollination is the relationship between the fig and the fig wasp (Rønsted et al., 2005), even though phylogenetic studies suggest that in some cases, fig wasp speciation might be induced by host shift rather than by strict cospeciation (Cook and Segar, 2010).

* Corresponding author.

E-mail addresses: thomas.marcou@yahoo.fr (T. Marcou), tomrevilla@gmail.com (T.A. Revilla), vlastimil.krivan@gmail.com (V. Křivan).

<https://doi.org/10.1016/j.jtbi.2024.111911>

Received 26 March 2024; Received in revised form 17 July 2024; Accepted 21 July 2024

Available online 26 July 2024

0022-5193/© 2024 Elsevier Ltd. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

Investigating the underlying mechanisms leading to coevolution would allow a better understanding of how mutualisms like pollination promote biodiversity. One way to explore such processes is by simulating the evolutionary dynamics of complex bipartite mutualistic networks using mathematical models (Nuismer et al., 2013; Guimarães et al., 2011; Minoarivelo and Hui, 2016; Hui et al., 2018; Guimarães et al., 2017). These models typically assume that the rules governing the dynamics of one partite are mirror images of rules governing the other, e.g., plant competition and pollinator competition both follow Lotka–Volterra equations (Bastolla et al., 2009). This approach is easier to generalize to many systems (plant–pollinator, plant–fungus, plant–ant, ant–myrmecophiles), but it can be lacking in ecological realism (Levins, 1966). An alternative approach, promoted by Holland and DeAngelis (2010), acknowledges the consumer–resource relationships behind numerous plant–animal mutualisms, where plants are the resource producers and pollinators are the consumers. Mechanistic implementations of this approach, for small community modules (Revilla and Křivan, 2016, 2018) or large communities (Valdovinos et al., 2013; Becker et al., 2022), could improve our understanding of plant–pollinator coevolutionary dynamics through well developed theoretical frameworks, such as resource competition theory (Grover, 1997), niche overlap and character displacement theories (MacArthur and Levins, 1967; MacArthur, 1970; May, 1974a; Roughgarden, 1972).

In this article, we use mathematical modeling to investigate evolutionary diversification in plant–pollinator communities by disruptive selection (Rueffler et al., 2006). We assume that plants and pollinators are mutualistic partners and can be seen as, respectively, primary producers and consumers. Mutualism depends here on plant and animal traits (metric characters that specify phenotypes) that must match to return benefits for both parties. At the same time, traits involved in plant–pollinator matching are assumed to affect plant competition for limiting factors, as well as indirect competition between pollinators for resources produced by the plants, such as nectar or pollen. Thus, an important goal of this article is to understand how species diversification and the impact of mutualisms are affected by the shape of species niches and the level of specialization/generalism.

Evolutionary Game Theory (EGT) (Maynard Smith and Price, 1973; Sigmund and Nowak, 1999) is a useful framework for studying trait evolution under natural selection. Maynard Smith and Price (1973) defined evolutionarily stable strategy (ESS) as “a strategy such that, if most of the members of a population adopt it, there is no ‘mutant’ strategy that would give higher reproductive fitness”. This approach is fully static: it predicts final or “optimal” trait values but does not model the dynamics of trait evolution. More recent approaches explicitly consider trait dynamics and its various feedbacks with ecological dynamics. One of these approaches is Adaptive Dynamics (Geritz et al., 1998, 2004). This approach separates the time scales of ecological and evolutionary dynamics, where ecological dynamics are assumed to run much faster than trait dynamics. Thus, population densities are supposed to be at an equilibrium that tracks trait changes. The approach that does not assume time scale separation between population and trait dynamics is called Darwinian Dynamics (Vincent and Brown, 2005, see also Bukkuri and Brown, 2021; Cohen et al., 1999). This approach was used, e.g., to investigate the conditions for disruptive selection (Doebeli and Dieckmann, 2000), or coevolution (Ripa et al., 2009).

Through analytical results and numerical simulations, we describe how the trophic organization of plant–pollinator communities, similarity-dependent competition, and the niche-widening effect of pollinators on the plants trigger a process of mutually assisted diversification for both groups.

2. Methods and results

Here, we develop a model that describes eco-evolutionary dynamics in plant–pollinator communities and branching events. We assume that, initially, there is a single plant (P) and a single pollinator (M) species.

Population dynamics of this system are described by differential equations where some, but not all, parameters depend on plant trait (x) and pollinator trait (y). Traits (also called phenotypes or strategies) undergo evolutionary dynamics by small mutations toward higher plant and pollinator fitness. Once the system reaches a stable population–trait equilibrium where neither traits nor population numbers change, we determine if disruptive selection occurs. If yes, an evolutionary branching event occurs, and the number of plant or pollinator morphs increases until an evolutionarily stable strategy (ESS) is attained. At an ESS, all resident plant and pollinator morphs are at their local fitness maxima, disruptive selection is not possible, and the community resists further invasion by novel, mutated morphs. Conditions for branching of the initial one-plant–one-pollinator system, and for the two-plant–one-pollinator system, can be obtained analytically (see Section 2.2). As the number of morphs increases, conditions for branching cannot be obtained analytically, and we numerically simulate plant and pollinator coevolution (see Section 2.3).

In the next section, we describe the population dynamics of a community that has already branched and consists of n plant morphs and m pollinator morphs.

2.1. Plant–pollinator eco-evolutionary dynamics

2.1.1. Population dynamics

The population dynamics of a community that has already branched to n plant and m pollinator morphs follow a trophic-based model of mutualism (see Appendix A)

$$\begin{aligned} \frac{dP_i}{dt} &= P_i \left\{ \frac{r \sum_{j=1}^m a(x_i, y_j) M_j}{1 + \sum_{j=1}^m a(x_i, y_j) M_j} \left(1 - \frac{\sum_{k=1}^n c(x_i, x_k) P_k}{K(x_i)} \right) - d \right\}, \\ & \quad i = 1, \dots, n \\ \frac{dM_j}{dt} &= M_j \left\{ e \sum_{i=1}^n \frac{a(x_i, y_j) P_i}{1 + \sum_{\ell=1}^m a(x_i, y_\ell) M_\ell} - g \right\}, \quad j = 1, \dots, m \end{aligned} \quad (1)$$

where P_i is the i th plant morph biomass density, and M_j is the j th pollinator morph biomass density. The plant population growth rate saturates with pollinator densities, with the maximum growth rate of r . Pollinator growth depends linearly on plant densities, and e is conversion efficiency from plant resources to pollinator births. Plants and pollinators die with intrinsic mortality d and g , respectively. These parameters are assumed to be identical for all morphs because they do not depend on plant or pollinator traits.

Now we describe parameters that are trait dependent, i.e., depend either on the plant or pollinator traits. As we have n plant morphs, there are n corresponding trait values x_i , $i = 1, \dots, n$ that are morph dependent, and similarly, there are m pollinator morph trait values y_j , $j = 1, \dots, m$. These trait parameters represent positions along a uni-dimensional niche space (Roughgarden, 1972), an abstraction of real-world Hutchinsonian niches (e.g., a “nectar tube length, flowering season, ..., flower shape” hyper-volume). Morphs with close trait values are expected to interact more strongly inside such niches than distant ones. In the case of plant–pollinator interactions, we assume these traits are essential for pollination and resource consumption (e.g., flower tube and butterfly proboscis lengths, flowering times, and pollinator activity times). The dependence of parameters on traits is given in the next section.

Plant recruitment is density-regulated by competition against adult plants (e.g., competition for space, mineral nutrients), following the Lotka–Volterra model where $K(x_i)$ is the plant’s environmental carrying capacity, and $c(x_i, x_k)$ are competition coefficients. The strength of plant–pollinator interactions depends on mutualistic coefficients $a(x_i, y_j)$ that relate the consumption of plant resources (e.g., nectar or pollen) by pollinators which, in turn, provide pollination services to plants. Mutualistic coefficients also indirectly control competition between pollinators for plant resources according to Schoener (1978)

Table 1
Model parameters and values used for figures and simulations.

Symbol	Description	Values/ranges	Units
r	Plant-specific growth rate	0.04	time ⁻¹
e	Pollinator conversion efficiency	0.04	time ⁻¹
d	Plant mortality rate	0.01	time ⁻¹
g	Pollinator mortality rate	0.01	time ⁻¹
$K(x_i)$	Plant carrying capacity	Eq. (2)	mass
$c(x_i, x_k)$	Competition coefficient	Eq. (4)	dimensionless
$a(x_i, y_j)$	Mutualist coefficient	Eq. (3)	mass ⁻¹
K_0	Scale of plant carrying capacity	15	mass
a_0	Scale of the mutualistic coefficient	1	mass ⁻¹
x_i	Plant i trait	$(-\infty, \infty)$	dimensionless
y_j	Pollinator j trait	$(-\infty, \infty)$	dimensionless
σ_k	Width of the carrying capacity kernel	10,14,16	dimensionless
σ_c	Width of the plant competition kernel	4,6,9	dimensionless
σ_m	Width of the plant-pollinator interaction kernel	4,8,12	dimensionless
$\mu_p \mu_m$	Rate of plant pollinator evolutionary change	1	time ⁻¹

energy-based model. Unlike other models commonly used to model bipartite mutualist networks, where dynamical equations are symmetric for both parties (e.g., Lotka–Volterra for plants and for pollinators; Minoarivelo and Hui, 2016), the equations for plants and animals are very different because of the distinct trophic roles of both groups. In the bulk of trophic interaction theory, competition at the higher level for resources is typically assumed to be in the form of indirect competition for multiple resources (Holt, 1977; Vandermeer and Pascual, 2006) without assuming direct competition in the form of interference, whereas mechanisms responsible for competition at the base trophic level (here the plants) are typically described by the Lotka–Volterra competition model. Thus, resource-consumer models are typically asymmetric and we follow the same approach here.

Without mutualism, plant and pollinator populations always go extinct in the model (1), i.e., they are obligate mutualists. Systems like (1) can be used to model mutualistic dynamics, from small community modules (Revilla and Křivan, 2016) to large interaction networks (Becker et al., 2022). This model is trophic-structured: the community has two trophic levels, a primary resource producer level (plants) and a primary resource consumer level (pollinators). But unlike victim-exploiter models (e.g., plant–grazer, host–parasite), the consumers do not “kill and eat” the producers. Table 1 lists model (1) parameters, with their values used in numerical simulations (see Appendix A).

2.1.2. Trait-dependent parameters

The dependence of plant i morph environmental carrying capacity on x_i is given by (Minoarivelo and Hui, 2016; Cressman et al., 2017)

$$K(x_i) = K_0 \exp\left(-\frac{x_i^2}{2\sigma_k^2}\right). \quad (2)$$

This “carrying capacity kernel” assumes that the optimal plant trait value is at $x = 0$ (we remark that trait values can attain both negative and positive values), at which the plant carrying capacity maximizes and equals K_0 . The width of the kernel, σ_k , can be related to the concept of “fundamental niche”, i.e., the environment’s tolerance to plant trait variation before considering the effects of competition or mutualism.

The strength of the mutualism between plant morph i and pollinator morph j depends on the trait difference (Doebeli and Dieckmann, 2000; Nuismer et al., 2013; Minoarivelo and Hui, 2016)

$$a(x_i, y_j) = a_0 \exp\left(-\frac{(x_i - y_j)^2}{2\sigma_m^2}\right), \quad (3)$$

where a_0 is the maximum strength when the two traits match ($x_i = y_j$), and σ_m is the width of the “mutualistic kernel”, e.g., effective range of trait-based mutualism.

The strength of competition between plant morphs i and k with trait values x_i and x_k , respectively, is (Minoarivelo and Hui, 2016; Cressman et al., 2017)

$$c(x_i, x_k) = \exp\left(-\frac{(x_i - x_k)^2}{2\sigma_c^2}\right), \quad (4)$$

where σ_c is the width of the “competition kernel”, e.g., effective range of trait-based plant competition. Eq. (4) implies that the closer the morphs, the stronger their competition due to multiple limiting factors (e.g., nutrient and energy scarcity, common herbivores). Thus, the maximum antagonism between two plant morphs is $c(x_i, x_k) = 1$, when they are identical $x_i = x_k$.

Fig. 1 illustrates how the plant competition coefficient $c(x_i, x_k)$, and the plant–pollinator mutualistic interaction coefficient $a(x_i, y_j)$ depend on trait values and the widths of interaction kernels. Besides these direct interactions, the model (1) also captures indirect interactions, such as competition between pollinators for plant resources. These interactions are also trait-dependent, but they are not shown in Fig. 1.

2.1.3. Evolutionary dynamics

From the previous assumptions, the fitness of a mutant plant individual with trait value x' (respectively y' for a mutant pollinator individual) depends on its trait value and also on trait values $\mathbf{x} = (x_1, x_2, \dots, x_n)$ and $\mathbf{y} = (y_1, y_2, \dots, y_m)$ and population densities $\mathbf{P} = (P_1, P_2, \dots, P_n)$ and $\mathbf{M} = (M_1, M_2, \dots, M_m)$ of the resident morphs already present in the community. From model (1), the expected per capita population growth rates of plant and pollinator mutant morphs are (Vincent and Brown, 2005; Geritz et al., 2004)

$$F(x'; \mathbf{x}, \mathbf{y}, \mathbf{P}, \mathbf{M}) = \frac{r \sum_{j=1}^m a(x', y_j) M_j}{1 + \sum_{j=1}^m a(x', y_j) M_j} \left(1 - \frac{\sum_{k=1}^n c(x', x_k) P_k}{K(x')}\right) - d \quad (5)$$

$$G(y'; \mathbf{x}, \mathbf{y}, \mathbf{P}, \mathbf{M}) = e \sum_{i=1}^n \frac{a(x_i, y') P_i}{1 + \sum_{\ell=1}^m a(x_i, y_\ell) M_\ell} - g.$$

Natural selection favors plant and pollinator trait values that increase individual fitness, which is conceptualized by

$$\frac{dx_i}{dt} = \mu_p \left. \frac{\partial F(x'; \mathbf{x}, \mathbf{y}, \mathbf{P}, \mathbf{M})}{\partial x'} \right|_{x'=x_i}, \quad (6)$$

$$\frac{dy_j}{dt} = \mu_m \left. \frac{\partial G(y'; \mathbf{x}, \mathbf{y}, \mathbf{P}, \mathbf{M})}{\partial y'} \right|_{y'=y_j},$$

where μ_p and μ_m represent some measure of heritability and can be seen as how fast plant and pollinator traits change. The meaning of equations in (6) is that a nearby trait substitutes the current trait only when the new trait value increases fitness. Thus, traits change in the direction of a higher fitness only. Functions F and G describe the adaptive landscape of plants and pollinators, and the system (6) can be interpreted as the selection gradient (Acerenza, 2016). Finally, the model describing the eco-evolutionary dynamics is

$$\begin{cases} \frac{dP_i}{dt} = P_i F(x_i; \mathbf{x}, \mathbf{y}, \mathbf{P}, \mathbf{M}), & \text{for } i = 1, \dots, n & (a) \\ \frac{dM_j}{dt} = M_j G(y_j; \mathbf{x}, \mathbf{y}, \mathbf{P}, \mathbf{M}), & \text{for } j = 1, \dots, m & (b) \\ \frac{dx_i}{dt} = \mu_p \left. \frac{\partial F(x'; \mathbf{x}, \mathbf{y}, \mathbf{P}, \mathbf{M})}{\partial x'} \right|_{x'=x_i}, & \text{for } i = 1, \dots, n & (c) \\ \frac{dy_j}{dt} = \mu_m \left. \frac{\partial G(y'; \mathbf{x}, \mathbf{y}, \mathbf{P}, \mathbf{M})}{\partial y'} \right|_{y'=y_j}, & \text{for } j = 1, \dots, m. & (d) \end{cases} \quad (7)$$

2.2. Evolutionary stability and disruptive selection

2.2.1. Evolutionarily stable strategy

The Evolutionarily Stable Strategy (ESS; Maynard Smith and Price, 1973) conceptualizes the endpoint of evolution. At the ESS, rare mutant morphs cannot invade resident morphs. An equilibrium denoted $(\hat{\mathbf{x}}, \hat{\mathbf{y}}, \hat{\mathbf{P}}, \hat{\mathbf{M}})$, of model (1) is an ESS if it is locally asymptotically stable and satisfies the ESS maximum principle (Vincent and Brown, 2005)

$$\begin{aligned} \max_{x'} F(x'; \hat{\mathbf{x}}, \hat{\mathbf{y}}, \hat{\mathbf{P}}, \hat{\mathbf{M}}) &= F(\hat{x}_i; \hat{\mathbf{x}}, \hat{\mathbf{y}}, \hat{\mathbf{P}}, \hat{\mathbf{M}}) = 0, & i = 1, \dots, n \\ \max_{y'} G(y'; \hat{\mathbf{x}}, \hat{\mathbf{y}}, \hat{\mathbf{P}}, \hat{\mathbf{M}}) &= G(\hat{y}_j; \hat{\mathbf{x}}, \hat{\mathbf{y}}, \hat{\mathbf{P}}, \hat{\mathbf{M}}) = 0, & j = 1, \dots, m \end{aligned} \quad (8)$$

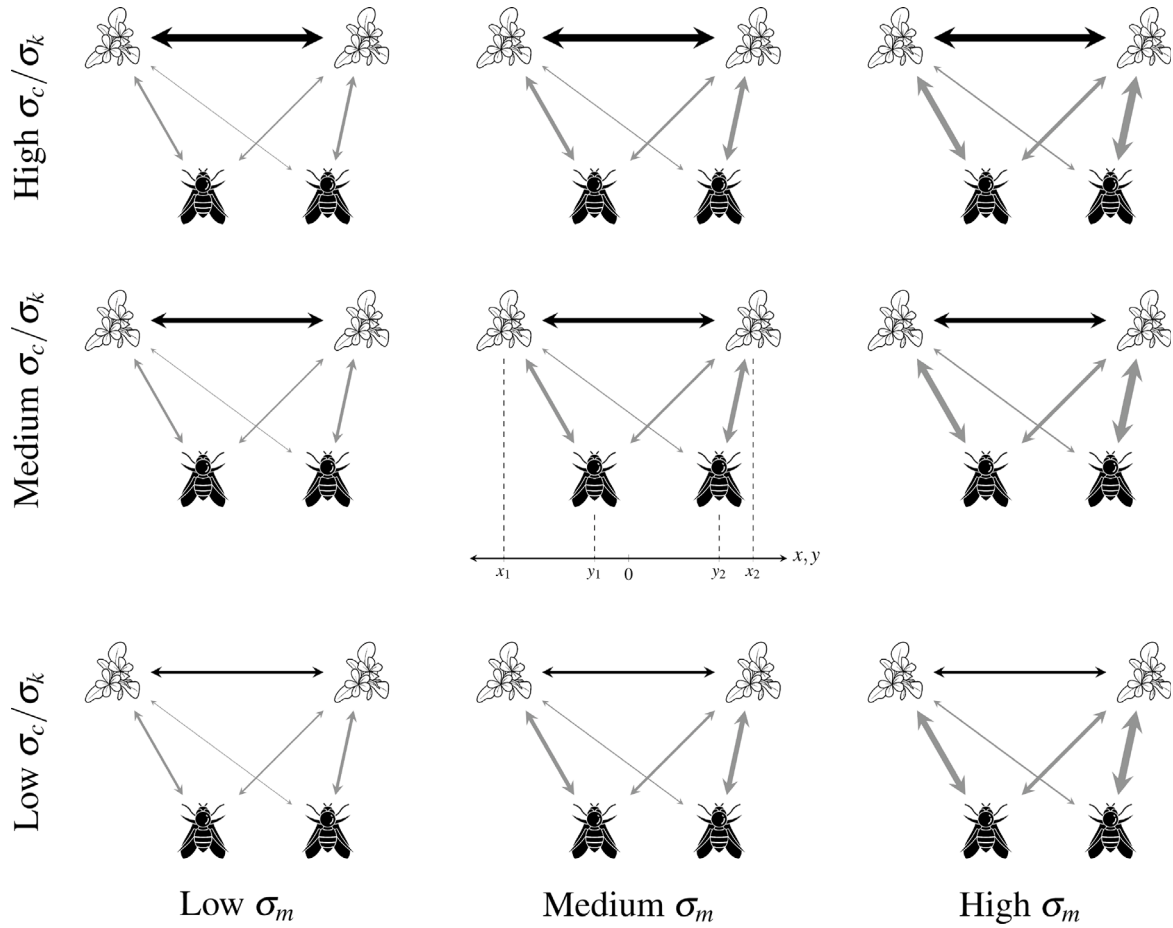


Fig. 1. Trait-based interactions. Thicknesses of gray (black) links are proportional to the relative magnitude of corresponding mutualistic (plant competition) coefficients $a(x_i, y_j)$ ($c(x_i, x_k)$). Mutualism between a plant morph with trait value x_i and a pollinator morph with trait value y_j weakens with the difference $|x_i - y_j|$ along the trait axis (pictured in the middle diagram), and strengthens with the width of the mutualistic kernel σ_m . Competition between plants increases with the width of the competition kernel σ_c relative to the carrying capacity kernel σ_k . Image: Flaticon.com.

where the maxima are calculated for each resident trait \hat{x}_i ($i = 1, \dots, n$) and \hat{y}_j ($j = 1, \dots, m$) over all mutant traits that are close enough to the resident trait. If an equilibrium does not satisfy the ESS maximum principle, a mutant with higher fitness can invade at least one plant or pollinator morph, and branching can occur (Geritz et al., 2004).

2.2.2. Plant first branching condition

When, initially, the community is composed of one plant and one pollinator morph, with densities P and M and trait values x and y , respectively, eco-evolutionary dynamics in (7) are

$$\begin{aligned} \frac{dP}{dt} &= P \left\{ \frac{ra(x, y)M}{1 + a(x, y)M} \left(1 - \frac{P}{K(x)} \right) - d \right\} \\ \frac{dM}{dt} &= M \left\{ \frac{ea(x, y)P}{1 + a(x, y)M} - g \right\} \\ \frac{dx}{dt} &= \mu_P \left\{ -(x - y) \frac{ra(x, y)M}{\sigma_m^2 (1 + a(x, y)M)^2} \left(1 - \frac{P}{K(x)} \right) - \frac{xP}{\sigma_k^2 K(x)} \right. \\ &\quad \left. \times \frac{ra(x, y)M}{1 + a(x, y)M} \right\} \\ \frac{dy}{dt} &= \mu_M \frac{eP(x - y)a(x, y)}{\sigma_m^2 (1 + a(x, y)M)}. \end{aligned} \quad (9)$$

Equations in (9) predict that at the evolutionary equilibrium where $\frac{dx}{dt} = \frac{dy}{dt} = 0$, plant and pollinator traits match and are equal to zero ($x = y = 0$, Appendix B). We denote the corresponding population equilibrium densities \hat{P} for the plant and \hat{M} for the pollinator. They are given in Appendix A and do not depend on σ . Assuming that system

(9) is at this eco-evolutionary equilibrium $(\hat{x}, \hat{y}, \hat{P}, \hat{M}) = (0, 0, \hat{P}, \hat{M})$, we find that the pollinator morph can never be invaded by a mutant pollinator (Appendix B). This means no pollinator branching in a single plant community is possible.

For the plant, the necessary and sufficient condition for branching is (Appendix B)

$$\sigma_k > \frac{\sigma_c}{\sqrt{1 - \left(\frac{\sigma_c}{\sigma_m}\right)^2 \frac{K_0 - \hat{P}}{(1 + a_0 \hat{M}) \hat{P}}}}. \quad (10)$$

This is illustrated in Fig. 2 as the region of the (σ_m, σ_k) plane above the solid line curve given by the right-hand side of (10). Condition (10) implies that plant branching requires two conditions to be met. First, because the denominator in (10) is smaller than one, $\sigma_k > \sigma_c$, that is, the plant niche must tolerate two competing plant populations. Indeed, σ_k can be seen as how broad the “fundamental niche” of the plant is, and σ_c is the “room” one morph occupies in this niche. Second, as the expression under the square root of (10) must be positive, we get that

$$\sigma_m > \sigma_c \sqrt{\frac{K_0 - \hat{P}}{(1 + a_0 \hat{M}) \hat{P}}} =: \sigma_m^*. \quad (11)$$

This inequality means the mutualistic niche must be wide enough for plants to branch. In particular, condition (11) shows that as the width of the competition kernel increases (but it is still smaller than σ_k), the width of the mutualistic kernel σ_m must increase too. This is an example of niche broadening, where mutualism allows plant species to overcome limitations imposed by competition.

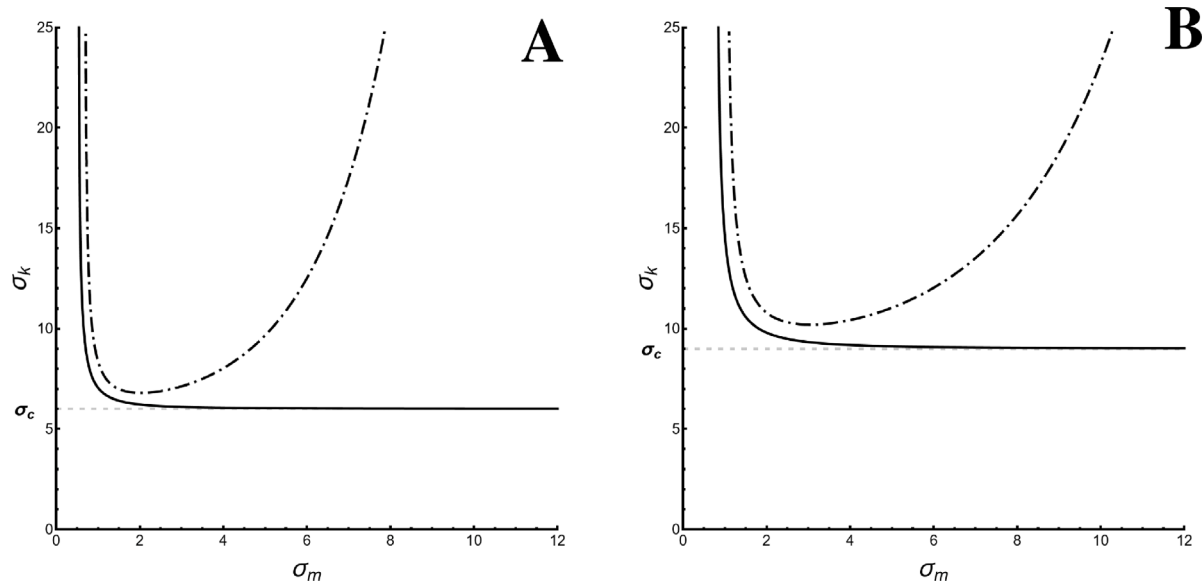


Fig. 2. Graphical representation of condition (10) for the first plant branching (solid line) and condition (12) for the first pollinator branching event when two plant morphs exist (dash-dot line) in (σ_m, σ_k) parameter space. Below the solid line single-plant–single-pollinator system cannot diversify. Above this curve, the plant splits into two morphs, and plant and pollinator evolutionary branching into several morphs can happen. In panel A $\sigma_c = 6$ and in B $\sigma_c = 9$. The other parameter values are given in Table 1.

Starting with one plant and one pollinator, we showed that the pollinator cannot branch, and the plant species can branch only if condition (10) is fulfilled. This first result shows that plant disruptive selection is driven by (trait) similarity-dependent competition (like in, e.g., Cressman et al. (2017) and Minoarivelo and Hui (2016)) but it is constrained by plant–pollinator (trait) matching. This is documented in Fig. 3, where the first branching occurs in the plant community at time $t_1 \approx 131425$, i.e., $\log_2(t_1) \approx 17$. We also observe that the two plant equilibrium trait values are symmetric, i.e., $\hat{x}_1 = -\hat{x}_2 \approx 6.136$. This symmetry arises from the assumption that competition, mutualistic interaction, and carrying capacity kernels are symmetric functions of traits with respect to zero. In the case of two plant species, this trait symmetry is similar to what happens in Cressman et al. (2017).

2.2.3. Pollinator first branching condition

The existence of two plant populations is necessary but not sufficient for pollinator disruptive selection. In other words, pollinator branching requires at least two plant morphs. Here, we provide a condition for pollinator branching in a community consisting of two plant morphs (P_1 and P_2 with trait values x_1 and x_2) and a single pollinator (M with trait value y). The eco-evolutionary dynamics of this community are described in Appendix B. Assuming symmetric plant trait equilibria, i.e., $\hat{x}_1 = -\hat{x}_2 = \hat{x}$, with $\hat{x} > 0$, it is also shown there that the condition for the pollinator to branch is

$$\hat{x} > \sigma_m. \quad (12)$$

This condition states that branching of the pollinator population requires the two plant morphs to be sufficiently different. In other words, (12) means that plant morphs 1 and 2 are considered separate, discrete energy sources from the pollinator’s perspective.

In Fig. 2 condition (12) for pollinator branching when two plant morphs exist holds in the region of (σ_m, σ_k) parameter values above the “u-shaped” dash-dot curve. As expected, this region is a subset of the region where the plant’s first branching condition (10) holds. But unlike the plant’s condition where large σ_m favors branching, pollinator branching is only limited to intermediate σ_m values. This is because for very large σ_m , pollinators tolerate large plant trait differences, which prevents disruptive selection. On the other hand, increasing σ_c facilitates first pollinator branching (cf. Panel A vs. Panel B in Fig. 2) because wide competition kernels lead to larger plant phenotype differences \hat{x} , making condition (12) more likely to hold.

Branching conditions for communities with more plants and pollinators cannot be obtained analytically, nor easily represented like in Fig. 2. In the next section, we analyze evolutionary branching cascades numerically.

2.3. Long-term branching analysis

2.3.1. Coevolutionary simulations

We perform simulations to study further branching events (see Appendix C for details). Each simulation starts with one plant and one pollinator species and with parameters satisfying condition (10) so that the plant can branch at least once. We then simulate the eco-evolutionary dynamics until an equilibrium is reached. If this equilibrium is an ESS, i.e., if all morphs are at local maxima of fitness functions F and G , the simulation stops. If it is not an ESS, it means that a mutant can invade at least one resident morph, and we thus add a new mutant morph (plant or pollinator) with low initial density and trait value close to a randomly selected invadable morph. We repeat this process until an ESS is reached. Panels A–D of Fig. 3 show the typical outcome of a simulation, while Panel E corresponds to the plant (top row) and pollinator (bottom row) adaptive landscapes at each branching event. The first nine branching events at times t_1, \dots, t_9 in Panel E show six branching events in the plant community and three in the pollinator community. The ESS is reached at time t_{10} .

Trait branching forms tree-like phylogenies (Panels B and D in Fig. 3). The timing between branching events increases rapidly (the time scale of Fig. 3 is logarithmic), in other words, branching slows down. The process stops after all resident populations attain (local) fitness maxima on the adaptive landscape, i.e., no mutant has higher fitness (see the final community state at time t_{10} in Panel E).

Fig. 3 is just one possible outcome of the simulation for given parameters, as the branching morphs and the direction of the mutation are chosen randomly at each branching event t_i . E.g., in time t_2 , a plant morph has been added, but a pollinator morph could have been added instead because both plant and pollinator morphs can be invaded at this time (see Panel E). This randomness leads to several possible final communities. Thus, for fixed values σ_k , σ_c , and σ_m we analyze all possible evolutionarily stable communities that can be reached through branching (see the next section and Fig. 4).

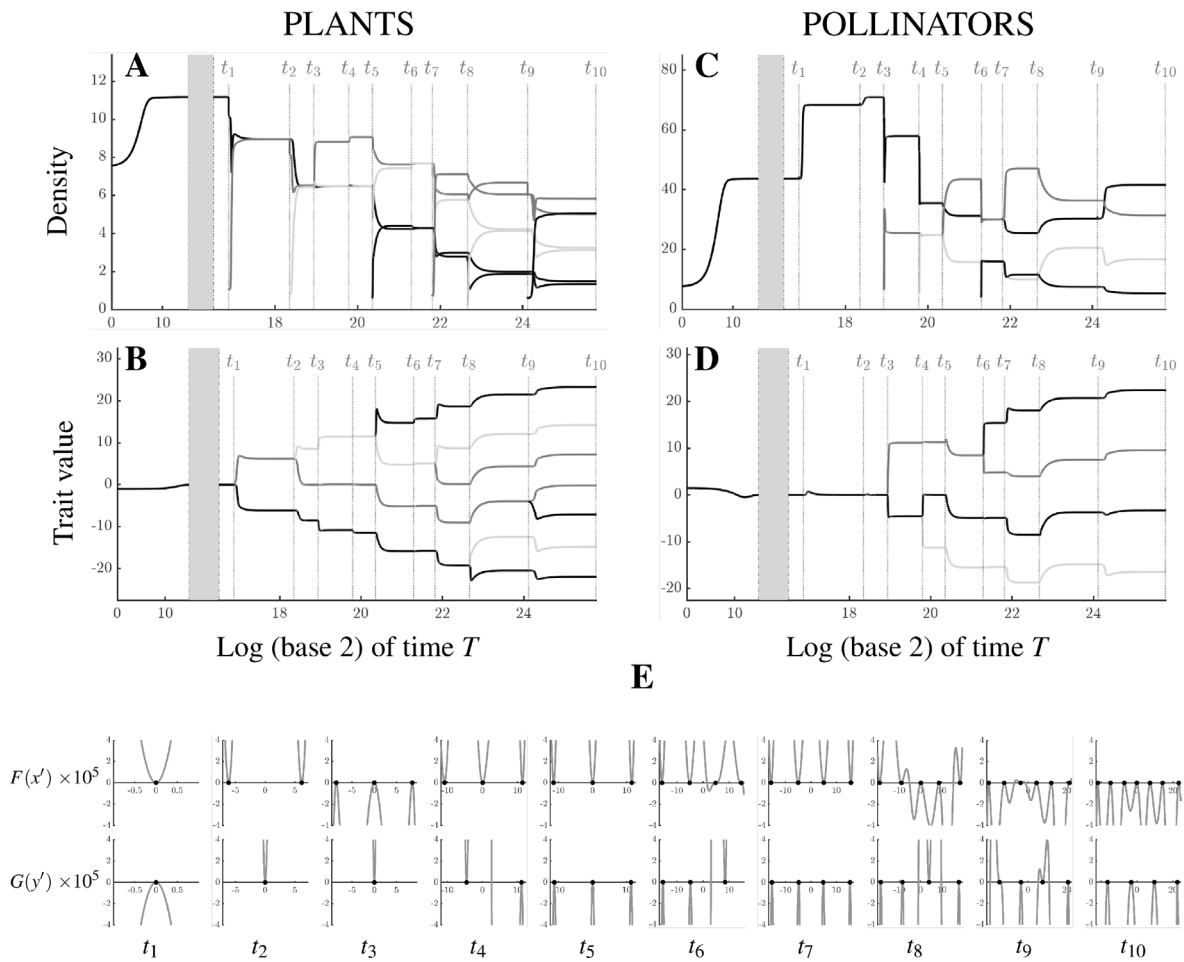


Fig. 3. Simulation of eco-evolutionary dynamics (7). Panels A and C show population dynamics, and panels B and D show trait evolution of plants and pollinators, respectively. Panel E shows adaptive landscapes (5) for plants (upper row, F) and pollinators (bottom row, G) at each branching event t_i , as a function of the mutant trait (x' for plants and y' for pollinators) in the resident population that is at an eco-evolutionary equilibrium shown in panels (A-D). The final community reached at t_{10} consists of 7 plants and 4 pollinators as all plants and pollinator traits are at the maxima of their fitness landscapes, and no further branching is possible. Parameters $\sigma_k = 14$, $\sigma_c = 6$ and $\sigma_m = 4$, and the rest as in Table 1. A time interval (represented by the gray box) has been omitted to better visualize branching.

2.3.2. Plant–pollinator diversification

In this section, we study the dependence of evolutionarily stable communities on parameters σ_k , σ_c , and σ_m . To do this, we fix two and vary the remaining one to see how it influences the final number of plant and pollinator morphs. These results are displayed in Fig. 4, where each panel shows the final number of plants (circle) and pollinators (star) morphs as a function of, respectively, σ_k , σ_c , and σ_m . We observe that there can be multiple numbers of morphs at one parameter value, which is because several evolutionarily stable communities may exist due to the particular sequence of invading morphs at branching events as described at the end of the previous section and in Appendix C.

To sum up, higher values of σ_k (Panel A) and smaller values of σ_c (Panel B) facilitate plant and pollinator branching, likely because tolerant environments (i.e., wider plant carrying capacity kernel) and weaker competition (narrower plant competition kernel) impose fewer constraints to plant branching. This, in turn, facilitates pollinator branching as there will be more plants. On the other hand, σ_m has contrasting effects. Whereas increasing it raises the number of plant morphs (Panel C), the number of pollinator morphs is hump-shaped. The positive influence of σ_m on plant diversity can be explained as follows. A larger σ_m implies a greater scope for mutualistic interaction so that plants can be more easily pollinated by a diverse array of pollinators, opening the door to more diversification through branching for both plants and pollinators. However, at some point, a large σ_m implies

a large overlapping of pollinator niches, making it more difficult for a mutant pollinator to invade, which explains the decreasing number of pollinator morphs for σ_m large enough.

We calculate the average interaction strength for each ESS community, averaging absolute values of the off-diagonal elements of the Jacobian matrix of the system (1). Unlike interaction coefficients ($c(x_i, y_j)$ and $a(x_i, x_k)$), Jacobian matrix elements account for all direct and indirect effects (e.g., apparent competition or mutualisms) between interacting pairs (plant–plant, plant–pollinator, pollinator–pollinator), weighed by abundances. Fig. 5A shows that our simulated communities are strongly biased towards weak interactions. This implies that the plant–pollinator coevolution drives communities in the direction that promotes local stability (*sensu* May, 1974b) and resilience (fast dampening of small perturbations). We also found that final communities tend to consist of approximately 1.5 plant morphs per pollinator, see Fig. 5B (correlation coefficient $R \approx 0.62$). Visual examination of many interaction graphs, like the one showcased in Fig. 5C, indicates that pollinators tend to specialize on two plant morphs, and plants interact strongly with one pollinator.

We also calculate connectance $\left(\frac{\text{No. of realized links}}{\text{No of plants} \times \text{No. of pollinators}} \right)$, nestedness (NODF, see Almeida-Neto et al., 2008), and modularity (LPBrim, see Liu and Murata, 2010) for each simulated evolutionarily stable community from Fig. 4. For each community, we created a binary interaction matrix $A = (a_{ij})$ with $a_{ij} = 1$ if interaction strength $a(x_i, y_j)$ between plant i and pollinator j is above a given threshold ϵ , and

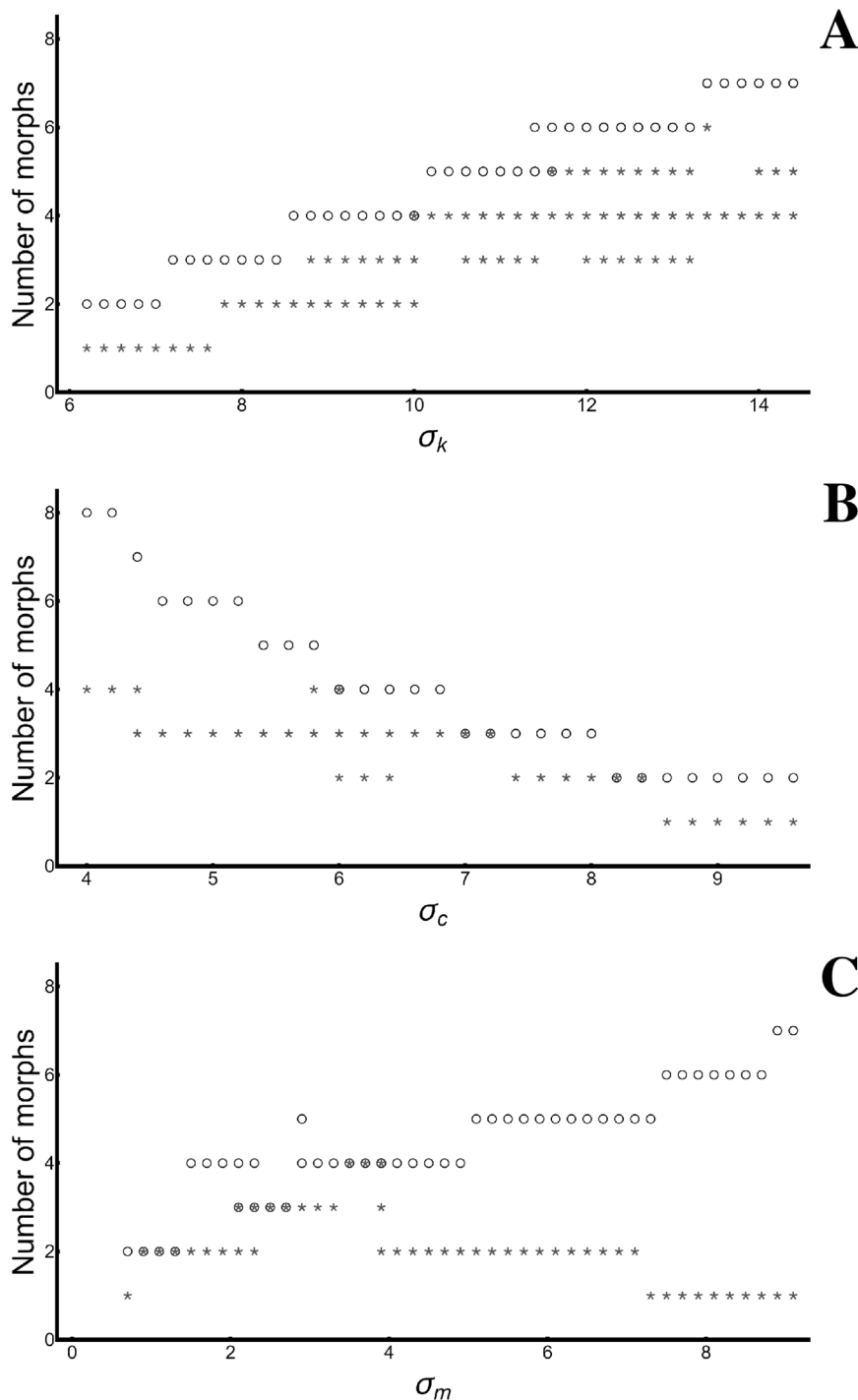


Fig. 4. Number of all possible plant (○) and pollinator (*) morphs attainable by evolutionary branching, as a function of kernel widths for environmental carrying capacity (σ_k , Panel A), competition (σ_c , Panel B) and mutualistic interaction (σ_m , Panel C). Parameters: $\sigma_c = 6, \sigma_m = 4$ in A; $\sigma_k = 10, \sigma_m = 4$ in B; $\sigma_k = 10, \sigma_c = 6$ in C; and the rest as in Table 1.

$a_{ij} = 0$ if below. Analyzing these communities with $\epsilon = 0.001$, we found av. connectance = 0.73 ± 0.2 , av. nestedness = 0.32 ± 0.27 , and av. modularity = 0.19 ± 0.15 . These results and those for $\epsilon = 0.01$ and $\epsilon = 0.0001$ are in the electronic supplement S1. It is shown there that average connectance tends to increase with the width of mutualistic kernel σ_m because pollinators can interact with more plants, which, in turn, decreases modularity. Nestedness is favored by intermediate values of σ_m , likely because lower values produce very small communities that are strongly linked, whereas large values produce communities with a single pollinator that are fully connected. The trend differs for the width of carrying capacity kernels σ_k . As σ_k increases and plants

diversify, pollinators can specialize on a limited set of plants, decreasing connectance and increasing modularity. Nestedness is also higher for intermediate σ_k , likely for the same reason as before: communities are structurally simpler for extreme values. Fig. 6 shows interaction matrices and associated interaction networks for two communities for threshold $\epsilon = 10^{-3}$ (that is 0.1% of the maximum possible interaction strength $a_0 = 1$). The interaction network in Panel A, which corresponds to the phylogeny tree shown in Fig. 3 and the network in Fig. 5(C) is moderately modular and weakly nested, while the one in Panel B is more nested and less modular. This is a consequence of a narrower fundamental plant niche in panel B.

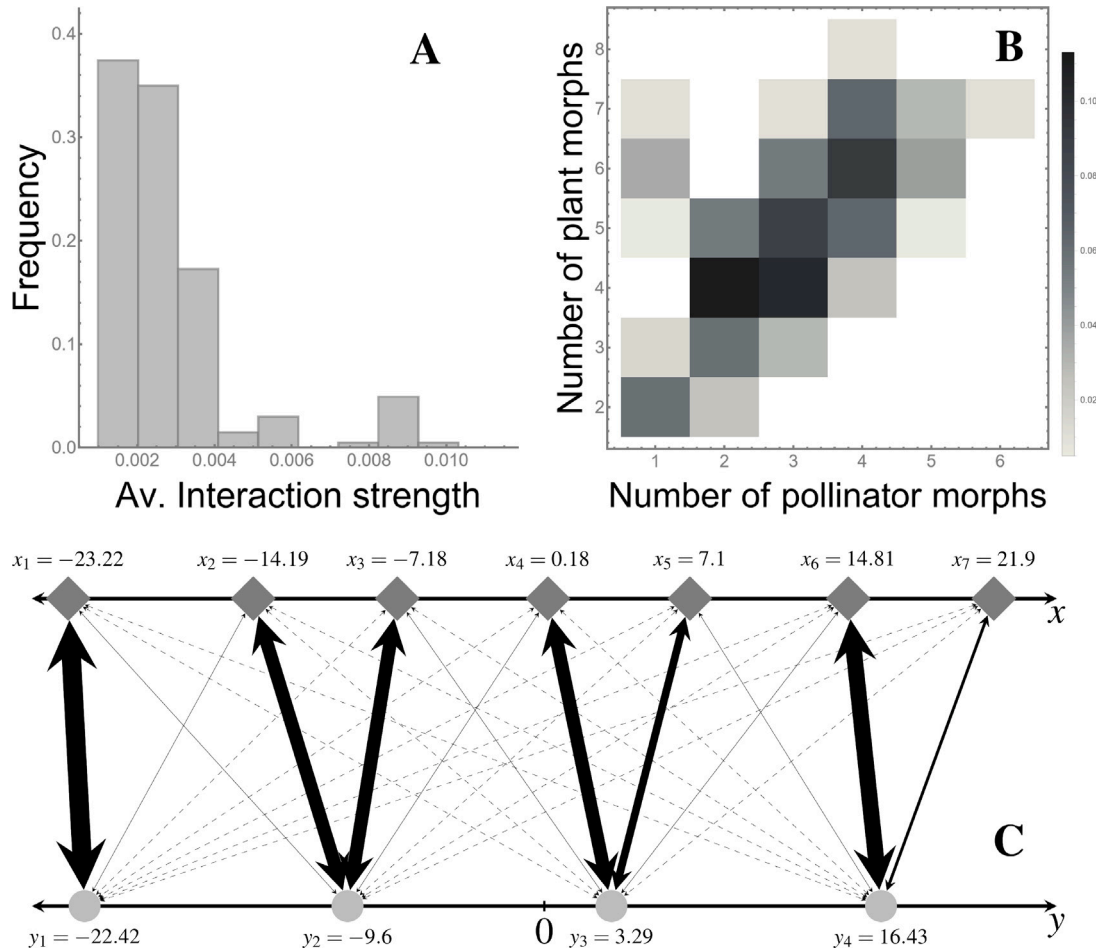


Fig. 5. Communities at the end of evolutionary simulations when ESS is reached. (A) Distribution of interaction strength in simulated communities at the ESS (see details in the main text). (B) Number of plant vs. number of pollinator morphs. Shading indicates the relative frequency of a combination. The slope of the plant vs. pollinator relationship is 1.517 ($R^2 \approx 0.6243$). (C) Example of a community with 7 plants (squares) and 4 pollinators (circle) morphs (final ESS from Fig. 3) distributed along trait axes x and y , respectively. The widths of mutualistic links (solid lines) are proportional to interaction strength that satisfies $a(x_i, y_j) > 10^{-3}$. Dashed lines represent all weak interactions satisfying $a(x_i, y_j) < 10^{-3}$. Parameters are those given in the caption of Fig. 3.

3. Discussion

In this article, we model the evolution of mutualism between plants and pollinators. Our model shows that mutualism increases plant environmental tolerance, making it easier for plants to branch into separate morphs in response to competition (e.g., for nutrients, light, or space). In response to competition for plant resources, pollinator branching requires the number of plant morphs to be larger than pollinator morphs, i.e., pollinator diversification tracks plant diversification. Evolutionary branching stops in a finite time when the system reaches an evolutionarily stable state. Analysis of resulting communities reproduces some features observed in the real plant–pollinator networks, such as a high frequency of weak interactions and a strong correlation between plant and pollinator diversities.

Our eco-evolutionary model considers trophic structures where plants produce nectar consumed by pollinators that provide pollination services to plants. Plants compete for space and resources, and pollinators compete for plants’ resources. Evolutionary modeling starts with a one-plant–one-pollinator system, and we analyze under which conditions a mutant plant or pollinator can invade this system. Such invasion events are termed branchings. We obtained two explicit conditions (10) and (11) for the first plant branching. The first condition implies that the plant’s environmental tolerance to trait change must be broader than the scope of competition, i.e., $\sigma_k > \sigma_c$. The second condition

shows that the effective tolerance (i.e., ability to branch) increases by density-dependent mutualistic feedback via pollinators, and the larger the mutualistic niche or pollinator generalism (σ_m), the easier plant branching is (see Fig. 2). Although the ecological dynamics (1) assumes that plants are obligate mutualists, our predictions concerning first branching conditions still hold if mutualism is facultative for plants (i.e., plants can reproduce vegetatively, see Appendix D). In this case, the first branching occurs for a wider set of σ_m and σ_k values; and just like in the obligate case, branching requires a minimum, nonzero width for the mutualistic kernel, like condition (11). Plants can start branching independently of animal traits and densities only when the interaction is commensalism (i.e., plants do not get pollination benefits, Appendix D).

The model also predicts that plant branching is necessary for first pollinator branching, i.e., the pollinator’s first evolutionary branching event lags behind plant branching events. This is reflected by condition (12) illustrated in Fig. 2: the parameter set where pollinator branching is possible is a subset of parameters that allow plant branching. Thus, the model predicts that community diversification is initiated by similarity-dependent competition between plants (Roughgarden, 1972; Cressman et al., 2017) and regulated by top-down control in the form of pollinator mutualism.

We also show that trait-based mutualism has contrasting effects on plant and pollinator evolutionary branching. A wide mutualistic kernel,

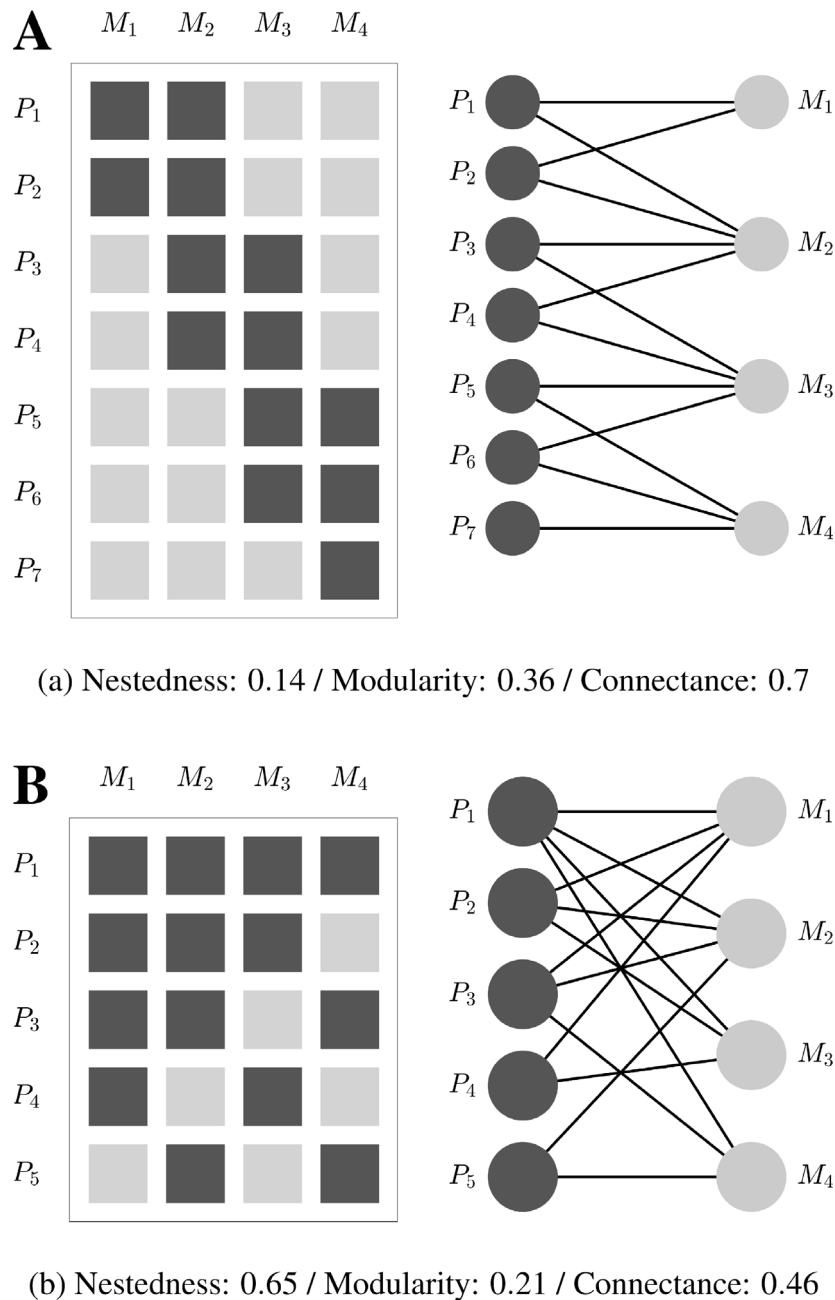


Fig. 6. Examples of two plant–pollinator evolutionarily stable interaction networks after removing weak mutualistic links satisfying $a(x_i, y_j) < 0.001$. The left panels show the interaction matrix with plants in rows and pollinators in the columns, and the right panels show the corresponding interaction network. Panel A ($\sigma_k = 14$, $\sigma_c = 6$ and $\sigma_m = 4$) is obtained from the network displayed in Fig. 5C. The network in panel B ($\sigma_k = 11.2$) assumes a narrower plant fundamental niche. Other parameters as in Table 1.

i.e., large σ_m , effectively enlarges plant niches, turning plant branching into an effective competition escape mechanism (i.e., inequality (10) holds). In contrast, a wide mutualistic kernel also means that pollinators turn into extreme generalists (when condition (12) does not hold), making pollinator branching unlikely because the mismatch between plant and pollinator traits is highly tolerable.

Conditions for further branching events (e.g., from 2 to 3 plant morphs) cannot be obtained analytically. Our numerical simulations suggest that these predictions for small communities (1 plant–1 pollinator, 2 plants–1 pollinator morphs) also hold for larger communities, which display phylogenetic cascades (Fig. 3) where pollinator branching follows branching of plant morphs. The diversity patterns associated with evolutionary stable strategies (ESS) indicate a positive

relation between the final number of plant morphs and mutualistic generalism, measured by the width of the mutualistic kernel, but a hump-shaped relation in the case of pollinators (Fig. 5).

Evolutionary stable communities predicted by our simulations are characterized by skewed distributions of interaction strengths, with a high frequency of weak and low frequency of strong interactions (Fig. 5A). This result is concordant with the empirical study by Vázquez et al. (2012), which also suggests that the interaction structure of plant–pollinator communities is similar to that of food webs. This bias towards weak interactions also happens with models of species assembly (Wootton and Emmerson, 2005), and it is thought to promote stability in large and complex communities (May, 1974b; McCann et al., 1998). Our finding is very relevant in the context of the stability of

mutualistic networks because simple models of mutualism are assumed to be destabilizing from a population dynamics perspective (e.g. May, 1974b, p. 224).

Our simulations predict that the number of plant and pollinator morphs increases with the width of the plant environmental carrying capacity kernel (σ_k , Fig. 4A) and a strong positive correlation between plant and pollinator diversities emerges from evolutionary branching, with approximately 1.5 plant morphs per pollinator (Fig. 5B). With our choice of parameter values final evolutionarily stable communities with six or seven plants per pollinator are rare and require wide mutualistic niches (large σ_m). This indicates a tendency towards pollinator specialization and plant niche packing, i.e., filling the plant resource niche while minimizing sharing. Empirical studies have found positive correlations between plant and pollinator diversities. For instance, in a phylogenetic study of bat and hummingbird pollination, Fleming et al. (2005) states, “The regional and local diversity of appropriate flowers controls the diversity of nectar-feeding bats and birds. This conclusion is strongly supported by the tight correlation between the number of nectar-bat or hummingbird flowers at a site and the number of nectar-bats and hummingbirds at that site”. A field experiment of Ebeling et al. (2008) also found a strong correlation, with the number of visiting pollinator species saturating with flowering species richness. Although this is not an evolutionary/phylogenetic study, the authors attribute the saturation effect to the limited availability of floral resources, one of the mechanisms causing competition and driving natural selection for the pollinators in our model.

We also explored the architecture of evolutionarily stable plant–pollinator networks obtained after eliminating very weak mutualistic links (see supplementary file S1). Empirical mutualistic networks tend to show nested interaction patterns (Bascompte and Jordano, 2007), where specialists tend to interact with species that form subsets of the species with which generalists interact. Our simulations show that nestedness as well as compartmentalization, where groups of plants and pollinators tend to form isolated modules, depend on the width of the three kernels as shown in the electronic supplement S1.

3.1. Bounded diversification

In our model, plant evolution is driven by two tendencies: (i) trait matching between plants, and (ii) trait matching between plants and pollinators. The first (i) causes similarity-dependent competition and the packing of plant niche (MacArthur and Levins, 1967; MacArthur, 1970; May, 1974a; Abrams, 1983), constrained by environmental tolerance (σ_k) and limiting similarity (σ_c). This is the mechanism directly responsible for plant evolutionary branching (this is demonstrated in Appendix D, which shows that similarity-dependent plant competition causes disruptive selection under commensalism, i.e., plants not being pollinated when nectar is consumed). The second (ii) tendency sets the effective size of realized niches. First, pollinator matching controls freedom of plant trait movement along the plant trait axis (large σ_m provides more freedom). Second, it improves trait-mismatch tolerance by raising pollinator densities (pollination service feedback). Thus, plant–pollinator mutualistic feedbacks constrain plant branching.

In contrast, pollinator evolution is driven by a single tendency: trait matching with plants, which is also indirectly responsible for pollinator resource competition. The competitive exclusion principle (Grover, 1997) prevents the stable coexistence of more pollinator morphs than is the number of discrete resources, i.e., nectar-providing plant morphs. As a result, pollinator diversification always lags behind plant diversification. Trophic trade-offs further bind diversification because matching one plant morph trait causes a mismatch with other plant morph traits. An important consequence of this trade-off is that the greater the pollinator generalism (σ_m , i.e., tolerance of trait-mismatch), the less likely pollinator evolutionary branching.

We can summarize the two previous paragraphs as follows. Pollination services widen plant realized niches, making plant evolutionary branching into multiple morphs a favorable strategy (10) in response to competition. This niche-widening effect relates positively with plant and pollinator densities (11), which get larger due to mutualism. For pollinators, disruptive selection occurs in response to the emergence of multiple resource suppliers (plant morphs), provided that generalism is limited, see (12). If pollinator branching happens, plant niches get wider again, and further diversification is favored (as shown by the simulations).

It is interesting to compare the evolutionary outcomes from our model with the results found by Cressman et al. (2017) in the case of pure competition, where all species belong to the same group (e.g., plants only) and population dynamics are described by Lotka–Volterra equations. They found that evolutionary branching never stops, leading to infinite niche packing with species traits repeatedly converging to fitness minima and their populations tending to zero. They concluded that finite diversity requires additional niche constraints, for example, positive carrying capacities restricted to finite domains in trait space or competition coefficients decreasing with trait differences but never approaching zero (Cressman et al., 2017).

In contrast with Cressman et al. (2017), our model predicts that evolutionary branching stops at a finite time. One reason is that, unlike competition, which promotes trait divergence, mutualism promotes trait matching (between plants and pollinators), i.e., convergent evolution. This tends to be restrictive for phenotype diversification (Yoder and Nuismer, 2010; Maliet et al., 2020; Raimundo et al., 2014), and in particular for the pollinators, which are obligate mutualists in our model. Another reason is that mutualistic benefits are limited for both parties. For pollinators, resource supply is limited by plant environmental carrying capacity. For plants, pollination experiences diminishing returns caused by resource competition between pollinators. Another way to see this is by extrapolating conditions (10) and (11) to large communities: as plant and pollinator morphs accumulate and their abundances (\hat{P}_i, \hat{M}_j) decline in response to competition, σ_k and σ_m values become insufficient for plant branching. This also could explain why time intervals between evolutionary branching events get progressively longer (Fig. 3).

It is important to stress the point that evolutionary branching of morphs according to our model (as well as e.g., Cressman et al., 2017; Minoarivelo and Hui, 2016), is not synonymous with *speciation*. Still, disruptive selection of the kind predicted here would enable sympatric speciation of polymorphic plant and pollinator populations, given appropriate mechanisms of reproductive isolation within each group, e.g., assortative mating (Doebeli and Dieckmann, 2000).

3.2. Trophic organization

Most mathematical and simulation models of bipartite mutualistic networks (e.g., Bastolla et al., 2009; Nuismer et al., 2013; Minoarivelo and Hui, 2016, 2018) described by the Lotka–Volterra type equations, do not capture the trophic structure of the network, because they do not consider explicitly plant resources consumed by pollinators. However, almost all plant–animal mutualisms are mediated by resource exchange (Holland and DeAngelis, 2010), and plants and pollinators are quite distinct in their roles as producers or consumers, respectively, with energy (e.g., nectar) flowing bottom–up and services (e.g., fertilization) flowing top–down, closing the mutualistic feedback. This means that the joint effects of inter-group mutualism and intra-group competition operate distinctly on plants and pollinators, and capturing this trophic asymmetry requires modeling their dynamics differently. In the case of the animals, competition is explicitly derived from resource consumption dynamics (of nectar or pollen), leading to the competitive equations originally proposed by Schoener (1978).

In the case of plants, our model does not specify the competition mechanism. Competition between plants is difficult to model because limiting factors such as space, light, and nutrients require different modeling approaches (Grover, 1997). In addition, there are additional sources of plant–plant antagonism connected with pollination, such as competition for pollinator visits and pollen loss caused by hetero-specific transfer (Mitchell et al., 2009; Beans, 2014). We avoided such complications by using Lotka–Volterra trait-dependent competition coefficients instead.

The different competitive dynamics between plants (direct competition for space) and pollinators (competition for resources) assumed by our model lead to a pattern of diversification where the number of pollinator morphs (consumer trophic level) arising from evolutionary branching cannot surpass (e.g., Figs. 3 and 5B) the number of plant morphs (producer trophic level). In this respect, the plant–pollinator community behaves like a bottom-up regulated food web. However, there is also top-down control via pollination services. The coupling between both controls enables indirect facilitation between plants and evolutionary diversification: by raising densities of shared pollinators (Revilla and Křivan, 2016), pollination benefits feed back to plants, broadening their niches and promoting disruptive selection.

3.3. Trait dependency

In our model, traits evolve along fitness gradients in directions that minimize niche overlaps and competition within groups (plant or pollinator). This is called *character displacement*. Character displacement has been sufficiently documented for animal communities, where competition is mainly driven by resource utilization overlap (Schluter, 2000). In the case of plants, studies suggest that character displacement plays an important role in minimizing competition. Still, empirical and experimental evidence for its role in niche differentiation is not as solid as in the case of animals (Beans, 2014). An important issue for the study of trait-dependent competition between plants is that according to Beans (2014), it combines ecological antagonisms like resource use overlap with interference on reproduction like inter-specific pollen transfer (IPT).

Following some previous works (Doebeli and Dieckmann, 2000; Nuismer et al., 2013; Minoarivelo and Hui, 2016; Hui et al., 2018; Minoarivelo and Hui, 2018; Becker et al., 2022) we consider a single trait that controls both competition between plants as well as plant–pollinator mutualism. This assumption is problematic because it seems very hard to conceive how a trait controlling pollination such as e.g., flower tube length, could influence plant competition, e.g., root length or foliage cover. However, it is not too far-fetched to think that flower traits involved with pollination could be connected, via ontogeny, with seed or fruit traits important for nutrient acquisition, competition, or dispersal during early life. For instance, the length of the nectar tube “*x*” and seed size “*z*” can be correlated, by having both traits depend on a common gene set that controls flower architecture. If so, selection on optimal seed or fruit size can indirectly alter flower architecture and vice-versa, through changes of the underlying genotype.

Multiple trait dependence for plants and pollinators remains an interesting problem for evolutionary modeling. This line of research may allow us to simulate the emergence of pollination syndromes (Rodríguez-Gironés and Santamaría, 2010) and phenotypic integration (Ordano et al., 2008). There is another good reason for considering multiple traits. As the reader can notice from Fig. 3, the pace of branching events slows down (the time scale is logarithmic). We think this is happening because a single niche dimension (line) can be “packed” or “filled” much faster than two- or three-dimensional space. A good starting point to test these ideas could be with simpler Lotka–Volterra type models, better suited to handle multi-dimensional niche overlaps (May, 1975), before attempting mechanistic-like trophic-based models.

CRediT authorship contribution statement

Thomas Marcou: Writing – review & editing, Writing – original draft, Methodology. **Tomás A. Revilla:** Writing – review & editing, Writing – original draft, Methodology. **Vlastimil Křivan:** Writing – review & editing, Writing – original draft, Methodology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This project has received funding from the European Union’s Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 955708. The opinions expressed in this document reflect only the author’s view and in no way reflect the European Commission’s opinions. The European Commission is not responsible for any use that may be made of the information it contains.

Appendix A. Plant and pollinator model

A.1. Ecological dynamics

System (1) from the main text can be derived according to the resource-based mechanism introduced by (Revilla, 2015; Revilla and Křivan, 2016)

$$\begin{aligned} \frac{dN_i}{dt} &= sP_i - wN_i - \sum_{j=1}^m b_{ij}N_iM_j \\ \frac{dP_i}{dt} &= f \sum_{j=1}^m b_{ij}N_iM_j \left(1 - \frac{\sum_{k=1}^n c_{ik}P_k}{K_i} \right) - dP_i \\ \frac{dM_j}{dt} &= q \sum_{i=1}^n b_{ij}N_iM_j - gM_j \end{aligned} \quad (\text{A.1})$$

where P_i is plant i density, M_j is pollinator j density, and N_i are resource (e.g., nectar or pollen) produced by plant i . This structured approach that separates the mutualists from the resources traces back to Scheuring (1992). The resource is supplied at a rate s and decays with rate w . Pollinators consume plant resources with the specific rate b_{ij} , and convert these into births with efficiency q . Plant recruitment correlates with pollinator consumption of plant resources with efficiency f , and is density-dependent modeled by the logistic growth with carrying capacity K_i and competition coefficients c_{ik} . Plant and pollinator death rates are d and g , respectively. We assume that plant resource has a much faster dynamic than plant and pollinator life cycles, so that their steady-state availability, $\tilde{N}_i = \frac{sP_i}{w + \sum_j b_{ij}M_j}$, tracks plant and pollinator densities instantaneously. Substituting \tilde{N}_i in the plant and pollinator dynamics allows us to reduce system (A.1) to

$$\begin{aligned} \frac{dP_i}{dt} &= \left\{ r \frac{\sum_{j=1}^m a_{ij}M_j}{1 + \sum_{j=1}^m a_{ij}M_j} \left(1 - \frac{\sum_{k=1}^n c_{ik}P_k}{K_i} \right) - d \right\} P_i \\ \frac{dM_j}{dt} &= \left\{ e \sum_{i=1}^n \frac{a_{ij}P_i}{1 + \sum_{\ell=1}^m a_{i\ell}M_\ell} - g \right\} M_j, \end{aligned} \quad (\text{A.2})$$

where $r = fs$, $e = qs$, and $a_{ij} = \frac{b_{ij}}{w}$. Parameters a_{ij} , K_i , and c_{ik} are trait dependent in the main text. In this model $dP_i/dt < 0$ if $P_i \geq K_i$ which means that pollination does not allow plants to exceed their carrying capacities.

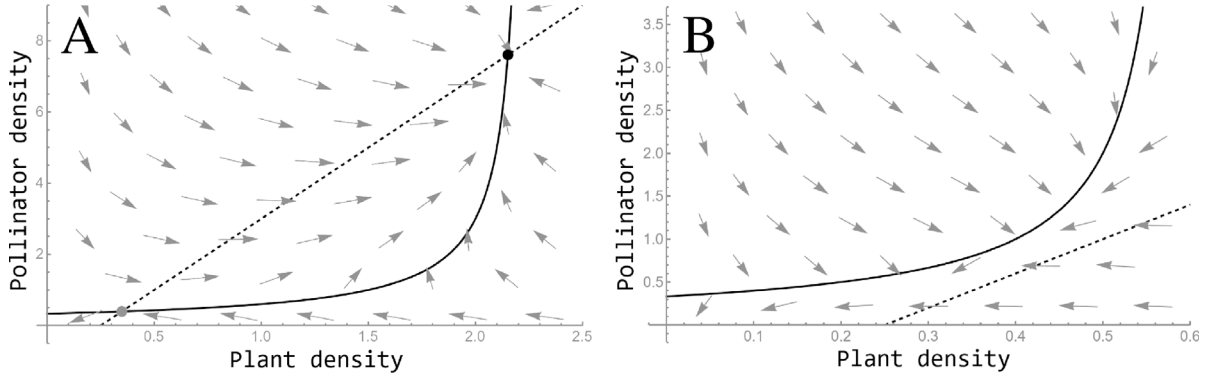


Fig. A.1. Population dynamics of system (A.5). The solid curve is the (non-trivial) nullcline of the plant, and the dotted line is the (non-trivial) nullcline of the pollinator. The vector field shows the dynamics of plants and pollinators. If (A.10) is true (panel A), there are two coexistence equilibria points at the intersection of nullclines: \hat{E} which is locally stable (black dot) and \tilde{E} which is unstable (gray dot). If (A.10) is not true (panel B), the nullclines do not intersect, and plant–pollinator coexistence is not possible. Parameters are those from Table 1, with $K_0 = 3$ in A and $K_0 = 0.8$ in B.

A.2. Eco-evolutionary equilibrium

Assuming one plant and one pollinator, system (7) becomes

$$\begin{aligned} \frac{dP}{dt} &= P \left\{ \frac{ra(x, y)M}{1 + a(x, y)M} \left(1 - \frac{P}{K(x)} \right) - d \right\} \\ \frac{dM}{dt} &= M \left\{ \frac{ea(x, y)P}{1 + a(x, y)M} - g \right\} \\ \frac{dx}{dt} &= \mu_p \left\{ -(x - y) \frac{ra(x, y)M}{\sigma_m^2 (1 + a(x, y)M)^2} \left(1 - \frac{P}{K(x)} \right) - \frac{xP}{\sigma_k^2 K(x)} \right. \\ &\quad \left. \times \frac{ra(x, y)M}{1 + a(x, y)M} \right\} \\ \frac{dy}{dt} &= \mu_m \frac{eP(x - y)a(x, y)}{\sigma_m^2 (1 + a(x, y)M)}. \end{aligned} \quad (\text{A.3})$$

Setting time derivatives to zero in the system (A.3), we find a trivial solution where $P = M = x = y = 0$. At a non-trivial eco-evolutionary equilibrium where the plant and the pollinator coexist at positive densities, $\frac{dy}{dt} = 0$ requires that $x = y$. Assuming now that $x = y$, we have

$$\frac{dx}{dt} = -\frac{xP}{\sigma_k^2 K(x)} \left(\frac{ra(x, x)M}{1 + a(x, x)M} \right) = -\frac{xP}{\sigma_k^2 K(x)} \left(\frac{ra_0 M}{1 + a_0 M} \right), \quad (\text{A.4})$$

and since $P > 0$ and $M > 0$ then $\frac{dx}{dt} = 0$ requires that $x = 0$. Thus, an equilibrium with viable plant and pollinator populations has $\hat{P} > 0$, $\hat{M} > 0$, $\hat{x} = 0$, $\hat{y} = 0$. Setting $x = y = 0$ makes $K(x) = K_0$, $a(x, y) = a_0$ and population dynamics in (A.3) are

$$\begin{aligned} \frac{dP}{dt} &= P \left\{ r \frac{a_0 M}{1 + a_0 M} \left(1 - \frac{P}{K_0} \right) - d \right\} = 0, \\ \frac{dM}{dt} &= M \left\{ e \frac{a_0 P}{1 + a_0 M} - g \right\} = 0. \end{aligned} \quad (\text{A.5})$$

Coexistence solutions correspond to intersections of non-trivial nullclines in the positive (P, M) quadrant. The pollinator's non-trivial nullcline

$$P = \frac{g(1 + a_0 M)}{ea_0}, \quad (\text{A.6})$$

is a line of positive slope intersecting the plant's axis at $P = \frac{g}{ea_0}$. The plant's non-trivial nullcline

$$P = K_0 \left(1 - \frac{d(1 + a_0 M)}{ra_0 M} \right), \quad (\text{A.7})$$

intersects the pollinator's axis at $M = \frac{d}{a_0(r-d)}$ and has vertical asymptote $P = K_0(r - d)/r$, indicating that $\hat{P} < K_0$ at its equilibrium (see

Fig. A.1 for a graphical representation of the isoclines). The non-trivial nullclines intersect at

$$\begin{aligned} \hat{E} &:= (\hat{P}, \hat{M}) = \left(\frac{g}{ea_0} \left(1 + \frac{B + \sqrt{D}}{2gr} \right), \frac{B + \sqrt{D}}{2a_0gr} \right) \\ \tilde{E} &:= (\tilde{P}, \tilde{M}) = \left(\frac{g}{ea_0} \left(1 + \frac{B - \sqrt{D}}{2gr} \right), \frac{B - \sqrt{D}}{2a_0gr} \right) \end{aligned} \quad (\text{A.8})$$

with

$$\begin{aligned} D &= (K_0 a_0 e(d - r) + gr)^2 - 4K_0 a_0 egrd, \\ B &= K_0 a_0 e(r - d) - gr. \end{aligned} \quad (\text{A.9})$$

The two equilibria exist in the positive (P, M) quadrant when

$$K_0 > \frac{gr}{a_0 e (\sqrt{d} - \sqrt{r})^2}. \quad (\text{A.10})$$

To check the stability of an eco-evolutionary equilibrium, we evaluate the Jacobian matrix of system (A.3) with P and M given by (A.8), and $x = y = 0$. Under these settings, the Jacobian matrix is block diagonal

$$\mathbf{J} = \begin{bmatrix} \mathbf{J}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{J}_2 \end{bmatrix},$$

where $\mathbf{0}$ denotes 2-by-2 zero matrix, and

$$\begin{aligned} \mathbf{J}_1 &= \begin{bmatrix} \frac{a_0 r M (K_0 - 2P)}{K_0 (1 + a_0 M)} - d & \frac{a_0 r P (K_0 - P)}{K_0 (1 + a_0 M)^2} \\ \frac{a_0 e M}{1 + a_0 M} & \frac{a_0 e P}{(1 + a_0 M)^2} - g \end{bmatrix}, \\ \mathbf{J}_2 &= \begin{bmatrix} -\frac{\mu_p r a_0 M (\sigma_k (K_0 - P) + K_0 \sigma_m^2 P (1 + a_0 M))}{\sigma_k \sigma_m^2 K_0 (1 + a_0 M)^2} & \frac{\mu_p r a_0 M (K_0 - P)}{\sigma_m^2 K_0 (1 + a_0 M)^2} \\ \frac{\mu_m e a_0 P}{\sigma_m^2 (1 + a_0 M)} & -\frac{\mu_m e a_0 P}{\sigma_m^2 (1 + a_0 M)} \end{bmatrix}. \end{aligned}$$

The trace of \mathbf{J}_2 is negative (recall from Appendix A that $P < K_0$) and its (factored) determinant $\frac{a_0^2 \mu_p \mu_m e r P^2 M}{\sigma_k \sigma_m^2 (1 + a_0 M)^2}$ is positive for $M > 0$. This means that \mathbf{J}_2 has eigenvalues with negative real parts, and stability depends on the eigenvalues of \mathbf{J}_1 only. Using Wolfram Mathematica we showed that when the two population equilibria exist, the low-density equilibrium \tilde{E} is unstable while the high-density equilibrium \hat{E} is locally stable. This is illustrated numerically in Fig. A.1. Fig. A.2 shows the temporal dynamics of coexisting plant and pollinator populations, and their traits with $\mu_p = \mu_m = 1$. Plants and pollinators approach ecological equilibrium very quickly (the stable point (\hat{P}, \hat{M}) given by (A.8)), but traits evolve towards evolutionary equilibrium (which is $\hat{x} = \hat{y} = 0$ in this case) at a much slower pace. This documents that even when $\mu_p = \mu_m = 1$, trait dynamics can operate on a much slower time scale than population dynamics.

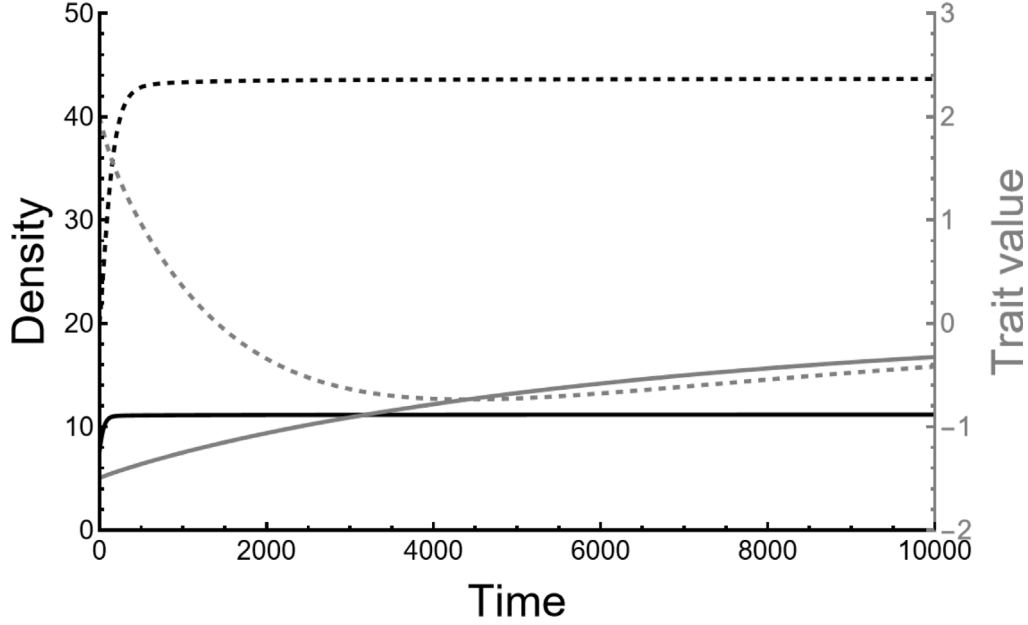


Fig. A.2. Temporal changes of plant (P , solid black) and pollinator (M , dashed black) densities, and of plant (x , solid gray) and pollinator (y , dash gray) traits. Parameters are those from Table 1.

Appendix B. First branching conditions

B.1. One plant and one pollinator

Here, we derive conditions for branching the plant population into two morphs. Appendix A shows that the eco-evolutionary equilibrium $(\hat{x}, \hat{y}, \hat{P}, \hat{M}) = (0, 0, \hat{P}, \hat{M})$ of system (9) from the main text is locally asymptotically stable, i.e., convergent stable (Vincent and Brown, 2005).

At the eco-evolutionary equilibrium $(\hat{x}, \hat{y}, \hat{P}, \hat{M}) = (0, 0, \hat{P}, \hat{M})$ the fitness of a plant individual with trait x' is

$$F(x'; 0, 0, \hat{P}, \hat{M}) = \frac{ra_0(x', 0)\hat{M}}{1 + a_0(x', 0)\hat{M}} \left(1 - \frac{c(x', 0)\hat{P}}{K(x')} \right) - d, \quad (\text{B.1})$$

and the fitness of a pollinator individual with trait y' is

$$G(y'; 0, 0, \hat{P}, \hat{M}) = \frac{ea_0(0, y')\hat{P}}{1 + a_0\hat{M}} - g. \quad (\text{B.2})$$

Eqs. (B.1) and (B.2) describe the adaptive landscape, respectively, of plants and pollinators. As $x = y = 0$ is a trait equilibrium of (9), we have that $F(x'; 0, 0, \hat{P}, \hat{M})|_{x'=0} = 0$ and $G(y'; 0, 0, \hat{P}, \hat{M})|_{y'=0} = 0$. For branching to happen, a mutant individual must have a positive fitness to invade the resident population. One way to check it is to compute the second derivative of F (or G) at 0. If it is negative, the equilibrium is a local maximum of the adaptive landscape and cannot be invaded (Apaloo et al., 2009). For the pollinator, the second derivative of G

$$\left[\frac{\partial^2 G}{\partial y'^2} \right]_{y'=0} = \left[\frac{ea_0(0, y')\hat{P}}{(1 + a_0\hat{M})\sigma_m^2} \left(\frac{y'^2}{\sigma_m^2} - 1 \right) \right]_{y'=0} = -\frac{ea_0\hat{P}}{(1 + a_0\hat{M})\sigma_m^2} < 0, \quad (\text{B.3})$$

is always negative, meaning a mutant pollinator cannot invade the pollinator species.

For the plant, the second derivative of F is

$$\left[\frac{\partial^2 F}{\partial x'^2} \right]_{x'=0}$$

$$= - \left\{ \frac{ra_0\hat{M}}{\sigma_m^2(1 + a_0\hat{M})^2} \left(1 - \frac{\hat{P}}{K_0} \right) + \frac{\hat{P}}{K_0} \left(\frac{1}{\sigma_k^2} - \frac{1}{\sigma_c^2} \right) \frac{ra_0\hat{M}}{1 + a_0\hat{M}} \right\} = S_F. \quad (\text{B.4})$$

Since $\hat{P} < K_0$, we observe that if $\sigma_k < \sigma_c$ then $S_F < 0$, and no plant branching is possible. In this case, neither the plant nor the pollinator species will branch, and the community is at an ESS with one plant and one pollinator species, with traits $x = y = 0$. Thus, a necessary condition for plant branching is

$$\sigma_k > \sigma_c. \quad (\text{B.5})$$

Condition for branching $S_F > 0$ becomes

$$\sigma_k^2 \sigma_m^2 (1 + a_0\hat{M}) \left(1 - \left(\frac{\sigma_c}{\sigma_m} \right)^2 \frac{K_0 - \hat{P}}{(1 + a_0\hat{M})\hat{P}} \right) > \sigma_c^2 \sigma_m^2 (1 + a_0\hat{M})\hat{P}, \quad (\text{B.6})$$

which yields condition (10) in the main text. Inequality (B.6) can hold only provided

$$\left(\frac{\sigma_c}{\sigma_m} \right)^2 \frac{K_0 - \hat{P}}{(1 + a_0\hat{M})\hat{P}} < 1 \quad (\text{B.7})$$

which yields condition (11) in the main text.

B.2. Two plants and one pollinator

Here we consider a community composed of two plant and one pollinator morphs. The G-functions F and G become

$$F(x'; \{x_1, x_2\}, y, \{P_1, P_2\}, M) = \frac{ra_0(x', y)M}{1 + a(x', y)M} \times \left(1 - \frac{\sum_{k=1}^2 c(x', x_k)P_k}{K(x')} \right) - d, \quad (\text{B.8})$$

$$G(y'; \{x_1, x_2\}, y, \{P_1, P_2\}, M) = e \left(\frac{a(x_1, y')P_1}{1 + a(x_1, y)M} + \frac{a(x_2, y')P_2}{1 + a(x_2, y)M} \right) - g. \quad (\text{B.9})$$

and the eco-evolutionary dynamics (7) are

$$\begin{aligned} \frac{dP_i}{dt} &= P_i F(x', \{x_1, x_2\}, y, \{P_1, P_2\}, M)|_{x'=x_i}, \quad i = 1, 2 \\ \frac{dM}{dt} &= M G(y'; \{x_1, x_2\}, y, \{P_1, P_2\}, M)|_{y'=y}, \\ \frac{dx_i}{dt} &= \mu_p \left[\frac{\partial F}{\partial x'} \right]_{x'=x_i}, \quad i = 1, 2 \\ \frac{dy}{dt} &= \mu_m \left[\frac{\partial G}{\partial y'} \right]_{y'=y} \end{aligned} \quad (\text{B.10})$$

where

$$\begin{aligned} \left[\frac{\partial F}{\partial x'} \right]_{x'=x_i} &= -(x_i - y) \frac{ra(x_i, y)M}{\sigma_m^2(1 + a(x_i, y)M)^2} \left(1 - \frac{P_i + c(x_i, x_j)P_j}{K(x_i)} \right) \\ &\quad - \frac{ra(x_i, y)M}{K(x_i)(1 + a(x_i, y)M)} \\ &\quad \times \left(\frac{x_i}{\sigma_k^2} (P_i + c(x_i, x_j)P_j) - \frac{x_i - x_j}{\sigma_c^2} c(x_i, x_j)P_j \right), \quad i, j = 1, 2, \quad i \neq j \end{aligned} \quad (\text{B.11})$$

and

$$\left[\frac{\partial G}{\partial y'} \right]_{y'=y} = \frac{e}{\sigma_m^2} \left(\frac{(x_1 - y)a(x_1, y)P_1}{1 + a(x_1, y)M} + \frac{(x_2 - y)a(x_2, y)P_2}{1 + a(x_2, y)M} \right). \quad (\text{B.12})$$

System (B.10) is too complex to calculate equilibria analytically. Similarly to Cressman et al. (2017), and supported by our numerical simulations, we assume that the evolutionary equilibrium of the plant species will be symmetric about 0, with $\hat{x}_1 = -\hat{x}_2 = \hat{x} > 0$. Then the pollinator trait equilibrium ($\left[\frac{\partial G}{\partial y'} \right]_{y'=y} = 0$) is $\hat{y} = 0$ and $\hat{P}_1 = \hat{P}_2 = \hat{P}$. To check if a mutant population can invade pollinators, we compute the second derivative of $G(y'; \{x_1, x_2\}, y, \{P_1, P_2\}, M)$ with respect to y' evaluated in $\hat{E} = (\hat{x}, -\hat{x}, 0, \hat{P}, \hat{P}, \hat{M})$:

$$\left[\frac{\partial^2 G(y'; \{x_1, x_2\}, y, \{P_1, P_2\}, M)}{\partial y'^2} \right]_{\hat{E}} = \frac{2e\hat{P}a(\hat{x}, 0)}{\sigma_m^2(1 + a(\hat{x}, 0)\hat{M})} \left(\frac{\hat{x}^2}{\sigma_m^2} - 1 \right) \quad (\text{B.13})$$

which is positive if $\hat{x} > \sigma_m$. This is condition (12) from the article's main body. The dashed-dot curve in Fig. 2 was obtained numerically.

Appendix C. Description of simulations

Evolutionary simulations are performed using the main text's system (7). The starting community consists of one plant and one pollinator population, with parameters (Table 1 and initial biomass densities) chosen to allow stable coexistence as described in Appendix A (i.e. $r > d$ and (A.10)). We then integrate the differential equations numerically until an eco-evolutionary equilibrium is reached and check if it is an ESS. If it is, we stop the simulation, as no mutants can invade the community anymore. However, if this equilibrium is not an ESS, it means that at least one resident morph, plant or pollinator, can be invaded by a mutated morph. We then add a new, mutated morph with a low initial density (10% of the resident invaded morph). Initially, the mutant's trait (e.g., x_m for a plant) is very close to the resident's (x_r , i.e., $|x_r - x_m| = 0.01$), and the mutation's direction is evenly picked, ($x_m > x_r$ or $x_m < x_r$, 50% chance each). The extended system (7) with an increased number of morphs is then simulated again. Numerical integration was performed using MATLAB R2023a function *ode15s*, designed to solve stiff problems. Such a method was used in Cressman et al. (2017) and Minoarivelo and Hui (2016) and has the advantage that there is no need to check if the eco-evolutionary equilibrium is convergent stable, as its locally asymptotically stability is given by the fact that it is reached through simulations.

If multiple morphs (plant and/or pollinator) become invadable simultaneously (i.e., they are at a minimum for their respective adaptive landscape), we select only one of these for invasion since it is unlikely

for two or more mutants to appear simultaneously. We repeat this process until an ESS is reached. The invasion morph's choice is important because, as explained in Cressman et al. (2017), the newly extended community (with one morph added) acts as the initial conditions for the next step and can influence the ESS reached, as shown in Fig. 4. Thus, we follow each choice separately to find all the possible ESSs for a given $\sigma_k, \sigma_c, \sigma_m$ combination.

Appendix D. Facultative mutualism or commensalism

The model in the main text assumes a mutually obligate association between plants and pollinators, as plants cannot exist without pollinators, and pollinators cannot exist without plants. Here, we consider two less restrictive cases where the interaction is facultative for plants or commensalism in which plants are not pollinated, but animal consumers remain dependent on the plant resources. Both cases require adding the term $r_0 P$ to the plant dynamics in (A.1), where $r_0 \geq 0$ is a vegetative growth rate independent from pollination. The plant G-function then becomes

$$F(x'; x, y, P, M) = \left(r_0 + \frac{ra(x', y)M}{1 + a(x, y)M} \right) \left(1 - \frac{c(x', x)P}{K(x')} \right). \quad (\text{D.1})$$

Depending on r_0, r and d we have

- Obligate mutualism if $r > d > r_0$: plants cannot survive in the absence of pollinators. This is like in the main text (where we set $r_0 = 0$).
- Facultative mutualism if $r > 0$ and $r_0 > d$: plants benefit from the pollinators but can survive when pollinators are absent (note that r could be larger or smaller than r_0).
- Commensalism if $r_0 > d > r = 0$: plants are not pollinated by the animals (but animals still benefit from plant resources just like in the previous cases).

We can then compute the plant's first branching condition:

$$\frac{ra_0\hat{M}}{\sigma_m^2(1 + a_0\hat{M})^2} \left(1 - \frac{\hat{P}}{K_0} \right) - \frac{\hat{P}}{K_0} \left(\frac{1}{\sigma_c^2} - \frac{1}{\sigma_k^2} \right) \left(r_0 + \frac{ra_0\hat{M}}{1 + a_0\hat{M}} \right) < 0. \quad (\text{D.2})$$

The pollinator's first branching condition is again given by (12) from the main text. This is because there is no change in the pollinator's fitness landscape formulation. It is important to notice that \hat{P} and \hat{M} in (D.2) are not the same as in (B.4), as this time population dynamics in (A.9) also depend on r_0 . We also compute numerically the first branching condition for pollinators. Fig. D.3 shows the plant (left panel) and pollinator (right panel) first branching boundaries in the (σ_m, σ_k) plane. The case from the main text, where mutualism is obligate for plants ($r_0 = 0$ and $r = 0.004$, Fig. 2), is delineated by solid curves, and the case where mutualism is facultative for plants ($r_0 = 0.015$ and $r = 0.004$) is delineated by dash-dot curves. In both cases, the shapes of the branching thresholds are the same, but the branching region is larger in the case of facultative mutualism. Branching thresholds for σ_m can be reduced by widening carrying capacity kernels by increasing σ_k , or by increasing vegetative growth rates (r_0), but they always remain positive. Thus, whether pollination is obligate or facultative, plant branching cannot occur without pollinators, as stated in the Discussion section.

Fig. D.3 also displays the first branching boundaries for the commensalistic case, where plants do not require pollinators ($r_0 = 0.015$ and $r = 0$). Here, the branching condition for the plant becomes $\sigma_k > \sigma_c$, like in Cressman et al. (2017), which is the region above the horizontal dashed line (left panel). The corresponding pollinator condition for branching is also different, as the pollinator can only branch inside the "horn-shaped" region of the plane delimited by the dashed curve (right panel). This result shows that when the animal consumer is a commensal, plant branching could happen without pollinators, and for σ_m values as low as zero.

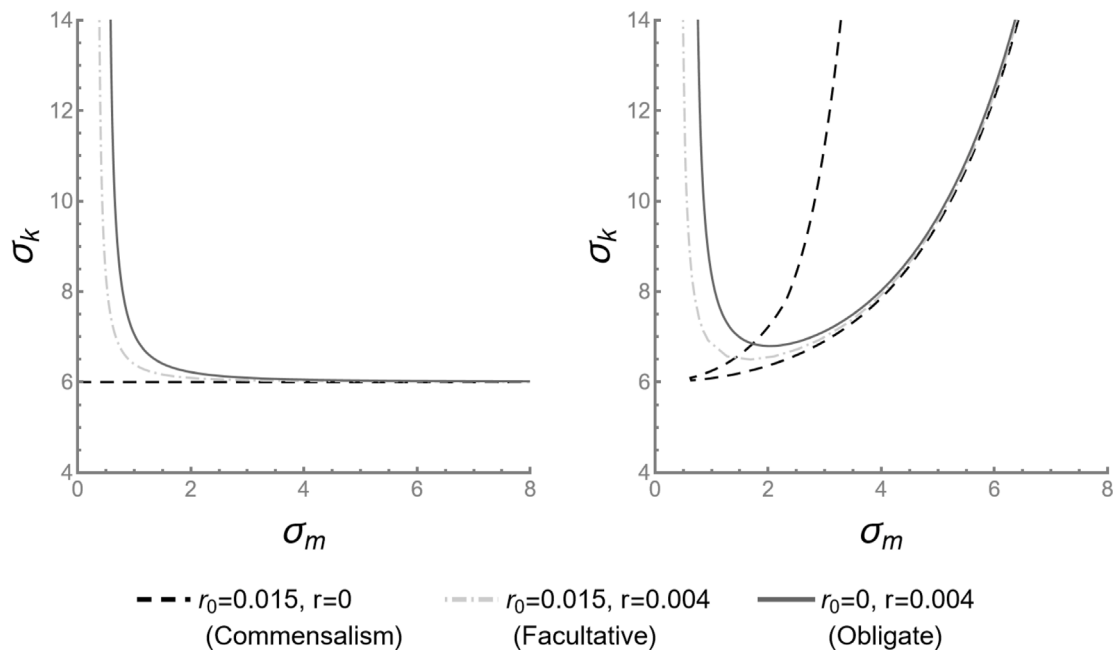


Fig. D.3. Graphical representation of plant (D.2, left panel) and pollinator ((12), right panel) first branching condition in (σ_m, σ_k) parameter space, for three different scenarios: commensalism ($r_0 = 0.015$, $r = 0$, black dashed curve), facultative ($r_0 = 0.015$, $r = 0.004$, light gray dash-dotted curve) and obligate ($r_0 = 0$, $r = 0.004$, dark gray solid curve) mutualism. Similarly to Fig. 2, above the curves the first plant branching (left panel) and the first pollinator branching (right panel) is possible.

Appendix E. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.jtbi.2024.111911>.

References

- Abrams, P.A., 1983. The theory of limiting similarity. *Annu. Rev. Ecol. Syst.* 14, 359–376. <http://dx.doi.org/10.1146/annurev.es.14.110183.002043>.
- Acerenza, L., 2016. Constraints, trade-offs and the currency of fitness. *J. Mol. Evol.* 82, 117–127. <http://dx.doi.org/10.1007/s00239-016-9730-3>.
- Almeida-Neto, M., Guimarães, P., Guimarães, Jr., P.R., Loyola, R.D., Ulrich, W., 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117 (8), 1227–1239. <http://dx.doi.org/10.1111/j.0030-1299.2008.16644.x>.
- Anderson, B., 2015. *Coevolution in Mutualisms*. Oxford University Press, pp. 107–130. <http://dx.doi.org/10.1093/acprof:oso/978019675654.003.0007>, (Chapter 7).
- Apaloo, J., Brown, J.S., Vincent, T.L., 2009. Evolutionary game theory: ESS, convergence stability, and NIS. *Evol. Ecol. Res.* 11, 489–515.
- Asar, Y., Ho, S.Y., Sauquet, H., 2022. Early diversifications of angiosperms and their insect pollinators: were they unlinked? *Trends Plant Sci.* 27, 858–869. <http://dx.doi.org/10.1016/j.tplants.2022.04.004>.
- Bascompte, J., 2019. Mutualism and biodiversity. *Curr. Biol.* 29, R467–R470. <http://dx.doi.org/10.1016/j.cub.2019.03.062>.
- Bascompte, J., Jordano, P., 2007. Plant-animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Syst.* 38, 567–593. <http://dx.doi.org/10.1146/annurev.ecolsys.38.091206.095818>.
- Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Luque, B., Bascompte, J., 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458, 1018–1020. <http://dx.doi.org/10.1038/nature07950>.
- Beans, C.M., 2014. The case for character displacement in plants. *Ecol. Evol.* 4 (6), 862–875.
- Becker, L., Blüthgen, N., Drossel, B., 2022. Stochasticity leads to coexistence of generalists and specialists in assembling mutualistic communities. *Amer. Nat.* 200 (3), 303–315.
- Benkman, C.W., Parchman, T.L., Mezquida, E.T., 2010. Patterns of coevolution in the adaptive radiation of crossbills. *Ann. New York Acad. Sci.* 1206, 1–16. <http://dx.doi.org/10.1111/j.1749-6632.2010.05702.x>.
- Breitkopf, H., Onstein, R.E., Cafasso, D., Schlüter, P.M., Cozzolino, S., 2015. Multiple shifts to different pollinators fuelled rapid diversification in sexually deceptive *Ophrys* orchids. *New Phytol.* 207, 377–389. <http://dx.doi.org/10.1111/nph.13219>.
- Brouat, C., García, N., Andary, C., McKey, D., 2001. Plant lock and ant key: pairwise coevolution of an exclusion filter in an ant-plant mutualism. *Proc. R. Soc. Lond. Ser. B* 268, 2131–2141. <http://dx.doi.org/10.1098/rspb.2001.1763>.
- Bukkuri, A., Brown, J.S., 2021. Evolutionary game theory: Darwinian dynamics and the g function approach. *Games* 12, <http://dx.doi.org/10.3390/g12040072>.
- Chomicki, G., Weber, M., Antonelli, A., Bascompte, J., Kiers, E.T., 2019. The impact of mutualisms on species richness. *Trends Ecol. Evol.* 34, <http://dx.doi.org/10.1016/j.tree.2019.03.003>.
- Cohen, Y., Vincent, T.L., Brown, J.S., 1999. A g-function approach to fitness minima, fitness maxima, evolutionary stable strategies and adaptive landscapes. *Evol. Ecol. Res.* 1, 923–943.
- Cook, J.M., Segar, S.T., 2010. Speciation in fig wasps. *Ecol. Entomol.* 35, 54–66. <http://dx.doi.org/10.1111/j.1365-2311.2009.01148.x>.
- Cressman, R., Halloway, A., McNickle, G., Apaloo, J., Brown, J., Vincent, T., 2017. Unlimited niche packing in a Lotka-Volterra competition game. *Theor. Popul. Biol.* 116, 1–17. <http://dx.doi.org/10.1016/j.tpb.2017.04.003>.
- Doebeli, M., Dieckmann, U., 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *Amer. Nat.* 156, S77–S101. <http://dx.doi.org/10.1086/303417>.
- Ebeling, A., Klein, A.-M., Schumacher, J., Weisser, W.W., Tschardt, T., 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos* 117, 1808–1815. <http://dx.doi.org/10.1111/j.1600-0706.2008.16819.x>.
- Fleming, T.H., Muchhala, N., Ornelas, J.F., 2005. New world nectar-feeding vertebrates: community patterns and processes, cap. 15: 163–186. In: Medellín, S.-C.V.y.R. (Ed.), *Contribuciones Mastozoológicas en Homenaje a Bernardo Villa*. UNAM Mexico, pp. 163–186, (Chapter 15).
- Geritz, S.A., Kisdi, É., Meszéná, G., Metz, J.A., 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* 12, 35–57. <http://dx.doi.org/10.1023/A:1006554906681>.
- Geritz, S.A., Kisdi, É., Meszéná, G., Metz, J.A., 2004. Adaptive dynamics of speciation: Ecological underpinnings. In: *Adaptive Speciation*. Cambridge University Press, pp. 54–75. <http://dx.doi.org/10.1017/CBO9781139342179.005>, (Chapter 4).
- Grover, J.P., 1997. *Resource Competition*. Chapman & Hall.
- Guimarães, P.R., Jordano, P., Thompson, J.N., 2011. Evolution and coevolution in mutualistic networks. *Ecol. Lett.* 14, 877–885. <http://dx.doi.org/10.1111/j.1461-0248.2011.01649.x>.
- Guimarães, P.R., Pires, M.M., Jordano, P., Bascompte, J., Thompson, J.N., 2017. Indirect effects drive coevolution in mutualistic networks. *Nature* 550, <http://dx.doi.org/10.1038/nature24273>.
- Holland, J.N., DeAngelis, D.L., 2010. A consumer-resource approach to the density-dependent population dynamics of mutualism. *Ecology* 91, 1286–1295. <http://dx.doi.org/10.1890/09-1163.1>.
- Holt, R.D., 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Popul. Biol.* 12, 197–229. [http://dx.doi.org/10.1016/0040-5809\(77\)90042-9](http://dx.doi.org/10.1016/0040-5809(77)90042-9).
- Hui, C., Minoarivelo, H.O., Landi, P., 2018. Modelling coevolution in ecological networks with adaptive dynamics. *Math. Methods Appl. Sci.* 41 (18), 8407–8422. <http://dx.doi.org/10.1002/mma.4612>.

- Levins, R., 1966. The strategy of model building in population biology. *Am. Sci.* 54 (4), 421–431.
- Litsios, G., Sims, C.A., Wüest, R.O., Pearman, P.B., Zimmermann, N.E., Salamin, N., 2012. Mutualism with sea anemones triggered the adaptive radiation of clownfishes. *BMC Evol. Biol.* 12, 212. <http://dx.doi.org/10.1186/1471-2148-12-212>.
- Liu, X., Murata, T., 2010. Community detection in large-scale bipartite networks. *Trans. Jpn. Soc. Artif. Intell.* 25 (1), 16–24. <http://dx.doi.org/10.1109/WI-IAT.2009.15>.
- MacArthur, R., 1970. Species packing and competitive equilibrium for many species. *Theor. Popul. Biol.* 1, 1–11. [http://dx.doi.org/10.1016/0040-5809\(70\)90039-0](http://dx.doi.org/10.1016/0040-5809(70)90039-0).
- MacArthur, R., Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species. *Amer. Nat.* 101, 377–385. <http://dx.doi.org/10.1086/282505>.
- Maliet, O., Loeuille, N., Morlon, H., 2020. An individual-based model for the evolutionary emergence of bipartite interaction networks. *Ecol. Lett.* 23 (11), 1623–1634.
- May, R.M., 1974a. On the theory of niche overlap. *Theor. Popul. Biol.* 5 (3), 297–332. [http://dx.doi.org/10.1016/0040-5809\(74\)90055-0](http://dx.doi.org/10.1016/0040-5809(74)90055-0).
- May, R.M., 1974b. Stability and Complexity in Model Ecosystems. In: Princeton Landmarks in Biology, Princeton University Press, Princeton.
- May, R.M., 1975. Some notes on estimating the competition matrix. *Ecology* 56 (3), 737–741.
- Maynard Smith, J., Price, G.R., 1973. The logic of animal conflict. *Nature* 246, 15–18. <http://dx.doi.org/10.1038/246015a0>.
- McCann, K.S., Hastings, A., Huxel, G.R., 1998. Weak trophic interactions and the balance of nature. *Nature* 395, 794–798. <http://dx.doi.org/10.1038/27427>.
- Minoarivelo, H.O., Hui, C., 2016. Trait-mediated interaction leads to structural emergence in mutualistic networks. *Evol. Ecol.* 30, 105–121. <http://dx.doi.org/10.1007/s10682-015-9798-z>.
- Minoarivelo, H.O., Hui, C., 2018. Alternative assembly processes from trait-mediated co-evolution in mutualistic communities. *J. Theoret. Biol.* 454, 146–153.
- Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M., Karron, J.D., 2009. New frontiers in competition for pollination. *Ann. Bot.* 103, 1403–1413. <http://dx.doi.org/10.1093/aob/mcp062>.
- Nuismer, S.L., Jordano, P., Bascompte, J., 2013. Coevolution and the architecture of mutualistic networks. *Evolution* 67, 338–354. <http://dx.doi.org/10.1111/j.1558-5646.2012.01801.x>.
- Ordano, M., Fornoni, J., Boege, K., Domínguez, C.A., 2008. The adaptive value of phenotypic floral integration. *New Phytol.* 179 (4), 1183–1192. <http://dx.doi.org/10.1111/j.1469-8137.2008.02523.x>.
- Raimundo, R.L., Gibert, J.P., Hembry, D.H., Guimarães, Jr., P.R., 2014. Conflicting selection in the course of adaptive diversification: the interplay between mutualism and intraspecific competition. *Amer. Nat.* 183 (3), 363–375.
- Revilla, T.A., 2015. Numerical responses in resource-based mutualisms: a time scale approach. *J. Theor. Biol.* 387, 39–46. <http://dx.doi.org/10.1016/j.jtbi.2015.04.012>.
- Revilla, T.A., Křivan, V., 2016. Pollinator foraging adaptation and coexistence of competing plants. *PLoS One* 11 (8), e0160076. <http://dx.doi.org/10.1371/journal.pone.0160076>.
- Revilla, T.A., Křivan, V., 2018. Competition, trait-mediated facilitation, and the structure of plant-pollinator communities. *J. Theor. Biol.* 440, 42–57. <http://dx.doi.org/10.1016/j.jtbi.2017.12.019>.
- Ripa, J., Storlind, L., Lundberg, P., Brown, J.S., 2009. Niche co-evolution in consumer-resource communities. *Evol. Ecol. Res.* 11.
- Rodríguez-Gironés, M.A., Santamaría, L., 2010. How foraging behaviour and resource partitioning can drive the evolution of flowers and the structure of pollination networks. *Open Ecol. J.* 3, 1–11. <http://dx.doi.org/10.2174/1874213001003040001>.
- Rønsted, N., Weiblen, G.D., Cook, J.M., Salamin, N., Machado, C.A., Savolainen, V., 2005. 60 Million years of co-divergence in the fig-wasp symbiosis. *Proc. R. Soc. Lond. Ser. B* 272, 2593–2599. <http://dx.doi.org/10.1098/rspb.2005.3249>.
- Roughgarden, J., 1972. Evolution of niche width. *Amer. Nat.* 106, 683–718.
- Rueffler, C., Dooren, T.J.V., Leimar, O., Abrams, P.A., 2006. Disruptive selection and then what? *Trends Ecol. Evol.* 21, 238–245. <http://dx.doi.org/10.1016/j.tree.2006.03.003>.
- Scheuring, I., 1992. “The orgy of mutualism” as an artefact: a stage structured model of plant-pollinator and seed-dispersal systems. *Abstr. Bot.* 16 (1), 65–70. <http://dx.doi.org/10.2307/43519288>.
- Schluter, D., 2000. Ecological character displacement in adaptive radiation. *Amer. Nat.* 156 (S4), S4–S16.
- Schoener, T.W., 1978. Effects of density-restricted food encounter on some single-level competition models. *Theor. Popul. Biol.* 13 (3), 365–381.
- Sigmund, K., Nowak, M.A., 1999. Evolutionary game theory. *Curr. Biol.* 9, R503–R505. [http://dx.doi.org/10.1016/S0960-9822\(99\)80321-2](http://dx.doi.org/10.1016/S0960-9822(99)80321-2).
- Thompson, J.N., 2013. Coevolution and Speciation. Princeton University Press, pp. 535–542. <http://dx.doi.org/10.1515/9781400848065-074>, (Chapter 6).
- Trager, M.D., Bhotika, S., Hostetler, J.A., Andrade, G.V., Rodriguez-Cabal, M.A., McKeon, C.S., Osenberg, C.W., Bolker, B.M., 2010. Benefits for plants in ant-plant protective mutualisms: A meta-analysis. *PLoS One* 5, e14308. <http://dx.doi.org/10.1371/journal.pone.0014308>.
- Valdovinos, F.S., Moisset de Espanés, P., Flores, J.D., Ramos-Jiliberto, R., 2013. Adaptive foraging allows the maintenance of biodiversity of pollination networks. *Oikos* 122 (6), 907–917. <http://dx.doi.org/10.1111/j.1600-0706.2012.20830.x>.
- Vandermeer, J., Pascual, M., 2006. Competitive coexistence through intermediate polyphagy. *Ecol. Complex.* 3, 37–43. <http://dx.doi.org/10.1016/j.ecocom.2005.05.005>.
- Vázquez, D.P., Lomáscolo, S.B., Maldonado, M.B., Chacoff, N.P., Dorado, J., Stevani, E.L., Vitale, N.L., 2012. The strength of plant–pollinator interactions. *Ecology* 93, 719–725. <http://dx.doi.org/10.1890/11-1356.1>.
- Vincent, T.L., Brown, J.S., 2005. Evolutionary Game Theory, Natural Selection, and Darwinian Dynamics. Cambridge University Press, <http://dx.doi.org/10.1017/CBO9780511542633>.
- Wootton, J.T., Emmerson, M., 2005. Measurement of interaction strength in nature. *Annu. Rev. Ecol. Syst.* 36, 419–444. <http://dx.doi.org/10.1146/annurev.ecolsys.36.091704.175535>.
- Yoder, J.B., Nuismer, S.L., 2010. When does coevolution promote diversification? *Amer. Nat.* 176 (6), 802–817.