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Eco-evolutionary dynamics of mutualistic-antagonistic systems: implications for plant-pollinator-herbivore communities

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Sorbonne Université

Ecole doctorale 227

Sciences de la Nature et de l'Homme: écologie et évolution

Thèse de doctorat d'Ecologie

Eco-evolutionary dynamics of mutualistic- antagonistic systems

Implications for plant-pollinator-herbivore communities

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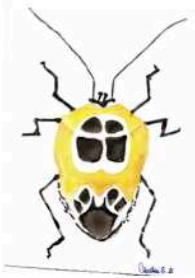
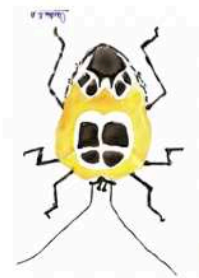
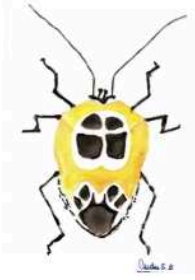
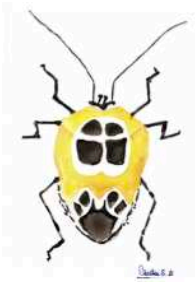


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I.
General
Introduction

This introduction is designed as an argumentation whose aim is to convince the reader of the relevance of studying the eco-evolutionary dynamics of mutualistic-antagonistic communities in order to gain insights into the mechanisms supporting multispecies coexistence in nature. The underlying reasoning is detailed in the three first sections as outlined here:

(1) Ecological communities consist of various species interacting in many diverse ways. The diversity of interspecific ecological interactions encompasses not only different types – competition, antagonism and mutualism – but also different pathways (direct vs. indirect).

(2) Eco-evolutionary dynamics – i.e. the interplay and feedback between ecological and evolutionary processes – are crucial to understanding multispecies coexistence and its maintenance over time, even more in the current context of global change in which strong selective pressures may lead to rapid evolutionary dynamics. Ecological interactions, which are usually mediated by traits that are variable and heritable, play a key role in community eco-evolutionary dynamics. In particular, different interactions are often associated with different eco-evolutionary processes.

(3) Understanding the eco-evolutionary processes supporting multispecies coexistence requires an integrative framework accounting for different types of interaction simultaneously. The reasons are twofold. On the one hand, species are often involved in several types of interactions simultaneously in natural communities. On the other hand, the combination of several interaction types leads to dynamics that significantly differ, and cannot be predicted, from the ones emerging when interactions are considered in isolation (i.e. non-additivity).

Plant-pollinator-herbivore communities are a particularly relevant study system to investigate the eco-evolutionary dynamics arising from the interplay of mutualistic and antagonistic interactions, as detailed in the fourth section of the introduction. In particular, several empirical studies document the non-additive dynamics arising from the interplay of pollination and herbivory, which is a key motivation of our investigation. Moreover, these communities appear particularly vulnerable to global changes, making their study of high applied relevance.

Finally, a fifth section presents the questions addressed in the three chapters of this PhD dissertation.

(1) The diversity of interspecific ecological interactions

"It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us" (Darwin 1859).

By starting the last paragraph of, perhaps, the most influential book of modern biology - *On the Origin of Species* – Charles Darwin emphasizes that ecological communities consist of several species interacting together in diverse ways, and that interspecific ecological interactions are at the very core of such communities. They are indeed key drivers of both the ecological and evolutionary dynamics within natural communities (Begon *et al.* 1986; Thompson 1999).

An interspecific ecological interaction can be defined as the modification of one or several characteristics of the population of one species by individuals of another species (Abrams 1987). Such characteristics can be, for instance, birth, mortality or growth rates, population size, or its spatial distribution. By altering these characteristics, the interaction modifies the survival and/or reproduction of the interacting populations, and thus their propensity to pass their genes to the next generations, i.e. their global fitness. According to its effect – positive (+), neutral (0), or negative (–) – on the global fitness of each interacting species, an interaction can be classified into one of six discrete categories (Odum 1983; Holland & Deangelis 2009) – competition (–, –), antagonism (+, –), mutualism (+, +), neutralism (0, 0), amensalism (0, –) and commensalism (0, +) - as presented in **Box 1**.

Box 1: Classification of interspecific ecological interactions

As presented in **table B1.1**, the interactions between two species (Sp. A & Sp. B) can be comprehensively classified according to the sign of the reciprocal effects between the two species. Three of these interactions – competition, antagonism, and mutualism - have been extensively studied in the literature. In what follows, I detail a bit what is meant by these three types of interactions, but also emphasize a few important results that I feel relevant in the context of the present dissertation.

		Effect on Sp. A		
		+	0	-
Effect on Sp. B	+	Mutualism		
	0	Commensalism	Neutralism	
	-	Antagonism	Amensalism	Competition

Table B1. 1: Classification of interspecific ecological interactions

Competition (-, -):

Competition is characterized by the two species having a negative impact on each other. Such an interaction is therefore symmetrical (qualitatively). Competitive interactions have early been identified a major process underlying “the struggle for existence” between species (Darwin 1859, chapter 3; Crombie 1947). Their key role in explaining multispecies coexistence and its maintenance over time have, since then, largely been demonstrated (Tilman 1982; Chesson 2000). Competition is notably stronger between species that occupy a similar ecological niche, which makes it an important driver of the evolution of niche dissimilarity (MacArthur & Levins 1967). In particular, competition should be the strongest between individuals of the same species (i.e. intraspecific competition). Often, competition arises from a common resource being shared by two (or more) species (Tilman 1982). The reciprocal negative effects between the interacting species mediated by their consumption of the shared resource correspond to exploitative competition (e.g. **Fig. B1 1.a**), but the two species can also directly interfere for accessing the resource (e.g. **Fig. B1 1.b**).

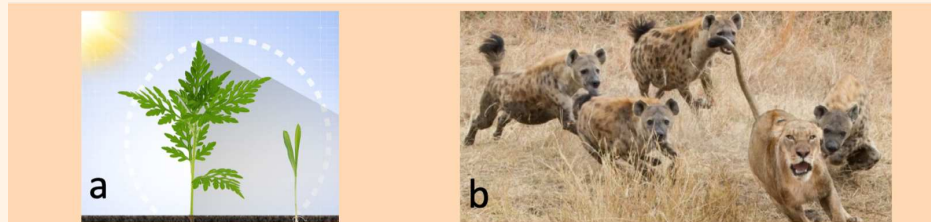


Fig. B1. 1: Examples of competitive interactions. **a.** Exploitative competition: two plant species competing for light. **b.** Interference competition: fight between hyenas and a lion.

Antagonism (+, -):

Antagonism is an asymmetrical ecological interaction in which one species benefits from the interaction at the expense of its interacting partner. Trophic interactions, such as predation or herbivory, are of such type. Predation (e.g. **Fig. B1 2.a**) is defined as the consumption by an organism (the predator) of either all or part of another organism (the prey), often resulting in the prey death (Begon *et al.* 1986). Herbivory refers to the consumption of plant material by animal species. Herbivory (e.g. **Fig. B1 2.b**) can be considered a type of predation, although the consumed plant individual is generally not killed (but see seed predation). Being the backbone supporting energy fluxes from photosynthetic plant species up to top predators, trophic interactions have been early characterized as one of the most important structuring element of natural communities (Lindeman 1942). They have notably been shown to be crucial for the stability of population dynamics (Rosenzweig 1971; McCann *et al.* 1998), as well as for the coexistence of multiple species (e.g. prey coexistence, Holt 1977).

Another example of antagonism is parasitism, i.e. an intimate interaction characterized by one organism (the parasite) living on or inside another organism (the host), using its host to acquire the resources needed to develop and reproduce, and resulting in a reduction of the host fitness. Generally, the parasite does not kill its host, except in the case of parasitoids (e.g. **Fig. B1 2.c**). An important feature of antagonistic interactions is that they tend to promote coevolutionary arms races (Dawkins & Krebs 1979), in which selection continuously favors a better exploitation by the exploiter species vs. a better defense of the exploited species (Red Queen hypothesis, Van Valen 1973). This is notably the case for plant-herbivore coevolution (Ehrlich & Raven 1964).

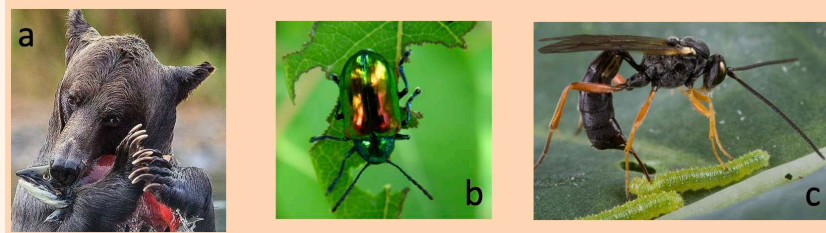


Fig. B1. 2: Examples of antagonistic interactions. **a. Predation:** a bear eats a salmon **b. Herbivory:** A dogbane beetle (*Chrysochus auratus*) feeding on *Apocynum cannabinum* (from Lemoine *et al.* 2014). **c. Parasitism:** a parasitic wasp (parasitoid, *Hyposoter ebeninus*) ovipositing into a caterpillar larvae (*Pieris rapae*) (from Harvey *et al.* 2010).

Mutualism (+, +):

Mutualism is characterized by being beneficial for both interacting species, and is thus a symmetrical ecological interaction (qualitatively). It involves the exchange of commodities in a “biological market”: each species exchanges a commodity it has access to for a commodity that is difficult or impossible for it to acquire (Bronstein *et al.* 1994). The mutualism can be obligate for one or both species, meaning that it cannot survive or reproduce without the interaction (e.g. coral and zooxanthellae, **Fig. B1 3.a**) or it can be facultative. Plants are notably involved in several mutualistic interactions with animal species, for instance providing food in exchange of pollen transport allowing reproduction – i.e. pollination (**Fig. B1 3.b**) – or seed dispersal (**Fig. B1 3.c**). Despite of their intrinsic positive feedback favoring instability (Levins 1974), mutualisms are widespread in nature (Janzen 1985), which led to an important body of literature addressing the question of their stability, both at the ecological (Vandermeer & Boucher 1978; Memmott *et al.* 2004) and evolutionary timescale (Bronstein *et al.* 1994; Toby Kiers *et al.* 2010). Because some intimate mutualism have coevolved over a huge period of time (e.g. Yuccas and Yucca moths, Pellmyr 2003), the study of mutualistic interactions can potentially shed lights on important eco-evolutionary processes underlying the diversification of life, as for instance in the case of flowering plant species (i.e. angiosperms) coevolving with their pollinators (Grant 1949).

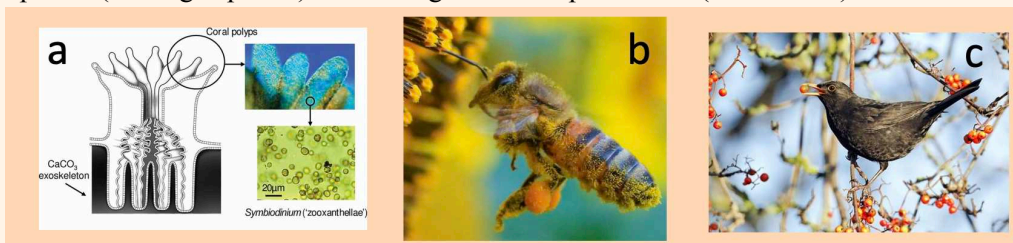


Fig. B1. 3: Examples of mutualistic interactions. **a. Coral and zooxanthellae:** this interaction is extremely intimate (symbiosis). The coral provides protection, as well as compounds needed for photosynthesis, in exchange, the algae provides the coral with nutrients resulting from photosynthesis. **b. Pollination:** A bee (*Apis sp.*), covered in pollen while pollinating. **c. Seed dispersal:** The seed is surrounded with an edible and nutritious fruit, consumed by the bird, leading to the dissemination of the seed in the spatial landscape when expelled in the animal feces.

Interspecific interactions can be direct or indirect

It is also possible to distinguish between direct and indirect ecological interactions. Indirect interactions (**Fig. 1**) correspond to the effect of one species on another that only arise in the presence of other species (Wootton 2002), while direct interactions are possible when considering the interacting pair in isolation (e.g. predation, pollination). An important ensuing distinction is that indirect interactions do not require species to co-occur in time nor space, contrary to direct interactions. There are at least two ways by which indirect interactions can arise (Wootton 2002).

First, the indirect interaction between two species can be mediated by their effect on the density of a third species, i.e. a density-mediated indirect interaction (Abrams *et al.* 1996, see **Fig. 1A**), arising from the coupling (due to shared species) of multiple direct interactions within ecological networks, such interactions are ubiquitous in natural communities in which they seem as important as direct pathways to explain coexistence patterns (Menge 1995; Burns *et al.* 2014). Isolating small sets of interacting species within ecological networks – i.e. modules or motifs – allows the study of such density-mediated indirect interactions (Milo *et al.* 2002). Trophic cascades, which propagates within a trophic chain (Carpenter *et al.* 1985) have notably been frequently reported in nature (e.g. wolf reintroduction in the Yellowstone National Park, Ripple & Beschta 2012). These dynamics are observed when an increase in the density of the top predator reduces the mesopredator abundance, which in turn increases the density of the basal prey (**Fig. 1A a**). Another important example is apparent competition between two species sharing a common enemy (Holt 1977). In the case of two prey sharing the same predator (**Fig. 1A b**) for instance, an increase in the density of either prey may reduce the density of the other prey owing to an increase of the predator density.

The second type of indirect interaction arises when the direct interaction between two species is modified by a third one (see **Fig. 1B**). This third species can, for instance, change the traits of individuals of one species – i.e. trait-mediated indirect interaction (Abrams *et al.* 1996, see **Fig. 1B.a**) – which, in turn, affects the direct interaction with the second species. A large number of empirical examples can be found in the review of Werner & Peacor (2003). For instance, Barber *et al.* (2012) demonstrate that early-season aboveground herbivore damage to cucumber (*Cucumis sativus*) reduces several subsequent interactions (below and aboveground) with both antagonists and mutualists, including pollinators. Notably, plant trait-mediated indirect interactions between pollinators and herbivores have largely been reported in the literature (Herrera 2000; Pohl *et al.* 2006; Kessler *et al.* 2011), with important consequences on the evolution of plant traits (Strauss & Whittall 2006). Instead of altering traits, the third

species can also alter the abiotic environment in which an interaction occurs (**Fig. 1B.b**). Ecosystem engineers (e.g. beavers) – i.e. species that significantly modify the physical characteristic of their habitat (Jones *et al.* 1997) - might for instance provide prey with refuges resulting in lower predation rates (e.g. Woodin 1981).

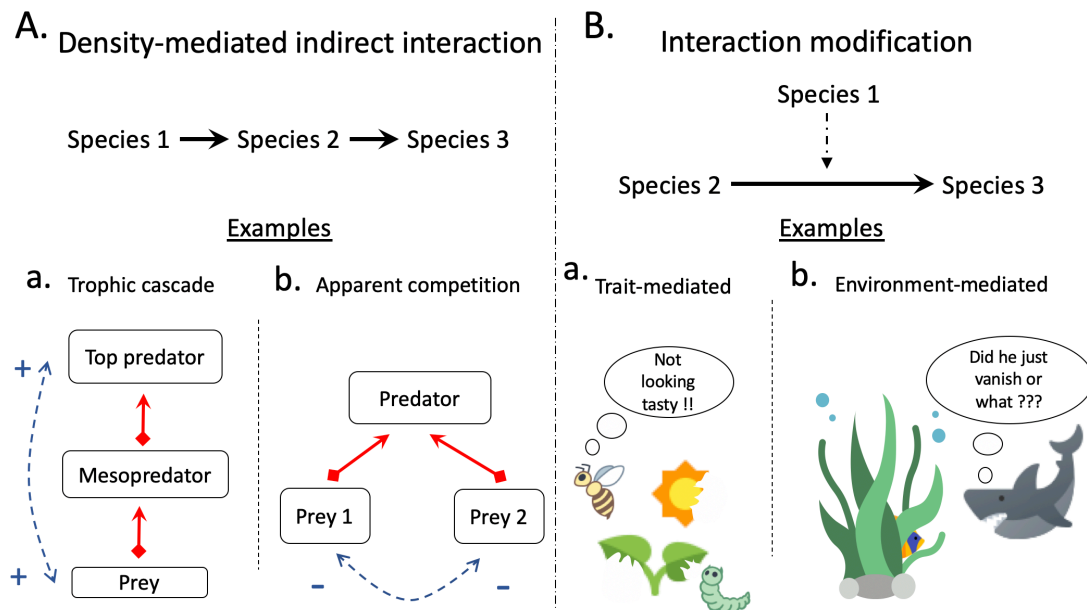


Fig. 1: Indirect ecological interactions. **A. Density-mediated indirect interactions.** In the examples, red arrows indicate trophic interactions while blue dotted arrows indicate indirect ecological interactions. **a. Trophic cascade:** an increase of the top predator density increases prey density as a result of the decline of the density of mesopredators. An increase in prey density increases mesopredators density, which in turn increases top predator density. **b. Apparent competition:** The increase of the density of either prey provokes a decline in the other prey density as a result of an increased predator density. **B. Interaction modification.** **a.** The avoidance of plant individuals that are damaged by herbivores is an example of trait-mediated interaction modification. **b.** Kelps can reduce predation on a given species by providing a place to hide. They are thus modifying the ecosystem spatial configuration, which in turn modifies trophic interactions.

Interspecific interactions are context-dependent

Indirect interactions readily demonstrate that interspecific ecological interactions may vary with the biotic environment in which they occur. Actually, far from being static (Chamberlain *et al.* 2014), interspecific interactions do vary in both sign (i.e. +, −, 0) and strength with time, space, and/or the abiotic and biotic environmental conditions. For instance, the global scale experiment of Callaway *et al.* (2002) documents a widespread shift of plant-plant interactions along the altitudinal gradient, with competition (−, −) dominating at low

elevations where abiotic stress is low, while facilitation (+, +) dominates at high elevations where abiotic stress is higher. Mutualism, in particular, have been frequently reported to grade into antagonism (e.g. Johnson *et al.* 1997; Yu & Pierce 1998; Maloof & Inouye 2000) when the costs of the interaction outweigh its benefits for one or both species (Bronstein 2001).

(2) The key role of interspecific interactions for community eco-evolutionary dynamics

What are eco-evolutionary dynamics?

Until the early '80s, ecological vs evolutionary processes were usually considered to act on such tremendously separate timescales (several generations vs. millions of years respectively, Slobodkin 1961) so that evolution could be safely ignored when investigating ecological questions. The accumulation of empirical evidence documenting significant evolutionary induced changes observable within a few generations in the wild (reviewed in Thompson 1998; Hendry & Kinnison 1999), however, led to an important paradigm shift (Reznick *et al.* 2019): understanding ecological dynamics requires to account for evolution as the latter often occurs at the same time as, and results in, alterations to ecological dynamics (Thompson 1998; Hairston *et al.* 2005). Multiple examples of fast evolution in the wild are now well-documented: fishery-induced selective pressures on Atlantic cod populations provoked a significant reduction of the age/size at maturation in just seven years (Olsen *et al.* 2004), preventing the recovery of population sizes decades after the establishment of a moratorium on its fishery by Canadian authorities (trade-off size vs. fecundity); the evolution toward longer legs favoring faster/longer dispersal in the invasive cane toad, reinforced by the spatial selection of the best dispersers at the expanding front (Phillips *et al.* 2010), enabled the speed of its range expansion across Australia to almost double in 20 years (Phillips *et al.* 2006); warming-induced selection on the Brown Argus butterfly resulted in the widening of its larval host range, with a documented genetic signature (Buckley *et al.* 2012), enabling a significant poleward range expansion across the UK in approximately 20 years (Pateman *et al.* 2012). All three examples highlight how the sole consideration of ecological processes impede the understanding, and even more the prediction, of the ecological dynamics over just a few decades. The effect of (evolutionary) phenotypic changes on population dynamics has notably been shown to be of similar magnitude as the one arising from (ecological) density-mediated processes in several cases (e.g. Yoshida *et al.* 2003; Hairston *et al.* 2005). It is this convergence of timescales

between ecological and evolutionary processes that put forth the prevailing role of eco-evolutionary dynamics.

As suggested by the three examples above, fast evolutionary dynamics are especially favored in the current context of global changes. The underlying rationale is straightforward (Loeuille 2019): the significant impact of global changes on species survival and/or fecundity (Brook *et al.* 2008; Barnosky *et al.* 2011) implies strong selective pressures fostering the fast evolution of any phenotype that is heritable, variable and associated with survival and/or fecundity. Accordingly, fast evolution has been reported in several contexts including overexploitation (Grift *et al.* 2003; Olsen *et al.* 2004), agricultural intensification (Manalil *et al.* 2011), species invasions (Carroll *et al.* 2005; Phillips *et al.* 2006), and climate change (Bradshaw & Holzapfel 2006; Franks *et al.* 2007; Pateman *et al.* 2012; Geerts *et al.* 2015). Quantifying the rates of phenotypic change across 68 study systems (i.e. a species in a geographic area), Hendry *et al.* (2008) estimate, for instance, that such rates are twice faster in “anthropogenic” (i.e. human-disturbed) than “natural” contexts. Note, however, that these rates encompass both evolutionary and plastic responses.

Because global change increases the prevalence of fast evolution, accounting for eco-evolutionary dynamics becomes all the more relevant, if not inescapable, for the management and conservation of biodiversity (Stockwell *et al.* 2003). For instance, the intensive use of antibiotics or chemical pesticides as of the early 20th century has led to the rapid emergence of a huge number of resistant phenotypes – bacteria, plants, animals (insects in particular) – which are nowadays responsible for huge economical extra costs associated with the development of new chemicals or the need to use bigger quantities (Palumbi 2001). Importantly, eco-evolutionary dynamics might also be part of the solution (Kinnison & Hairston 2007), in agricultural management in particular (Loeuille *et al.* 2013). For instance, turning directional selection into fluctuating selection by regularly changing the chemical used on a given agricultural field could reduce the strength of selection toward resistance (Palumbi 2001; Loeuille *et al.* 2013). In managing biodiversity, eco-evolutionary dynamics are therefore a double-edged sword, as perfectly illustrated by the process of evolutionary rescue (Gomulkiewicz & Holt 1995). Evolutionary rescue happens when adaptive evolutionary change restores positive growth in declining populations and prevents extinction (**Fig. 2**). This is typically the process involved in the emergence of resistance discussed above. A pest population exposed to pesticides (i.e. environmental stress in **Fig. 2**) for the first time starts

declining because of the increased mortality (red curve in **Fig. 2**) while the frequency of resistant phenotypes increases as a result of their fitness advantage in the new environment (blue curve in **Fig. 2**). Resistant phenotypes are present in low frequencies before pesticide exposure and/or appear by de novo mutations, indicating that population size, standing genetic variation and generation times positively correlate with the probability of evolutionary rescue (Gomulkiewicz & Holt 1995; Carlson *et al.* 2014). The mean population fitness increases with the frequency of resistant phenotypes, potentially enabling population recovery before extinction (Fig. 2). Note that a successful evolutionary rescue implies that population density recovers above the threshold below which it is significantly threatened by low-density processes such as demographic stochasticity, Allee effects or inbreeding. But evolutionary rescue has also enabled the persistence of species that play an important role in the functioning of ecosystems, such as the phytoplankton species of many polluted Canadian lakes (Bell 2012) or marine fish populations whose habitat suffered severe hydrocarbon contaminations (Oziolor *et al.* 2019). Above all, an “evolutionary enlightened” management and conservation planning, aware of the various factors underlying the evolutionary rescue process, could turn it into a formidable ally in the preservation of biodiversity (Carlson *et al.* 2014).

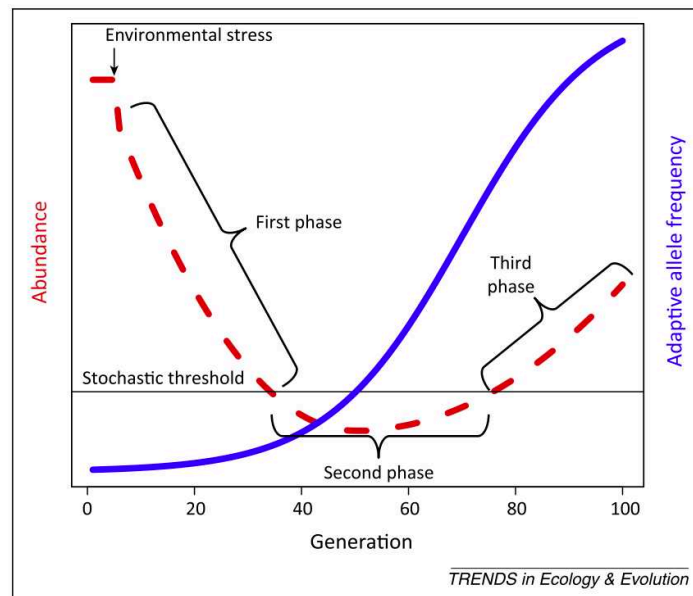


Fig. 2 (taken from Carlson *et al.* 2014): Evolutionary rescue following an environmental disturbance. Population abundance (red dotted line) first decreases while the frequency of adapted phenotypes (blue line) increases. If the latter increase is fast enough, the population stabilizes before recovering above the stochastic threshold below which the population is vulnerable to extinction owing to low-density processes.

The convergence between ecological and evolutionary timescales bears a crucial implication that constitutes the essence of eco-evolutionary dynamics. Mediated by its phenotypic traits, the interaction between an individual and its environment (biotic and abiotic) – i.e. its ecology – leads to the emergence of selective pressures acting on those same traits. The consecutive evolutionary-induced change then alters the individual ecology, which in turn modifies the selective pressures on its traits (**Fig. 3**). Ecology and evolution thus incessantly feedback into each other, creating the eco-evolutionary feedback loop (Ferriere & Legendre 2012, see **Fig. 3**).

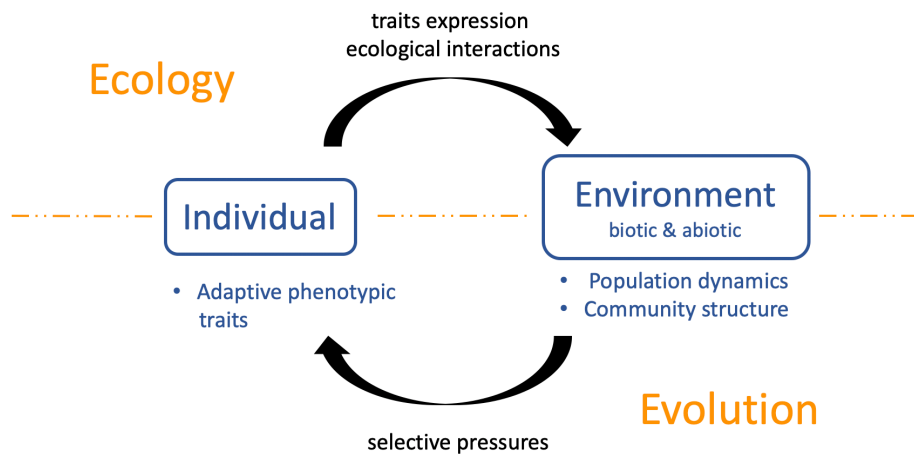


Fig. 3 (adapted from Ferriere & Legendre 2012): The eco-evolutionary feedback loop. The interaction between an individual and its environment (ecological interactions in particular) determine the population and community dynamics, which in turn lead to selective pressures through which evolution modifies the individual traits, and thus the interaction between the individual and its environment (i.e. its ecology). Note that the result is the intertwining between ecology and evolution, which are markedly separated here (orange dotted line) for illustrative purposes.

Why are interspecific interactions key to eco-evolutionary dynamics?

Interspecific ecological interactions are intrinsically subject to the eco-evolutionary feedback loop because, on the one hand, they affect the fitness of an individual by modifying one or several of its characteristics (e.g. mortality rate, see section (1)) and, on the other hand, they are essentially mediated by individual traits that are subject to evolution (i.e. variable, heritable). As such, they play a critical role in community eco-evolutionary dynamics. Before developing in more detail this mechanistic argument, I would like to point out another argument demonstrating the crucial role of ecological interactions: an important part of the variability of eco-evolutionary dynamics is explained by the variability of interspecific interactions. Such an idea can be illustrated by considering the outcome of an evolutionary rescue process within an explicit pairwise community context (**Box 2, adapted from Loeuille 2019**).

Box 2: Evolutionary rescue within a pairwise community context
(adapted from Loeuille, 2019)

Consider two species (species 1 and 2, **Fig. B2 1**) within the same habitat but that do not interact together. The habitat is brutally disturbed so that the two species are no longer adapted, and their populations start declining. Adaptive evolution, however, enables the two species to survive but the evolutionary rescue process is faster for species 2 than species 1 (**Fig. B2 1**), due to a higher initial standing genetic variation for instance.

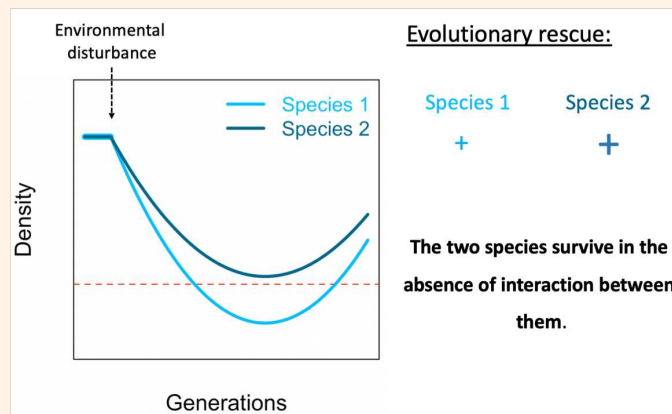


Fig. B2 1: Two concomitant evolutionary rescue processes for two species within the same habitat. The evolutionary rescue of species 2 is faster than that of species 1 due to a higher prior standing genetic variation. This more efficient process is figured by a bigger + symbol.

Now imagine, in addition, that these two species interact. We show that the eco-evolutionary outcome qualitatively depends on the type of interspecific interaction (**Fig. B2 2**). If the two species are competitors (**Fig. B2 2.a**), the increased negative effect of species 2 on species 1 along the evolutionary trajectories (increase of $\frac{Species2_{Density}}{Species1_{Density}}$, see **Fig. B2 1**) is likely to provoke the extinction of species 1 despite the ongoing adaptive evolution. In contrast, if the two species are mutualists (**Fig. B2 2.c**), the increased positive effect of species 2 on species 1 along the evolutionary trajectories facilitates the evolutionary rescue of species 1, favoring the maintenance of diversity. In the case of a trophic interaction (**Fig. B2, 2.b&c**), the outcome also depends on which species – predator or prey – experiments a faster evolutionary rescue (i.e. is species 2 here). If it is the predator (**Fig. B2. 2.b**), the increased relative predation along evolutionary dynamics would favor the prey extinction. If there are no alternative prey, this could even provoke the extinction of both species. If it is the prey (**Fig. B2. 2.c**), the increased positive bottom-up effect would foster the evolutionary rescue of the predator, thus contributing to the maintenance of diversity. The maintenance of species diversity as a result of evolutionary rescue thus strongly depends on the type of ecological interaction considered.

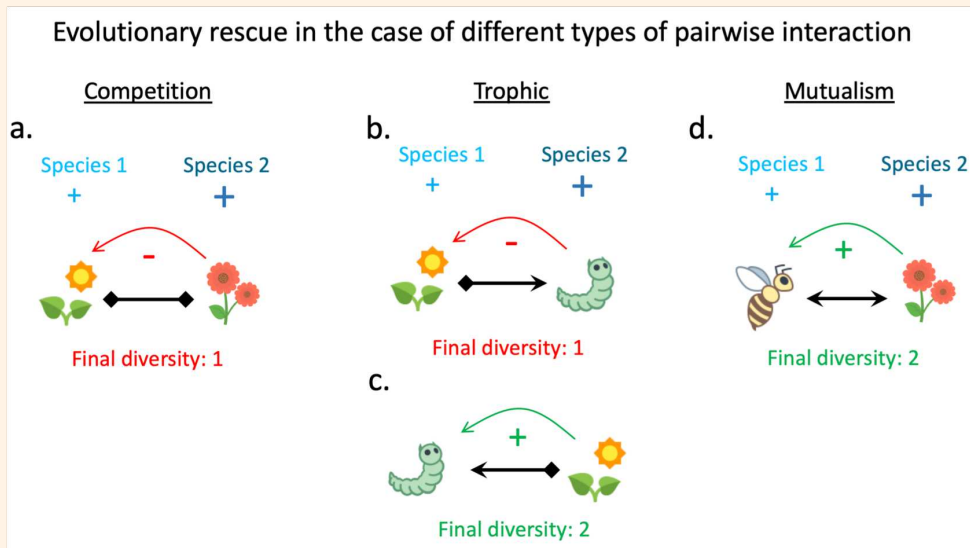


Fig. B2 1: The eco-evolutionary outcome depends on the type of interspecific interaction. As figured by the bigger + symbol, the evolutionary rescue of species 2 is faster (more efficient) than that of species 1. **a. Competition scenario.** **b & c. Trophic scenarios:** In b, the predator experiments faster evolutionary rescue while, in c, it is the prey. **d. Mutualism scenario**

Let us now complexify a bit the ecological setting. Imagine that the evolutionary rescue process in response to the environmental disturbance involves the evolution of a trait that determines the strength of the interspecific interaction between the two species. For instance, climate warming exerts strong selective pressures on a large and diverse set of species toward earlier phenologies (i.e. timing of seasonal activities of plants and animals) (Parmesan & Yohe 2003). The phenology overlap between two interacting species can be considered as a proxy of the intensity of the interspecific interaction (Visser & Gienapp 2019), so that by altering phenologies, climate change also modifies the intensity of direct ecological interactions. For our example, we consider the phenologies of our two-interacting species (1 & 2) – here the distribution of their densities through time (Gaussian curves in **Fig. B2. 3a**) – which emerge from the distribution of a focal phenological trait within the population (e.g. flowering time, egg hatching date). Before warming, the mean traits are matching (**Fig. B2 3a**). After a few generations, warming is responsible for a shift toward an earlier mean phenological trait in both species, but the shift is more important in species 2 than species 1 owing to a faster evolution due to a higher initial standing genetic variation (**Fig. B2 3b**). From now on, how will this initial mismatch interact with the community context to affect the ongoing evolutionary rescue processes (**Fig. B2 3c**)? As summarized in **table B2.1**, it critically depends on the type of interspecific interaction under consideration.

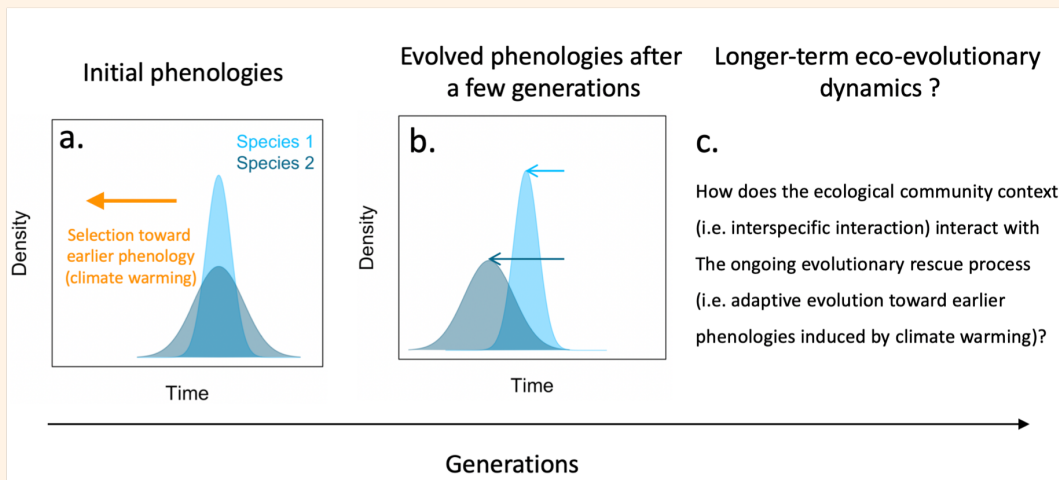


Fig. B2 3: Working example: adaptive evolution toward earlier phenologies in two interacting species as a result of climate warming. **a. Initial phenologies.** Mean traits initially coincide. The orange arrow depicts warming-induced selective pressures. **b. Evolved phenologies after a few generations** (i.e. initial steps of the evolutionary rescue processes). Species 2 displays a bigger initial shift of phenology owing to a greater initial standing genetic variation (the Gaussian standard deviation is a proxy of such variability). **c. What about the longer-term eco-evolutionary dynamics?** The early phenological mismatch (see b) affects subsequent population densities, as well as the strength of the selection toward earlier phenologies, which are both important for evolutionary rescue. Underlying assumption: fitness is significantly affected by both the warming and the interspecific interaction.

There are at least two important factors for evolutionary rescue which are straightforward to consider in our setting – population densities and the strength of selection toward earlier phenologies – and are affected by the community context. In the competition scenario, the partial release from competition induced by the early phenological mismatch (**Fig. B2 3b**) increases both species densities. Moreover, mutants of species 2 that present an earlier phenology benefit from the additional advantage of experiencing less competition from species 1, while the same mutants of species 1 suffer an increased competition from species 2. This implies that the selection toward earlier phenologies is stronger (resp. weaker) for species 2 (resp. species 1). The mutualism scenario displays an opposite pattern: (1) the mismatch is responsible for a decrease in the densities of both species; (2) the selection toward earlier phenologies is weaker (resp. stronger) for species 2 (resp. species 1) as the mutualism selects for an increased overlap of phenologies. In the trophic scenario finally, the early phenological mismatch increases the prey density but decreases that of the predator. Additionally, the trophic interaction leads to the selection of an increased phenological overlap in the predator, and a reduced overlap in the prey. When the prey (species 2) has initially evolved faster than its predator (species 1), it thus contributes positively to the selection toward earlier phenologies for both the prey and the predator. In contrast, when the prey (species 1) has initially evolved slower than its predator (species 2), it contributes negatively to the selection toward earlier phenologies for both species.

Interspecific interaction	Species?		Effect of early mismatch on population densities	Effect of early mismatch on the strength of selection toward an earlier phenology	How does the community context affect the evolutionary rescue processes?
Competition	1(+)	Competitor	+	–	Open question
	2(+)	Competitor	+	+	+
Trophic	1(+)	Predator	–	+	Open question
	2(+)	Prey	+	+	+
	1(+)	Prey	+	–	Open question
	2(+)	Predator	–	–	–
Mutualism	1(+)	Mutualist	–	+	Open question
	2(+)	Mutualist	–	–	–

Table B2 1: Eco-evolutionary dynamics after warming critically depend on the type of interspecific interaction.

Both the population density and the strength of selection toward earlier phenologies accelerates the shift toward earlier phenologies (breeder equation (Lush 1937; Lande 1982), canonical equation of adaptive dynamics (Dieckmann & Law 1996, see **Box 3**), and hence the evolutionary rescue process. Population density, in addition, positively correlates with the probability of evolutionary rescue, notably because it increases the standing genetic variation and offers more opportunities of de novo mutations before extinction (Carlson *et al.* 2014). As such, when the community context positively contributes to those two factors, the evolutionary rescue process is all the more probable (**table B2 1, 6th column**). In our example, the community context facilitates evolutionary rescue when the two species are competing, or in the case of a trophic interaction under the condition that the prey evolved initially faster. In contrast, when it is the predator that evolved initially faster, or when the two species are mutualistic partners, evolutionary rescue is slowed down.

To at least some extent, most interspecific ecological interactions depend on a given set of traits of the interacting species. These traits are often morphological, behavioral, physiological and/or phenological, all categories displaying a minimal level of heritability (Mousseau & Roff 1987). Several examples are developed in the following lines.

Morphological traits appear to be the most heritable (Mousseau & Roff 1987). Among these, body size has notably been shown to play a critical role in trophic interactions. Predators (except herbivores) are almost always bigger than their prey (Warren & Lawton 1987; Memmott *et al.* 2000). Above all, trophic interactions are significantly constrained by predator-prey body size ratios as indicated by a large set of studies describing and analyzing the structure of natural food webs (Cohen *et al.* 1993, 2003; Layman *et al.* 2005; Brose *et al.* 2006; Vucic-Pestic *et al.* 2010; Naisbit *et al.* 2011). The study of Brose *et al.* (2006) – the one with the most important dataset including several types of predators, prey and habitats – nicely illustrates the wide applicability of such scaling, with the relationship between predator and prey size explaining 86% of the observed variance (major axis regression). Of course, the scaling between predator and prey body size also significantly varies depending on the type of predator/prey (vertebrate vs. invertebrate, endotherm vs ectotherm), the type of habitat (aquatics vs. terrestrial), the taxa considered and even the prey/predator size itself (Cohen *et al.* 1993; Brose *et al.* 2006; Naisbit *et al.* 2011). Even within “similar species”, differences exist as illustrated by the study of Scharf *et al.* (2000) on marine fish predators from continental shelf waters off the northern US coast. Their study notably demonstrates that the species considered could be classified into two distinct size-based feeding strategies, with some species mainly consuming prey that are 10% to 20% their size, while other species frequently consume prey that are bigger than half their size. Their study also illustrates that body size, which is thus structuring trophic interactions, can be highly variable within species. As body size can be highly heritable (e.g. Garnett 1981; Noordwijk *et al.* 1988; Castillo-Juárez *et al.* 2007; Silventoinen *et al.* 2008; Schneider *et al.* 2011), trophic interactions are potentially an important driver of eco-evolutionary dynamics.

The same reasoning can be applied to competitive interactions, as they often emerge as a result of indirect trophic interactions (e.g. exploitative competition, apparent competition (Holt 1977)). In zooplankton for instance, the superior grazing ability of bigger species makes them stronger competitors (Gianuca *et al.* 2016). Body size has also been shown to play a key part in interspecific competition, with bigger individuals benefiting from an advantage in defending their territory (e.g. Johnsson *et al.* 1999) or bigger males preventing smaller ones from accessing females (e.g. Bisazza *et al.* 2009).

Other morphological traits are also involved in interspecific interactions. A classic example is the matching between beak size and consumed seed size in Darwin's finches which has likely played a role in their radiation in the Galapagos archipelago from a common ancestor approximately 3 million years ago (Schluter & Grant 1984; Grant & Grant 2003). In one of the islands, contemporary evolution of beak size has been documented as a result of drought-induced modification of the relative abundance of different sized seeds (Boag & Grant 1981; Grant & Grant 1995), clearly indicating ongoing eco-evolutionary dynamics (Hendry 2017). Another classic example is the matching between flower and insect pollinator morphologies which affects the strength and efficiency of pollination (Alexandersson & Johnson 2002; Klumpers *et al.* 2019). The study of Alexandersson & Johnson (2002) on the hawkmoth-pollinated South African iris, for instance, shows that variations in flower-tube length are associated with variations in both fruit and seed set as a result of more or less efficient pollination in relationship with the length of hawkmoth tongue. Surprisingly, the authors conclude on directional selection acting on flower-tube length without any reference to the heritability of this character. The authors are, nevertheless, certainly right as flower traits are indeed relatively heritable (Ashman & Majetic 2006).

Phenological traits – i.e. the seasonal timing of life cycle events – are straightforward to relate to interspecific interactions as interacting species usually need to cooccur in time in order to interact. Indeed, several empirical studies focusing on a single interaction – trophic (e.g. Muniz *et al.* 2012), mutualistic (e.g. Cruz-Neto *et al.* 2011) or competitive (e.g. Fargione & Tilman 2005) – demonstrate the importance of matching phenologies. Other studies, at the community level, emphasize the structuring role of phenological traits in natural trophic (e.g. Edwards & Richardson 2004), mutualistic (e.g. Jordano *et al.* 2003) or competitive networks (e.g. Ramos *et al.* 2014). There is a growing interest in studying the relationship between phenology and ecological interactions because climate change, by modifying the abiotic parameters (e.g. temperature, daylength...) often used as environmental cues to trigger a given life cycle event, differentially affects phenologies resulting in temporal mismatches between interacting species (Parmesan 2006; Renner & Zohner 2018). Notably, earlier plant phenologies have been consistently reported resulting in a significant advance in the onset of Spring worldwide (Parmesan & Yohe 2003; Badeck *et al.* 2004; Menzel *et al.* 2006), which suggests that plant-animal interactions might be particularly impacted. Deacy *et al.* (2017), for instance, report that warming-induced earlier fruit production in the red elderberry altered its trophic interaction with the Kodiak brown bear, with far-reaching consequences at the community and

ecosystem levels. The phenological shift led to the red elderberry being available during the period when the sockeye salmon spawned in tributary streams, resulting in a strong decline of salmon consumption by bears, which preferred to forage on berries. Far-reaching consequences are expected as the “keystone” interaction between bears and salmon – bears usually kill 25%-75% of the salmon – provides approximately one-quarter of the riparian nitrogen budget (Helfield & Naiman 2006).

Phenological traits seem heritable, as indicated by several studies on bird migration dates (e.g. Møller 2001; Pulido *et al.* 2001) or plant flowering times (e.g. Kochmer & Handel 1986; Andrés & Coupland 2012). Some studies even exhibit the genetic signature of warming-induced phenological shifts, demonstrating the role of evolution in shaping phenologies (Bradshaw & Holzapfel 2001; Berteaux *et al.* 2004; Franks *et al.* 2007).

Given the huge diversity of life on earth, the diversity of traits that might play a part in a given interspecific interaction is virtually infinite. I would therefore briefly conclude this section by mentioning some other traits that are important for plant-pollinator and plant-herbivore interactions.

Floral traits, which have a genetic basis and are thus heritable (Ashman & Majetic 2006), have been shown to play a key role in both types of interaction (Strauss & Whittall 2006). Examples include flower color, shape, size or number, as well as floral VOCs (i.e. volatile organic compounds), nectar quality and quantity. Pollinators and herbivores may indeed display preferences in relationship with these floral traits (e.g. flower colors, Stanton 1987; McCall *et al.* 2013). Behavioral traits, which display a significant level of heritability according to the meta-analysis by Stirling *et al.* (2002), are thus likely involved. Some studies notably report herbivores that preferentially consume plant species bearing abundant developing fruits (e.g. Herrera 2000), while other report pollinators that discriminate against damaged plant individuals (e.g. Pohl *et al.* 2006).

Plants also rely on chemical defense – i.e. production of toxic secondary metabolites – to protect themselves against herbivory (Johnson 2011). In response, some herbivores developed detoxification enzymes that make them able to consume defended plant phenotypes (Després *et al.* 2007). Both the production of chemical defenses and counter-defenses have been shown to exhibit a reasonable degree of genetic variation, and are thus subject to evolution (Després *et al.* 2007; Johnson 2011). Becerra *et al.* (2009) even demonstrate the macroevolutionary signature resulting from such chemical escalation between plants and herbivores.

(3) The need to account for diverse interspecific interactions simultaneously

Accounting for diverse interspecific interactions simultaneously is required as (1) species are often, if not always, involved in several interactions simultaneously and (2) the dynamics resulting from the combination of several interactions differ from the linear combination of the dynamics ensuing from single interactions considered in isolation.

Diverse ecological interactions coexist simultaneously in natural communities

Consider, for instance, a fig tree (genus *Ficus*) in an Asian tropical forest ecosystem. Several *Lepidoptera* caterpillars may feed on its leaves, including the plain tiger (*Danaus chrysippus*) or the brown awl (*Badamia exclamationis*). Its fruits are also a key resource for several frugivores (Shanahan *et al.* 2001) including fruit bats (*Pteropodidae* family), several primate species such as gibbons (*Hylobatidae* family) or langurs (*Cercopithecidae* family), and birds such as the fig-parrot (*Psittaculidae* family) or the bulbul (*Pycnonotidae* family). These frugivores may also enable seed dispersal and thus act as mutualistic partners of the plant (Shanahan *et al.* 2001). For its reproduction, the fig tree relies on fig wasps (*Hymenoptera*, *Agaonidae* family), whose females enter immature fruits to deposit their eggs. By doing so, females also deposit pollen from the fig tree where they grew and matured, before emerging to search for a fig fruit where to lay eggs to complete their life-cycle (Ramirez 1974). Wasps from other families can deposit eggs without entering the fruit, thus acting as parasites to the fig and/or the pollinating wasps (Ramirez 1974). As approximately 90% of terrestrial plant species (Fitter & Moyersoen 1996), the fig tree, in addition, relies on its mutualistic interaction (symbiosis) with mycorrhizal fungi to obtain important nutrients from the soil (e.g. phosphorus). Because it is involved in so many interaction webs, several authors consider the fig tree to be a keystone species of many tropical forests across the globe (e.g. Lambert & Marshall 1991; Nason *et al.* 1998; Shanahan *et al.* 2001).

The fig tree is not an isolated case. Virtually all plant species are consumed by herbivore species. Approximately 80% of terrestrial plant species are flowering plants (i.e. angiosperms, Christenhusz & Byng 2016), of which around 90% rely on animals for pollination (Ollerton *et al.* 2011). Several other mutualistic interactions are also widespread within plant species (Bronstein *et al.* 2006), including seed-dispersal in exchange for food, or protection in exchange

for habitat, as well as belowground interactions with fungi or bacteria involving the exchange of nutrients (Trappe 1977; Carlsson & Huss-Danell 2003). Terrestrial plant species might therefore be a critical node of ecological interaction networks.

Animal species are also involved in diverse types of interactions. In particular, every mutualistic interaction is connected to the trophic network of each interacting partner, as well as their respective competitive networks with the species occupying a similar ecological niche (MacArthur & Levins 1967). For instance, all animals possess in their gut a community of microorganisms – the gut microbiota (Gilbert *et al.* 2012) – which has been shown to influence many aspects of the host ecology, including health, physiology and behavior (Redfern *et al.* 2017; Wong *et al.* 2017). Gut microbiota might therefore influence other ecological interactions, trophic and competitive in particular, but this research topic is still in its infancy.

Another interaction in which animal species are often involved is parasitism (definition in **Box 1**). Although much smaller than their hosts, parasites could represent a substantial amount of the biomass within a given ecosystem, as shown by Kuris *et al.* (2008). Moreover, incorporating the parasites into the pelagic food web of a subarctic lake more than doubled the links within the network (Amundsen *et al.* 2009). Such a tremendous impact on network topology is likely to impact the whole food web functioning.

The study conducted by Kéfi *et al.* (2015) is particularly relevant to conclude this section. The authors characterize a comprehensive ecological network consisting of 104 species of the marine intertidal community of the central Chilean coast, including all known trophic interactions, as well as diverse non-trophic links between them. Non-trophic interactions notably include various facilitative interactions, refuge provisioning as well as competition for space. The authors found that non-trophic interactions accounted for more than two-thirds of the interactions within this ecological network. Their study clearly emphasizes that natural ecological communities consist of diverse species interacting in many diverse ways, simultaneously.

The non-additive effect of diverse ecological interactions

The decisive argument in favor of an integrative approach accounting for diverse interactions simultaneously is that the understanding derived from single-interaction

approaches might not apply in real communities where several interaction types coexist (Fontaine *et al.* 2011). Pursuing the example of mapping parasitic interactions into food webs, the study of Amundsen *et al.* (2009) not only shows an increase in the number of links, but also a significant alteration of the topology and structure of the trophic network. In line with several other studies (Lafferty *et al.* 2006), their results indicate that important network properties, such as connectance (i.e. the proportion of realized interactions) or nestedness (i.e. the tendency of subnetworks to be nested within each other), are modified. Because such properties have been shown to strongly influence the stability of ecological networks (e.g. Thébault & Fontaine 2010), a thorough understanding of food web stability requires to account for the effect of parasitic interactions.

The interplay of mutualistic and antagonistic interactions can also strongly influence community stability, as illustrated by the theoretical work of Mougi & Kondoh (2012). The authors investigated the relationship between the complexity of an ecological network – i.e. the product of species richness and connectance – and its stability. This relationship has been central in community ecology since May (1972) theoretically demonstrated that stability decreases with complexity within randomly assembled communities. Because it was paradoxical given the complexity of real communities in nature, May's work was followed by a huge amount of research on the subject – i.e. the complexity-stability debate – resulting in major advances in community ecology. In particular, the non-random assembly of natural communities is likely the key element to resolve the initial paradox (De Ruiter *et al.* 1995; Neutel *et al.* 2007; Landi *et al.* 2018). In their work, Mougi & Kondoh (2012) compare networks that differ in the proportion of mutualistic vs. trophic interactions. They found a negative complexity-stability relationship when either type of interaction is predominant, but a positive relationship when the two interactions are of similar proportions. Their study thus provides compelling evidence that key biodiversity patterns resulting from the combination of diverse interaction may strongly differ from the combination of patterns derived from considering ecological interactions in isolation.

Non-additivity most often arises from one interaction modifying the strength of another interaction, i.e. interaction modification (**Fig. 1B**).

A large amount of literature reports that tropically transmitted parasites often increase the susceptibility of their intermediate hosts to predation, notably by modifying their behavior (Moore 1995; Kuris 2005). Pacific killifishes (*Fundulus parvipinnis*) infected by the

trematode *Euhaplorchis californiensis* are, for instance, 30 times more likely to be eaten by avian predators than unparasitized fishes owing to a much more conspicuous behavior (Lafferty & Kimo Morris 1996). Similarly, but in the context of a mutualistic interaction this time, several bacteria of the *Drosophila* (i.e. fruit fly) gut microbiota have been shown to modify the foraging behavior of their host, by modifying its olfactory system, so that it preferentially consumes food containing the given focal bacteria (Wong *et al.* 2017).

Interaction modifications have especially been reported in the interactions involving plant species. In particular, plants connect aboveground and belowground ecosystems, with the strength of interactions occurring aboveground modifying the strength of belowground interactions (e.g. Barber *et al.* 2012), and conversely (e.g. Barber & Gorden 2014). As pointed out by the review of Wardle *et al.* (2004), such processes even lead to ecological feedback between aboveground and belowground communities, advocating for a more integrative approach. Indirect interaction between pollinators and herbivores mediated by the modification of plant traits have also been frequently reported. Examples include herbivore preference towards plants bearing abundant developing fruits as a result of strong pollination (Herrera 2000), as well as pollinator avoidance of damaged plant individuals owing to the change in floral display (e.g. Cardel & Koptur 2010) or plant chemistry (e.g. Kessler *et al.* 2011). Herbivory-induced changes of plant chemistry may also modify the interaction between herbivores and their predators, as some volatiles emitted upon damage can attract the latter in order to defend against herbivory (e.g. Kessler & Baldwin 2001).

The various examples exhibited so far illustrate how diverse ecological interactions often interplay in a non-linear manner so that non-additive dynamics might be widespread in natural communities. This is why several relatively recent works emphasize that the study of communities involving several types of interactions simultaneously should significantly improve our understanding of biodiversity functioning (Fontaine *et al.* 2011; Kéfi *et al.* 2012). In particular, the interplay of pollination and herbivory have been shown not only to induce non-additive ecological dynamics (e.g. Herrera 2000; Lundin *et al.* 2013; Sutter & Albrecht 2016), but also to lead to complex evolutionary dynamics that cannot be predicted from the insights obtained from single-interaction studies (e.g. Herrera *et al.* 2002; Gómez 2005). As such, the study of plant-pollinator-herbivore communities appears especially relevant to unravel the complexity of the eco-evolutionary dynamics that might emerge from the interplay of mutualistic and antagonistic interactions.

(4) Why study plant-pollinator-herbivore communities?

Plant-pollinator-herbivore communities play a pivotal role in terrestrial ecosystems. Tremendously widespread across the globe, plant species are present in almost every terrestrial ecosystem (Woodward *et al.* 2004). Photosynthesis enables plant species to turn atmospheric carbon into organic one (Lambers *et al.* 2008). As primary producers, plant species provide the organic matter and energy supporting whole food webs, which flows through trophic interactions from herbivores up to top predators. Because photosynthesis is virtually responsible for all the biochemical production of organic matter, plant species are crucial to the functioning of biodiversity (Field *et al.* 1998). As the first link connecting the autotroph plant trophic level to the rest of the food web, plant-herbivore interactions are also key. On the other hand, a vast majority of terrestrial plant species rely on animal pollination for reproduction (Ollerton *et al.* 2011; Christenhusz & Byng 2016), making plant-pollinator interactions critical to the functioning of terrestrial biodiversity.

Plant-pollinator-herbivore communities are also crucial for human food provisioning. Pollination is, indeed, important for agricultural production as three-quarters of the leading food crops exhibit increased fruit or seed set as a result of animal pollination (Klein *et al.* 2007). Gallai *et al.* (2009) estimate that the economic value of such an ecosystem service amounts to €153 billion worldwide, representing approximately 10% of the world agricultural production each year. Herbivores, in contrast, provide an ecosystem dis-service by damaging cultivated plant species (Zhang *et al.* 2007). Oerke (2006), for instance, estimates that the worldwide yield loss of five major crops (e.g. wheat, rice) attributable to herbivory ranges from 8 to 15% of their total annual production.

Owing to such importance, plant-pollinator and plant-herbivore interactions have been extensively studied in the literature. Being our central motivation for investigating antagonistic-mutualistic communities, their non-additive effects on both ecological and evolutionary dynamics have notably been reported several times.

Manipulating the presence-absence of pollinators and herbivores, two-level fully factorial designs have frequently been used to measure how the interplay of pollination and herbivory affects seed and fruit production. These studies often exhibit an interactive effect showing that the negative effects of herbivory on plant yield is observed only in the presence

of pollinators (Herrera 2000; Herrera *et al.* 2002; Gómez 2005). Similar results have been obtained in studies that indirectly manipulated the level of herbivory by modifying the density of herbivores' predators (i.e. pest control, Lundin *et al.* 2013; Sutter & Albrecht 2016). Based on the authors' observations, herbivore preference towards pollinated plant individuals has often been presented as the underlying mechanism, but other processes have also been reported. Sutter & Albrecht (2016), for instance, show that herbivory-induced lifetime reduction is responsible for dividing by two the number of pollination visits received by an individual flower. Other studies simulating herbivore damage (e.g. petal clipping) shows that pollinator avoidance of damaged plant individuals is also involved (e.g. Pohl *et al.* 2006), in line with several field observations (e.g. Cardel & Koptur 2010).

The ecological interplay described so far implies that the selective pressures imposed on plant species cannot be understood from the sole consideration of pollination nor herbivory (e.g. Galen & Cuba 2001; Brody 2008; Ramos & Schiestl 2019). A large number of plant traits are notably often involved in an ecological trade-off – i.e. a trade-off that manifests itself only in the presence of a given ecological interaction (Strauss *et al.* 2002) – between attracting pollinators and deterring herbivores. For instance, more defended plant phenotypes can be less visited by pollinators (Strauss *et al.* 1999), phenotypes that produce more nectar to attract pollinators may also attract more herbivores (Adler & Bronstein 2004). Actually, shared animal preferences for plant phenotypes are tremendously widespread (Asikainen & Mutikainen 2005; Strauss & Whittall 2006; Theis *et al.* 2014). As a result, plant traits are often under conflicting selection from the interplay of pollination and herbivory. An important question is whether it can also lead to disruptive selection, as various studies demonstrate its role in supporting the maintenance of plant polymorphism (Ehrlén *et al.* 2002; Irwin *et al.* 2003; Frey 2004).

Finally, the study of plant-pollinator-herbivore communities is of high applied relevance given that these communities are particularly impacted by global change. Insect species, which represent an important part of herbivores and/or pollinators, are rapidly declining in abundance and diversity worldwide, so that 40% of the species are expected to go extinct over the next few decades (Sánchez-Bayo & Wyckhuys 2019). Specific reviews focusing on pollinator species, including birds and mammals (Regan *et al.* 2015), yield similar alarming results (Potts *et al.* 2010; Ollerton 2017). As for non-insect herbivores, a recent comparative study of extinction risks among mammals, birds and reptiles, and across trophic levels suggests that herbivores might be at a higher risk of extinction (Atwood *et al.* 2020). All studies emphasize the role of habitat degradation, loss and fragmentation driven by intensive agriculture and urbanization, as

well as invasive species and climate change in driving such biodiversity losses (Potts *et al.* 2010; Regan *et al.* 2015; Sánchez-Bayo & Wyckhuys 2019; Atwood *et al.* 2020). Note the disturbing paradox of agriculture being the main driver of pollinators decline (Potts *et al.* 2010; Regan *et al.* 2015).

(5) Questions addressed in this PhD thesis

The present PhD thesis investigates the eco-evolutionary dynamics of a three-species module consisting of a plant species interacting with both a pollinator and a herbivore species (**Fig. 4**).

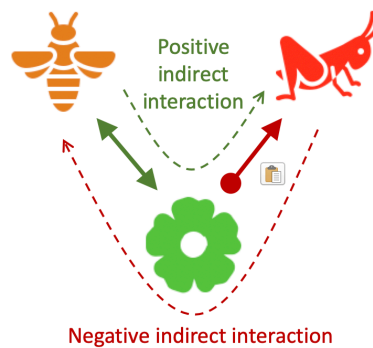


Fig. 4: Schematic representation of the plant-pollinator-herbivore module. Mediated by plant density, the indirect interaction between animal species is positive for herbivores and negative for pollinators.

First, we study how stable coexistence depends on the relative strengths of pollination vs. herbivory. We show that when herbivory is much stronger than pollination, coexistence is lost as a result of pollinator extinction. When pollination is much stronger than herbivory, coexistence is no longer stable. As a result, stable coexistence requires a balanced interaction pattern. We notably unravel in detail the processes – indirect density-mediated interactions and feedback loops – underlying the observed pattern. We discuss how our result may be related to the ecological trade-off – i.e. attracting pollinators vs. deterring herbivores – being widespread.

We then introduce a plant trait involved in both interactions. Each plant-animal interaction gets stronger as the matching between the plant phenotype and the respective animal phenotype increases. We investigate the potential eco-evolutionary dynamics arising from such a framework by combining numerical simulations with analytical results derived from adaptive dynamics (details in **Box 3**).

Box 3: The framework of adaptive dynamics

The traits of a given population change under the action of natural selection. Such trait evolution may then modify the strength of the ecological interactions, as well as the densities within the community. As a result, the selective pressures on our focal population, and in turn trait evolution, are modified. Adaptive dynamics are an analytical framework, developed in the 90s (Metz *et al.* 1992; Dieckmann & Law 1996; Geritz *et al.* 1997, 1998), that allows the theoretical study of evolutionary dynamics by explicitly accounting for such a feedback between ecology and evolution. As such, it is a powerful tool to investigate the eco-evolutionary dynamics that may occur within natural communities.

Considering a population imbedded (clonal reproduction) in a given ecological context (ecological interactions...), adaptive dynamics describe the evolution through time of a given population trait (noted s here) under the action of random mutations. At the core of adaptive dynamics, the eco-evolutionary feedback loop is accounted for by deriving fitness from the explicit population dynamics (Metz *et al.* 1992). Two important assumptions are made. Firstly, population dynamics occur on an ecological timescale that is much faster than the evolutionary timescale on which trait changes are observed. This, in essence, corresponds to mutations being rare so that they always occur within a monomorphic resident population at ecological equilibrium. Secondly, mutations are of small phenotypic amplitude. In such a context, a mutant with a new phenotype s_{mut} invades the resident population if its expected long-term per capita growth rate, when rare and in the environment set by the resident (i.e. ecological equilibrium N^*) – i.e. its **fitness of invasion** $\omega(s_{mut}, s)$ (equation 1) – is positive.

$$\omega(s_{mut}, s) \stackrel{\text{def}}{=} \left. \frac{dN_{mut}}{N dt} \right]_{N_{mut} \ll N^*} \quad (1)$$

When a mutant invades, it replaces the resident population, thus becoming the new resident. The consecutive sequence of trait substitution defines the long-term evolutionary dynamics. Although intrinsically stochastic, such evolutionary dynamics can be deterministically approximated under the assumption of adaptive dynamics (Dieckmann and Law, 1996), leading to **the canonical equation of adaptive dynamics** (equation 2)..

$$\frac{ds}{dt} = CN^* \mu \sigma^2 \left. \frac{\partial \omega(s_{mut}, s)}{\partial s_{mut}} \right]_{s_{mut}=s} \quad (2)$$

The expected rate of trait substitution is proportional to **the selection gradient**, i.e. the derivative of the invasion fitness with respect to the mutant's trait ($\left. \frac{\partial \omega(s_{mut}, s)}{\partial s_{mut}} \right]_{s_{mut}=s}$). It is also proportional to the population evolvability, which depend on the population size N^* , as well as on the phenotypic variability brought by the mutation regime $\mu \sigma^2$, with μ and σ^2 the mutation frequency and phenotypic amplitude, respectively. C is an homogenizing constant that notably depends on the specific mutation regime (e.g. symmetry).

Evolutionary equilibria s^* , which are characterized by $\frac{ds}{dt} = 0$, thus correspond to the trait values at which the selection gradient vanishes. These **evolutionary singularities** can be classified according to two properties: convergence and invasibility. Convergence indicates that the trait evolves toward the singularity in its vicinity. Invasibility specifies whether the singularity may be invaded by nearby mutants. It is often referred to as evolutionary stability in other frameworks (Maynard Smith & Price 1973). These properties depend on the sign of the second derivatives of the fitness of invasion, as indicated by equations 3&4.

Convergence	$\frac{d}{ds} \left\{ \frac{\partial \omega(s_{mut}, s)}{\partial s_{mut}} \right\}_{s_{mut}=s} \Big _{s=s^*} < 0$	(3)
Invasibility	$\frac{\partial^2 \omega(s_{mut}, s)}{\partial s_{mut}^2} \Big _{s_{mut}=s=s^*} < 0$	(4)

Four types of singularities may then be considered (Geritz *et al.* 1998). Two singularities are convergent: the non-invasible continuously stable strategy (CSS, Eshel, 1983) and the invasible branching point (BP, Geritz *et al.* 1997). Branching points are of particular interest as they yield the emergence of a dimorphic population, which can be viewed as the first step toward sympatric speciation. Non-convergent singularities are the invasible repellor and the non-invasible garden of Eden. Evolutionary dynamics can be fully determined by knowing the position and type of all singularities.

Here, adaptive dynamics have been illustrated in the case of one trait evolution, but the framework can be adapted to account for the evolution of several traits simultaneously, thus allowing to investigate coevolutionary scenarios (Dieckmann & Law 1996; Kisdi 2006). Relaxing some assumptions such as clonal reproduction (Collet *et al.* 2011) or populations being at ecological equilibrium is also possible (Dieckmann & Law 1996).

Firstly, we study plant phenotype evolution while fixing animal phenotypes. We are interested in the different types of evolutionary dynamics that can arise, as well as in their consequences on the interaction pattern and the maintenance of multispecies coexistence. We notably show that disruptive selection may arise from the interplay of pollination and herbivory, leading to a dimorphic plant population.

Secondly, we study the (co)evolution of animal species within such a two-species floral landscape, plant phenotypes being fixed. We are interested in (1) the potential for diversification in animals in response to the diversity of plant resources and (2) the impact of animal evolution on interspecific plant competition and its consequences for plant coexistence. We show that the opposite sign in eco-evolutionary feedback – negative for herbivores and positive for pollinators – is responsible for the emergence of strongly contrasting eco-evolutionary dynamics when comparing pollinator vs. herbivore evolution. Moreover, coevolution may lead to dynamics that significantly differ from the ones obtained when only one animal is evolving, with notably fluctuating selection acting on both animal phenotypes, that dampens over time.

Our results shed light on the processes that may underlie the evolutionary emergence of diverse plant-pollinator-herbivore communities, as well as on the potential for achieving such emergence within our modelling framework, akin to what has been achieved two decades ago for trophic networks (Loeuille & Loreau 2005; Allhoff *et al.* 2015). We notably illustrate how such emerging networks can be used to assess the eco-evolutionary resilience of natural communities confronted with global change (Yacine *et al.* 2021, see appendix).

References (section I)

- Abrams, P.A. (1987). On classifying interactions between populations. *Oecologia*, 73, 272–281.
- Abrams, P.A., Menge, B.A., Mittelbach, G.G., Spiller, D.A. & Yodzis, P. (1996). The Role of Indirect Effects in Food Webs. In: *Food Webs*. Springer US, Boston, MA, pp. 371–395.
- Adler, L.S. & Bronstein, J.L. (2004). Attracting antagonists: Does floral nectar increase leaf herbivory? *Ecology*, 85, 1519–1526.
- Alexandersson, R. & Johnson, S.D. (2002). Pollinator-mediated selection on flower-tube length in a hawkmoth-pollinated *Gladiolus* (Iridaceae). *Proc. R. Soc. B Biol. Sci.*, 269, 631–636.
- Allhoff, K.T., Ritterskamp, D., Rall, B.C., Drossel, B. & Guill, C. (2015). Evolutionary food web model based on body masses gives realistic networks with permanent species turnover. *Sci. Rep.*, 5, 10955.
- Amundsen, A., Lafferty, K.D., Knudsen, R., Primicerio, R., Klemetsen, A. & Kuris, A.M. (2009). Food web topology and parasites in the pelagic zone of a subarctic lake. *J. Anim. Ecol.*, 78, 563–572.
- Andrés, F. & Coupland, G. (2012). The genetic basis of flowering responses to seasonal cues. *Nat. Rev. Genet.*, 13, 627–639.
- Ashman, T.L. & Majetic, C.J. (2006). Genetic constraints on floral evolution: A review and evaluation of patterns. *Heredity (Edinb.)*, 96, 343–352.
- Asikainen, E. & Mutikainen, P. (2005). Preferences of pollinators and herbivores in gynodioecious *Geranium sylvaticum*. *Ann. Bot.*, 95, 879–886.
- Atwood, T.B., Valentine, S.A., Hammill, E., McCauley, D.J., Madin, E.M.P., Beard, K.H., *et al.* (2020). Herbivores at the highest risk of extinction among mammals, birds, and reptiles. *Sci. Adv.*, 6, eabb8458.
- Badeck, F.W., Bondeau, A., Böttcher, K., Doktor, D., Lucht, W., Schaber, J., *et al.* (2004). Responses of spring phenology to climate change. *New Phytol.*, 162, 295–309.
- Barber, N.A., Adler, L.S., Theis, N., Hazzard, R. V & Kiers, E.T. (2012). Herbivory reduces plant interactions with above-and belowground antagonists and mutualists. *Ecology*, 93, 1560–1570.
- Barber, N.A. & Gorden, N.L.S. (2014). How do belowground organisms influence plant-pollinator interactions? *J. Plant Ecol.*, 8, 1–11.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., *et al.* (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51–57.
- Becerra, J.X., Noge, K. & Venable, D.L. (2009). Macroevolutionary chemical escalation in an ancient plant-herbivore arms race. *Proc. Natl. Acad. Sci. U. S. A.*, 106, 18062–18066.
- Begon, M., Harper, J.L. & Townsend, C.R. (1986). *Ecology: Individuals, Populations, and Communities*. Blackwell scientific publications.
- Bell, G. (2012). Evolutionary rescue and the limits of adaptation. *Philos. Trans. R. Soc. B Biol. Sci.*, 368, 20120080–20120080.
- Berteaux, D., Réale, D., McAdam, A.G. & Boutin, S. (2004). Keeping pace with fast climate change: Can Arctic life count on evolution? *Integr. Comp. Biol.*, 44, 140–151.
- Bisazza, A., Novarini, N. & Pilastro, A. (2009). Male body size and male-male competition: Interspecific variation in poeciliid fishes. *Ital. J. Zool.*, 63, 365–369.
- Boag, P.T. & Grant, P.R. (1981). Intense natural selection in a population of Darwin's finches (geospizinae) in the Galápagos. *Science*, 214, 82–85.

- Bradshaw, W.E. & Holzapfel, C.M. (2001). Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl. Acad. Sci.*, 98, 14509–14511.
- Bradshaw, W.E. & Holzapfel, C.M. (2006). Evolutionary response to rapid climate change. *Science*, 312, 1477–1478.
- Brody, A.K. (2008). Effects of Pollinators, Herbivores, and Seed Predators on Flowering Phenology. *Ecology*, 78, 1624–1631.
- Bronstein, J.L. (2001). The Costs of Mutualism. *Am. Zool.*, 41, 825–839.
- Bronstein, J.L., Alarcón, R. & Geber, M. (2006). The evolution of plant-insect mutualisms. *New Phytol.*, 172, 412–428.
- Bronstein, J.L., Dieckmann, U. & Ferrière, R. (1994). *Coevolutionary Dynamics and the Conservation of Mutualisms*.
- Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008). Synergies among extinction drivers under global change. *Trends Ecol. Evol.*
- Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.F., *et al.* (2006). Consumer-resource body-size relationships in natural food webs. *Ecology*, 87, 2411–2417.
- Buckley, J., Butlin, R.K. & Bridle, J.R. (2012). Evidence for evolutionary change associated with the recent range expansion of the British butterfly, *Aricia agestis*, in response to climate change. *Mol. Ecol.*, 21, 267–280.
- Burns, T.P., Rose, K.A. & Brenkert, A.L. (2014). Quantifying direct and indirect effects of perturbations using model ecosystems. *Ecol. Modell.*, 293, 69–80.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., *et al.* (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417, 844–847.
- Cardel, Y.J. & Koptur, S. (2010). Effects of florivory on the pollination of flowers: An experimental field study with a perennial plant. *Int. J. Plant Sci.*, 171, 283–292.
- Carlson, S.M., Cunningham, C.J. & Westley, P.A.H. (2014). Evolutionary rescue in a changing world. *Trends Ecol. Evol.*, 29, 521–530.
- Carlsson, G. & Huss-Danell, K. (2003). Nitrogen fixation in perennial forage legumes in the field. *Plant Soil*, 253, 353–372.
- Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R. (1985). Cascading Trophic Interactions and Lake Productivity. *Bioscience*, 35, 634–639.
- Carroll, S.P., Loye, J.E., Dingle, H., Mathieson, M., Famula, T.R. & Zalucki, M.P. (2005). And the beak shall inherit - Evolution in response to invasion. *Ecol. Lett.*, 8, 944–951.
- Castillo-Juárez, H., Carlos, J., Casares, Q., Campos-Montes, G., Cabrera Villela, C., Martínez Ortega, A., *et al.* (2007). Heritability for body weight at harvest size in the Pacific white shrimp, *Penaeus (Litopenaeus) vannamei*, from a multi-environment experiment using univariate and multivariate animal models. *Aquaculture*, 273, 42–49.
- Chamberlain, S.A., Bronstein, J.L. & Rudgers, J.A. (2014). How context dependent are species interactions? *Ecol. Lett.*, 17, 881–890.
- Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.
- Christenhusz, M.J.M. & Byng, J.W. (2016). The number of known plants species in the world and its annual increase. *Phytotaxa*, 261, 201–217.

- Cohen, J.E., Jonsson, T. & Carpenter, S.R. (2003). Food Webs, Body Size, and Species Abundance in Ecological Community Description. *Proc. Natl. Acad. Sci.*, 100, 1781–1786.
- Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldana, J. (1993). Body Sizes of Animal Predators and Animal Prey in Food Webs. *J. Anim. Ecol.*, 62, 67.
- Collet, P., Metz, J.A.J. & Méléard, S. (2011). *A rigorous model study of the adaptive dynamics of Mendelian diploids*.
- Crombie, A.C. (1947). Interspecific Competition. *J. Anim. Ecol.*, 16, 44.
- Cruz-Neto, O., Machado, I.C., Duarte, J.A. & Lopes, A.V. (2011). Synchronous phenology of hawkmoths (Sphingidae) and Inga species (Fabaceae-Mimosoideae): Implications for the restoration of the Atlantic forest of northeastern Brazil. *Biodivers. Conserv.*, 20, 751–765.
- Darwin, C. (1859). *On the Origin of Species*. Cambridge, MA: Harvard University Press.
- Dawkins, R. & Krebs, J.R. (1979). Arms races between and within species. *Proc. R. Soc. B Biol. Sci.*, 205, 489–511.
- Deacy, W.W., Armstrong, J.B., Leacock, W.B., Robbins, C.T., Gustine, D.D., Ward, E.J., *et al.* (2017). Phenological synchronization disrupts trophic interactions between Kodiak brown bears and salmon. *Proc. Natl. Acad. Sci. U. S. A.*, 114, 10432–10437.
- Després, L., David, J.P. & Gallet, C. (2007). The evolutionary ecology of insect resistance to plant chemicals. *Trends Ecol. Evol.*, 22, 298–307.
- Dieckmann, U. & Law, R. (1996). The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.*, 34, 579–612.
- Edwards, M. & Richardson, A.J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, 430, 881–884.
- Ehrlén, J., Käck, S. & Ågren, J. (2002). Pollen limitation, seed predation and scape length in *Primula farinosa*. *Oikos*, 97, 45–51.
- Ehrlich, P.R. & Raven, P.H. (1964). Butterflies and Plants: A Study in Coevolution. *Evolution (N. Y.)*, 18, 586.
- Eshel, I. (1983). Evolutionary and continuous stability. *J. Theor. Biol.*, 103, 99–111.
- Fargione, J. & Tilman, D. (2005). Niche differences in phenology and rooting depth promote coexistence with a dominant C4 bunchgrass. *Oecologia*, 143, 598–606.
- Ferriere, R. & Legendre, S. (2012). Eco-evolutionary feedbacks, adaptive dynamics and evolutionary rescue theory. *Philos. Trans. R. Soc. B Biol. Sci.*, 368, 20120081.
- Field, C.B., Behrenfeld, M.J., Randerson, J.T. & Falkowski, P. (1998). Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science*, 281, 237–240.
- Fitter, A.A.H. & Moyersoen, B. (1996). Evolutionary Trends in Root-Microbe Symbioses. *Philos. Trans. Biol. Sci.*, 351, 1367–1375.
- Fontaine, C., Guimarães Jr, P.R., Kéfi, S., Loeuille, N., Memmott, J., van der Putten, W.H., *et al.* (2011). The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.*, 14, 1170–1181.
- Franks, S.J., Sim, S. & Weis, A.E. (2007). Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proc. Natl. Acad. Sci. U. S. A.*, 104, 1278–1282.

- Frey, F.M. (2004). Opposing natural selection from herbivores and pathogens may maintain floral-color variation in *Claytonia virginica* (Portulacaceae). *Evolution (N. Y.)*, 58, 2426–2437.
- Galen, C. & Cuba, J. (2001). Down the tube: Pollinators, predators, and the evolution of flower shape in the alpine skypilot, *Polemonium viscosum*. *Evolution (N. Y.)*, 55, 1963–1971.
- Gallai, N., Salles, J.M., Settele, J. & Vaissière, B.E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.*, 68, 810–821.
- Garnett, M.C. (1981). Body Size, Its Heritability and Influence on Juvenile Survival Among Great Tits, *Parus Major*. *Ibis (Lond. 1859)*, 123, 31–41.
- Geerts, A.N., Vanoverbeke, J., Vanschoenwinkel, B., Van Doorslaer, W., Feuchtmayr, H., Atkinson, D., *et al.* (2015). Rapid evolution of thermal tolerance in the water flea *Daphnia*. *Nat. Clim. Chang.*, 5, 665–668.
- Geritz, S.A.H., Kisdi, É., Meszéna, G. & Metz, J.A.J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, 12, 35–57.
- Geritz, S.A.H., Metz, J.A.J., Kisdi, É. & Meszéna, G. (1997). Dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.*, 78, 2024–2027.
- Gianuca, A.T., Pantel, J.H. & De Meester, L. (2016). Disentangling the effect of body size and phylogenetic distances on zooplankton top-down control of algae. *Proc. R. Soc. B Biol. Sci.*
- Gilbert, S.F., Sapp, J. & Tauber, A.I. (2012). A symbiotic view of life: We have never been individuals. *Q. Rev. Biol.*, 87, 325–341.
- Gómez, J.M. (2005). Non-additive effects of herbivores and pollinators on *Erysimum mediohispanicum* (Cruciferae) fitness. *Oecologia*, 143, 412–418.
- Gomulkiewicz, R. & Holt, R.D. (1995). When does Evolution by Natural Selection Prevent Extinction? *Evolution (N. Y.)*, 49, 201–207.
- Grant, B.R. & Grant, P.R. (2003). What Darwin's Finches Can Teach Us about the Evolutionary Origin and Regulation of Biodiversity. *Bioscience*, 53, 965–975.
- Grant, P.R. & Grant, B.R. (1995). Predicting microevolutionary responses to directional selection on heritable variation. *Evolution (N. Y.)*, 49, 241–251.
- Grant, V. (1949). Pollination Systems as Isolating Mechanisms in Angiosperms. *Evolution (N. Y.)*, 3, 82–97.
- Grift, R.E., Rijnsdorp, A.D., Barot, S., Heino, M. & Dieckmann, U. (2003). Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Mar. Ecol. Prog. Ser.*, 257, 247–257.
- Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T. & Fox, J.A. (2005). Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.*, 8, 1114–1127.
- Harvey, J.A., Poelman, E.H. & Gols, R. (2010). Development and host utilization in *Hyposoter ebeninus* (Hymenoptera: Ichneumonidae), a solitary endoparasitoid of *Pieris rapae* and *P. brassicae* caterpillars (Lepidoptera: Pieridae). *Biol. Control*, 53, 312–318.
- Helfield, J.M. & Naiman, R.J. (2006). Keystone interactions: Salmon and bear in riparian forests of Alaska. *Ecosystems*, 9, 167–180.
- Hendry, A.P. (Andrew P.. (2017). *Eco-evolutionary dynamics*. Princeton University Press.
- Hendry, A.P., Farrugia, T.J. & Kinnison, M.T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Mol. Ecol.*, 17, 20–29.

- Hendry, A.P. & Kinnison, M.T. (1999). Perspective: The pace of modern life: Measuring rates of contemporary microevolution. *Evolution (N. Y.)*, 53, 1637–1653.
- Herrera, C.M. (2000). Measuring the Effects of Pollinators and Herbivores: Evidence for Non-Additivity in a Perennial Herb. *Ecology*, 81, 2170–2176.
- Herrera, C.M., Medrano, M., Rey, P.J., Sánchez-Lafuente, A.M., Garcia, M.B., Guitián, J., *et al.* (2002). Interaction of pollinators and herbivores on plant fitness suggests a pathway for correlated evolution of mutualism- and antagonism-related traits. *Proc. Natl. Acad. Sci.*, 99, 16823–16828.
- Holland, N.J. & Deangelis, D.L. (2009). Consumer-resource theory predicts dynamic transitions between outcomes of interspecific interactions. *Ecol. Lett.*, 12, 1357–1366.
- Holt, R.D. (1977). Predation, apparent competition, and the structure of prey communities. *Theor. Popul. Biol.*, 12, 197–229.
- Irwin, R.E., Strauss, S.Y., Storz, S., Emerson, A. & Guibert, G. (2003). The Role of Herbivores in the Maintenance of a Flower Color Polymorphism in Wild Radish. *Ecology*, 84, 1733–1743.
- Janzen, D. (1985). The natural history of mutualisms. In: *The Biology of Mutualism* (ed. Boucher, D.H.). pp. 40–49.
- Johnson, M.T.J. (2011). Evolutionary ecology of plant defences against herbivores. *Funct. Ecol.*, 25, 305–311.
- Johnson, N.C., Graham, J.H. & Smith, F.A. (1997). Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytol.*, 135, 575–585.
- Johnsson, J.I., Nöbbelin, F. & Bohlin, T. (1999). Territorial competition among wild brown trout fry: Effects of ownership and body size. *J. Fish Biol.*, 54, 469–472.
- Jones, C.G., Lawron, J.H. & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, 78, 1946–1957.
- Jordano, P., Bascompte, J. & Olesen, J.M. (2003). Invariant properties in coevolutionary networks of plant-animal interactions. *Ecol. Lett.*, 6, 69–81.
- Kéfi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., Brose, U., *et al.* (2015). Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology*, 96, 291–303.
- Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., *et al.* (2012). More than a meal... integrating non-feeding interactions into food webs. *Ecol. Lett.*, 15, 291–300.
- Kessler, A. & Baldwin, I.T. (2001). Defensive function of herbivore-induced plant volatile emissions in nature. *Science*, 291, 2141–2144.
- Kessler, A., Halitschke, R. & Poveda, K. (2011). Herbivory-mediated pollinator limitation: Negative impacts of induced volatiles on plant-pollinator interactions. *Ecology*, 92, 1769–1780.
- Kinnison, M.T. & Hairston, N.G. (2007). Eco-evolutionary conservation biology: Contemporary evolution and the dynamics of persistence. *Funct. Ecol.*, 21, 444–454.
- Kisdi, É. (2006). Trade-off geometries and the adaptive dynamics of two co-evolving species. *Evol. Ecol. Res.*, 8, 959–973.
- Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., *et al.* (2007). Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.*, 274, 303–313.
- Klumpers, S.G.T., Stang, M. & Klinkhamer, P.G.L. (2019). Foraging efficiency and size matching in a plant-pollinator community: the importance of sugar content and tongue length. *Ecol. Lett.*, 22, 469–479.

- Kochmer, J.P. & Handel, S.N. (1986). Constraints and Competition in the Evolution of Flowering Phenology. *Ecol. Monogr.*, 56, 303–325.
- Kuris, A.M. (2005). Trophic transmission of parasites and host behavior modification. *Behav. Processes*, 68, 215–217.
- Kuris, A.M., Hechinger, R.F., Shaw, J.C., Whitney, K.L., Aguirre-Macedo, L., Boch, C.A., *et al.* (2008). Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature*, 454, 515–518.
- Lafferty, K.D., Dobson, A.P. & Kuris, A.M. (2006). Parasites dominate food web links. *PNAS*, 103, 11211–11216.
- Lafferty, K.D. & Kimo Morris, A. (1996). Altered behavior of parasitized killifish increases susceptibility to predation by bird final hosts. *Ecology*, 77, 1390–1397.
- Lambers, H., Chapin, F.S. & Pons, T.L. (2008). Photosynthesis. In: *Plant Physiological Ecology*. Springer New York, New York, NY, pp. 11–99.
- Lambert, F.R. & Marshall, A.G. (1991). Keystone Characteristics of Bird-Dispersed Ficus in a Malaysian Lowland Rain Forest. *J. Ecol.*, 79, 793.
- Lande, R. (1982). A quantitative genetic theory of life history evolution. *Ecology*, 63, 607–615.
- Landi, P., Minoarivelo, H.O., Brännström, Å., Hui, C. & Dieckmann, U. (2018). Complexity and stability of ecological networks: a review of the theory. *Popul. Ecol.*, 60, 319–345.
- Layman, C.A., Winemiller, K.O., Arrington, D.A. & Jepsen, D.B. (2005). Body size and trophic position in a temperate estuarine food web. *Ecology*, 86, 2530–2535.
- Lemoine, N.P., Burkepile, D.E. & Parker, J.D. (2014). Variable effects of temperature on insect herbivory. *PeerJ*, 2014, e376.
- Levins, R. (1974). Discussion paper: the qualitative analysis of partially specified systems. *Ann. N. Y. Acad. Sci.*, 231, 123–138.
- Lindeman, R. (1942). The Trophic-Dynamic aspect of ecology. *Ecology*.
- Loeuille, N. (2019). Eco-evolutionary dynamics in a disturbed world: Implications for the maintenance of ecological networks [version 1; referees: 2 approved]. *F1000Research*, 8, 1–11.
- Loeuille, N., Barot, S., Georgelin, E., Kylafis, G. & Lavigne, C. (2013). Eco-evolutionary dynamics of agricultural networks: Implications for sustainable management. *Adv. Ecol. Res.*, 49, 339–435.
- Loeuille, N. & Loreau, M. (2005). Evolutionary emergence of size-structured food webs. *Proc. Natl. Acad. Sci.*, 102, 5761–5766.
- Lundin, O., Smith, H.G., Rundlöf, M. & Bommarco, R. (2013). When ecosystem services interact: Crop pollination benefits depend on the level of pest control. *Proc. R. Soc. B Biol. Sci.*, 280, 20122243.
- Lush, J.L. (1937). *Animal breeding plans. Anim. Breed. plans*. Iowa State College Press.
- MacArthur, R. & Levins, R. (1967). The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *Am. Nat.*, 101, 377–385.
- Maloof, J.E. & Inouye, D.W. (2000). Are nectar robbers cheaters or mutualists? *Ecology*, 81, 2651–2661.
- Manalil, S., Busi, R., Renton, M. & Powles, S.B. (2011). Rapid Evolution of Herbicide Resistance by Low Herbicide Dosages. *Weed Sci.*, 59, 210–217.
- May. (1972). Will a large complex system be stable? *Nature*, 239, 137–138.

- Maynard Smith, J. & Price, G.R. (1973). The logic of animal conflict. *Nature*, 246, 15–18.
- McCall, A.C., Murphy, S.J., Venner, C. & Brown, M. (2013). Florivores prefer white versus pink petal color morphs in wild radish, *Raphanus sativus*. *Oecologia*, 172, 189–195.
- McCann, K., Hastings, A. & Huxel, G.R. (1998). Weak trophic interactions and the balance of nature. *Nature*, 395, 794–798.
- Memmott, J., Martinez, N.D. & Cohen, J.E. (2000). Predators, parasitoids and pathogens: Species richness, trophic generality and body sizes in a natural food web. *J. Anim. Ecol.*, 69, 1–15.
- Memmott, J., Waser, N.M. & Price, M. V. (2004). Tolerance of pollination networks to species extinctions. *Proc. R. Soc. B Biol. Sci.*, 271, 2605–2611.
- Menge, B.A. (1995). Indirect effects in marine rocky intertidal interaction webs: Patterns and importance. *Ecol. Monogr.*, 65, 21–74.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., *et al.* (2006). European phenological response to climate change matches the warming pattern. *Glob. Chang. Biol.*, 12, 1969–1976.
- Metz, J.A.J., Nisbet, R.M. & Geritz, S.A.H. (1992). How should we define “fitness” for general ecological scenarios? *Trends Ecol. Evol.*, 7, 198–202.
- Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D. & Alon, U. (2002). Network motifs: Simple building blocks of complex networks. *Science*, 298, 824–827.
- Møller, A.P. (2001). Heritability of arrival date in a migratory bird. *Proc. R. Soc. B Biol. Sci.*, 268, 203–206.
- Moore, J. (1995). The Behavior of Parasitized Animals. *Bioscience*, 45, 89–96.
- Mougi, A. & Kondoh, M. (2012). Diversity of interaction types and ecological community stability. *Science*, 337, 349–351.
- Mousseau, T.A. & Roff, D.A. (1987). Natural selection and the heritability of fitness components. *Heredity (Edinb.)*, 59, 181–197.
- Muniz, D.G., Freitas, A.V.L. & Oliveira, P.S. (2012). Phenological relationships of *Eunica bechina* (Lepidoptera: Nymphalidae) and its host plant, *Caryocar brasiliense* (Caryocaraceae), in a Neotropical savanna. *Stud. Neotrop. Fauna Environ.*, 47, 111–118.
- Naisbit, R.E., Kehrl, P., Rohr, R.P. & Bersier, L.F. (2011). Phylogenetic signal in predator-prey body-size relationships. *Ecology*, 92, 2183–2189.
- Nason, J.D., Herre, E.A. & Hamrick, J.L. (1998). The breeding structure of a tropical keystone plant resource. *Nature*, 391, 685–687.
- Neutel, A.M., Heesterbeek, J.A.P., Van De Koppel, J., Hoenderboom, G., Vos, A., Kaldewey, C., *et al.* (2007). Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449, 599–602.
- Noordwijk, A.J.V., Balen, J.H.V. & Scharloo, W. (1988). Heritability of body size in a natural population of the Great Tit (*Parus major*) and its relation to age and environmental conditions during growth. *Genet. Res.*, 51, 149–162.
- Odum, T.H. (1983). *Systems ecology; An introduction*. John Wiley and Sons, New York, NY.
- Oerke, E.C. (2006). Crop losses to pests. *J. Agric. Sci.*, 144, 31–43.
- Ollerton, J. (2017). Pollinator Diversity: Distribution, Ecological Function, and Conservation. *Annu. Rev. Ecol. Evol. Syst.*, 48, 353–76.
- Ollerton, J., Winfree, R. & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120,

321–326.

- Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B., *et al.* (2004). Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, 428, 932–935.
- Oziolor, E.M., Reid, N.M., Yair, S., Lee, K.M., VerPloeg, S.G., Bruns, P.C., *et al.* (2019). Adaptive introgression enables evolutionary rescue from extreme environmental pollution. *Science*, 364, 455–457.
- Palumbi, S.R. (2001). Humans as the world’s greatest evolutionary force. *Science*, 293, 15–24.
- Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annu. Ecol. Evol. Syst.*, 37, 637–669.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- Pateman, R.M., Hill, J.K., Roy, D.B., Fox, R. & Thomas, C.D. (2012). Temperature-Dependent Alterations in Host Use Drive Rapid Range Expansion in a Butterfly. *Science*, 336, 1028–1030.
- Pellmyr, O. (2003). Yuccas, Yucca Moths, and Coevolution: A Review. *Source Ann. Missouri Bot. Gard.*, 90, 35–55.
- Phillips, B.L., Brown, G.P. & Shine, R. (2010). Life-history evolution in range-shifting populations. *Ecology*, 91, 1617–1627.
- Phillips, B.L., Brown, G.P., Webb, J.K. & Shine, R. (2006). Invasion and the evolution of speed in toads. *Nature*, 439, 803.
- Pohl, N., Carvallo, G., Botto-Mahan, C. & Medel, R. (2006). Nonadditive effects of flower damage and hummingbird pollination on the fecundity of *Mimulus luteus*. *Oecologia*, 149, 648–655.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends Ecol. Evol.*, 25, 345–353.
- Pulido, F., Berthold, P., Mohr, G. & Querner, U. (2001). Heritability of the timing of autumn migration in a natural bird population. *Proc. R. Soc. B Biol. Sci.*, 268, 953–959.
- Ramirez, W.B. (1974). Coevolution of *Ficus* and *Agaonidae*. *Ann. Missouri Bot. Gard.*, 61, 770.
- Ramos, D.M., Diniz, P. & Valls, J.F.M. (2014). Habitat filtering and interspecific competition influence phenological diversity in an assemblage of Neotropical savanna grasses. *Brazilian J. Bot.*, 37, 29–36.
- Ramos, S.E. & Schiestl, F.P. (2019). Rapid plant evolution driven by the interaction of pollination and herbivory. *Science*, 364, 193–196.
- Redfern, A., Suchodolski, J. & Jergens, A. (2017). Role of the gastrointestinal microbiota in small animal health and disease. *Vet. Rec.*, 181, 370–370.
- Regan, E.C., Santini, L., Ingwall-King, L., Hoffmann, M., Rondinini, C., Symes, A., *et al.* (2015). Global Trends in the Status of Bird and Mammal Pollinators. *Conserv. Lett.*, 8, 397–403.
- Renner, S.S. & Zohner, C.M. (2018). Climate Change and Phenological Mismatch in Trophic Interactions Among Plants, Insects, and Vertebrates. *Annu. Rev. Ecol. Evol. Syst.*, 49, 165–182.
- Reznick, D.N., Losos, J. & Travis, J. (2019). From low to high gear: there has been a paradigm shift in our understanding of evolution. *Ecol. Lett.*
- Ripple, W.J. & Beschta, R.L. (2012). Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biol. Conserv.*, 145, 205–213.

- Rosenzweig, M.L. (1971). Paradox of Enrichment - Destabilization of Exploitation Ecosystems in Ecological Time. *Science*, 171, 385-.
- De Ruiter, P.C., Neutel, A.M. & Moore, J.C. (1995). Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science*, 269, 1257–1260.
- Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.*, 232, 8–27.
- Scharf, F.S., Juanes, F. & Rountree, R.A. (2000). Predator size - Prey size relationships of marine fish predators: Interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar. Ecol. Prog. Ser.*, 208, 229–248.
- Schluter, D. & Grant, P.R. (1984). Determinants of morphological patterns in communities of Darwin's finches. *Am. Nat.*, 123, 175–196.
- Schneider, J.R., Chadee, D.D., Mori, A., Romero-Severson, J. & Severson, D.W. (2011). Heritability and adaptive phenotypic plasticity of adult body size in the mosquito *Aedes aegypti* with implications for dengue vector competence. *Infect. Genet. Evol.*, 11, 11–16.
- Shanahan, M., Samson, S.O., Compton, S.G. & Corlett, R. (2001). Fig-eating by vertebrate frugivores: A global review. *Biol. Rev. Camb. Philos. Soc.*, 76, 529–572.
- Silventoinen, K., Magnusson, P.K.E., Tynelius, P., Kaprio, J. & Rasmussen, F. (2008). Heritability of body size and muscle strength in young adulthood: A study of one million Swedish men. *Genet. Epidemiol.*, 32, 341–349.
- Slobodkin, L.B. (1961). *Growth and Regulation of Animal Populations*. New York.
- Stanton, M.L. (1987). Reproductive biology of petal color variants in wild populations of *Raphanus sativus*. I. Pollinator response to colour morphs. *Am. J. Bot.*, 74, 178–187.
- Stirling, D.G., Réale, D. & Roff, D.A. (2002). Selection, structure and the heritability of behaviour. *J. Evol. Biol.*, 15, 277–289.
- Stockwell, C.A., Hendry, A.P. & Kinnison, M.T. (2003). Contemporary evolution meets conservation biology. *Trends Ecol. Evol.*, 18, 94–101.
- Strauss, S.Y., Rudgers, J.A., Lau, J.A. & Irwin, R.E. (2002). Direct and ecological costs of resistance to herbivory. *Trends Ecol. Evol.*, 17, 278–285.
- Strauss, S.Y., Siemens, D.H., Decher, M.B. & Mitchell-Olds, T. (1999). Ecological Costs of Plant Resistance To Herbivores in the Currency of Pollination. *Evolution (N. Y.)*, 53, 1105–1113.
- Strauss, S.Y. & Whittall, J.B. (2006). Non-pollinator agents of selection on floral traits. In: *Ecology and evolution of flowers* (eds. Harder, L.D. & Barrett, S.C.H.). Oxford University Press on Demand, New York, NY, USA, pp. 120–138.
- Sutter, L. & Albrecht, M. (2016). Synergistic interactions of ecosystem services: Florivorous pest control boosts crop yield increase through insect pollination. *Proc. R. Soc. B Biol. Sci.*, 283, 20152529.
- Thébaud, E. & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, 329, 853–856.
- Theis, N., Barber, N.A., Gillespie, S.D., Hazzard, R. V. & Adler, L.S. (2014). Attracting mutualists and antagonists: Plant trait variation explains the distribution of specialist floral herbivores and pollinators on crops and wild gourds. *Am. J. Bot.*, 101, 1314–1322.
- Thompson, J.N. (1998). Rapid evolution as an ecological process. *Trends Ecol. Evol.*, 13, 329–332.

- Thompson, J.N. (1999). Specific hypotheses on the geographic mosaic of coevolution. *Am. Nat.*, 153, 1–14.
- Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press.
- Toby Kiers, E., Palmer, T.M., Ives, A.R., Bruno, J.F. & Bronstein, J.L. (2010). Mutualisms in a changing world: An evolutionary perspective. *Ecol. Lett.*, 13, 1459–1474.
- Trappe, J.M. (1977). Selection of Fungi for Ectomycorrhizal Inoculation in Nurseries. *Annu. Rev. Phytopathol.*, 15, 203–222.
- Van Valen, L. (1973). A new evolutionary law. *Evol. Theor.*, 1, 1–30.
- Vandermeer, J.H. & Boucher, D.H. (1978). Varieties of mutualistic interaction in population models. *J. Theor. Biol.*, 74, 549–558.
- Visser, M.E. & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nat. Ecol. Evol.*
- Vucic-Pestic, O., Rall, B.C., Kalinkat, G. & Brose, U. (2010). Allometric functional response model: Body masses constrain interaction strengths. *J. Anim. Ecol.*, 79, 249–256.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., Van Der Putten, W.H. & Wall, D.H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, 304, 1629–1633.
- Warren, P.H. & Lawton, J.H. (1987). Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? *Oecologia*, 74, 231–235.
- Werner, E.E. & Peacor, S.D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083–1100.
- Wong, A.C.N., Wang, Q.P., Morimoto, J., Senior, A.M., Lihoreau, M., Neely, G.G., *et al.* (2017). Gut Microbiota Modifies Olfactory-Guided Microbial Preferences and Foraging Decisions in *Drosophila*. *Curr. Biol.*, 27, 2397–2404.
- Woodin, S.A. (1981). Disturbance and Community Structure in a Shallow Water Sand Flat. *Ecology*, 62, 1052–1066.
- Woodward, F.I., Lomas, M.R. & Kelly, C.K. (2004). Global climate and the distribution of plant biomes. *Philos. Trans. R. Soc. B Biol. Sci.*, 359, 1465–1476.
- Wootton, J.T. (2002). Indirect effects in complex ecosystems: Recent progress and future challenges. *J. Sea Res.*, 48, 157–172.
- Yacine, Y., Allhoff, K.T., Weinbach, A. & Loeuille, N. (2021). Collapse and rescue of evolutionary food webs under global warming. *J. Anim. Ecol.*, 90, 710–722.
- Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F. & Hairston, N.G. (2003). Rapid evolution drives ecological dynamics in a predator–prey system. *Nature*, 424, 303–306.
- Yu, D.W. & Pierce, N.E. (1998). A castration parasite of an ant-plant mutualism. *Proc. R. Soc. B Biol. Sci.*, 265, 375–382.
- Zhang, W., Ricketts, T.H., Kremen, C., Carney, K. & Swinton, S.M. (2007). Ecosystem services and dis-services to agriculture. *Ecol. Econ.*, 64, 253–260.

II.

Chaper I

Stable coexistence in plant-pollinator-herbivore communities requires balanced mutualistic vs antagonistic interactions

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Stable coexistence in plant-pollinator-herbivore communities requires balanced mutualistic vs antagonistic interactions

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Running headline

Stable coexistence: pollination vs. herbivory

Statement of authorship

N.L. and Y.Y. conceived the ideas. The analytical work was done by Y.Y. Results were analyzed by both N.L. and Y.Y. Y.Y. wrote the first draft of the manuscript that has been subsequently reviewed and edited by N.L. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility statement

No data were used in the present work.

The manuscript is submitted as a Research Paper and contains an abstract of 149 words, the main text of 5081 words, 69 references, 4 figures, and 2 tables.

Abstract

Ecological communities consist of multiple species interacting in diverse ways. Understanding the mechanisms supporting coexistence requires accounting for such diversity. Because most works focus either on mutualism or predation, how pollination and herbivory interactively determine the stable coexistence in plant-pollinator-herbivore communities is still poorly understood. Studying the typical three-species module of such communities, we determine the conditions allowing stable coexistence then investigate how its maintenance constrains the relative interaction strengths. Our results show that coexistence is possible if pollination is sufficiently strong relative to herbivory, while its stability is possible if herbivory is sufficiently strong relative to pollination. A balance between pollination and herbivory is therefore required. Interestingly, shared preferences for plant phenotypes, that would favor such balance, have been frequently reported in the empirical literature. The identified ecological trade-off between attracting pollinators and deterring herbivores therefore also appears as an emergent property of stable plant-pollinator-herbivore communities.

Keywords

Community ecology, Herbivory, Lotka-Volterra, Network motif, Plant-Animal interactions, Pollination

1. Introduction

Multiple species interacting closely together form an ecological community. A topic of long-standing interest in community ecology is to understand what mechanisms drive the coexistence of species and its maintenance over time. It is now well established that the way ecological interactions connect species - the type of interactions, the network topology as well as the distribution of interaction strengths - plays a decisive role. Combining modeling approaches with empirical data, several works indicate for instance that weak trophic interactions are crucial to maintain the stability of complex food webs (McCann et al., 1998; Neutel et al., 2002). Deriving general laws is, however, difficult. The network properties and topologies favoring the maintenance of coexistence indeed vary with the type of interaction characterizing the community, mutualism or antagonism in particular (Thébault and Fontaine, 2010). The ecological processes and structural patterns supporting the maintenance of coexistence within single-interaction-type communities can, moreover, considerably differ from the ones at play within communities with several interaction kinds (e.g. Mougi and Kondoh, 2012; Sauve et al., 2014). Studies of such communities should therefore significantly improve our understanding of ecological communities, especially given that most species get simultaneously involved in a diversity of interaction networks (Fontaine et al., 2011; Kéfi et al., 2012). Most terrestrial plant species ($\approx 90\%$ of flowering plants, Ollerton et al., 2011), for instance, are involved in a mutualistic interaction with their animal pollinators, while suffering from herbivorous predation (antagonism). Plant-pollinator-herbivore communities are, in addition, of particular interest due to their critical role in agricultural production (Klein et al., 2007; Oerke, 2006), as well as the serious threats global change poses to them (Atwood et al., 2020; Potts et al., 2010). The study of stable coexistence within these communities is thus of high applied relevance while offering the opportunity to gain new conceptual insights into the functioning of mutualistic-antagonistic communities.

Understanding stable coexistence within plant-pollinator-herbivore communities requires explicitly accounting for both the mutualistic (i.e. plant-pollinator) and the antagonistic (i.e. plant-herbivore) interaction. A large body of empirical evidence indeed documents non-additive effects of pollination and herbivory on plant densities, in both uncultivated (Gómez, 2005; Herrera, 2000; Herrera et al., 2002; Pohl et al., 2006) and cultivated (Lundin et al., 2013; Strauss and Murch, 2004; Sutter and Albrecht, 2016) plant species. The strength of the mutualistic interaction is affected by the antagonistic interaction and vice versa, explaining such

an interactive effect. Herbivores may, for instance, preferentially consume plant species bearing abundant flowers or developing fruits as a result of strong pollination (Herrera, 2000; Herrera et al., 2002). By decreasing floral display, herbivore damages can reduce pollination (Adler et al., 2001; Cardel and Koptur, 2010; Pohl et al., 2006). In addition to floral display, herbivory-induced changes in plant chemistry can also deter pollinators (Kessler et al., 2011).

Indirect interactions between two species within a community can also be mediated by their effect on the density of a third species (Wootton, 2002). Ubiquitous in natural communities, such indirect effects play a key part in the maintenance of coexistence (Burns et al., 2014; Menge, 1995). By isolating the structural building blocks of complex ecological networks - modules or motifs - it becomes easier to unravel such indirect effects and their implications for community maintenance (Milo et al., 2002). Modules are therefore small sets of interacting species characteristic of the studied community, whose study enables deeper insights into the mechanisms at play at the broader scale (Milo et al., 2002; Stouffer and Bascompte, 2010).

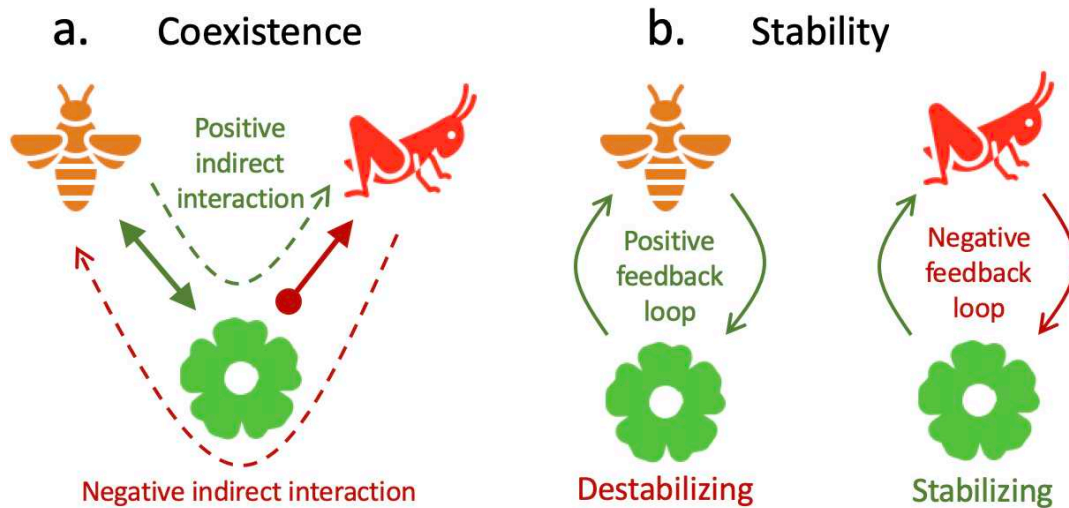
In plant-pollinator-herbivore communities, the typical module consists of two animal species - a pollinator and a herbivore - sharing a common resource plant species (Fig. 1A.a). The resulting indirect interaction between pollinators and herbivores is an antagonism (Fig. 1A.a, Holland *et al.* 2013). Pollinators allow the community to sustain a higher herbivore density by increasing plant productivity while herbivores, on the other hand, decrease pollinator density by reducing resource availability. Theoretical works indicate that the presence of pollinators can even make the herbivore population viable (Georgelin and Loeuille, 2014; Mougi and Kondoh, 2014a). As illustrated by Georgelin & Loeuille (2014), direct vs. indirect ecological effects can be of similar magnitude. Their study indeed reports a constant herbivore density despite increasing herbivore mortality. In their model, over a wide range of herbivore mortalities, the direct mortality-induced losses on herbivores are totally offset by the indirect gain resulting from a higher pollinator density consecutive to the herbivorous predation release on plants. Further increasing mortality, however, leads to the abrupt collapse of the herbivore population, which illustrates that combining different interactions also has important implications in terms of community stability (Mougi and Kondoh, 2014b).

Mutualisms, such as pollination, intrinsically entail positive feedback loops (Fig. 1A.b). Positive feedbacks are destabilizing (Levins, 1974; Neutel and Thorne, 2014) as they tend to amplify the direct effect of a perturbation. As a result, unstable behaviors have been identified in theoretical models of mutualism, including tipping points (Lever et al., 2014) or unbounded

population growths driven by an “orgy of mutual benefaction” (May, 1981). The latter is, however, seldom observed in nature. One possible explanation is that antagonistic interactions, such as predation, could prevent this behavior in real systems. Negative feedback loops born from antagonistic interactions (Neutel and Thorne, 2014) could restore stability by counterbalancing the positive loops arising from mutualisms (Fig. 1A.b). This hypothesis implies that the relative magnitude of pollination vs. herbivory plays a critical role, which is in line with the findings of several theoretical investigations on mutualistic-antagonistic modules (Georgelin and Loeuille, 2014; Holland et al., 2013; Mougi and Kondoh, 2014b; Sauve et al., 2016a).

The goal of the present paper is to understand how stable coexistence within plant-pollinator-herbivore communities constrains the relative strengths of pollination and herbivory, i.e. the relative per capita effects of each interacting animal species on plant population growth. In contrast with most previous theoretical works on mutualistic-antagonistic modules, the relationships governing stable coexistence we obtain are analytical. Such relationships between pollination and herbivory are derived from the population dynamics of the characteristic three-species module (Fig. 1A.a), in which both animal intake rates (i.e. functional responses) are assumed linear to achieve analytical tractability. We discuss such an assumption at the end of the present work (section 4). Finally, the per-capita effect of plant-animal interactions on community dynamics is mediated by animal densities, which in turn depend on other ecological parameters such as animal mortalities or intraspecific competition rates. We therefore extend our analysis by studying their influence, which confirms the robustness of our results. In what follows, we show that stable coexistence within plant-pollinator-herbivore communities requires a balance between the strengths of pollination and herbivory. Such a pattern ensues from the opposite effect each interaction has on coexistence and stability (Fig. 1A). Coexistence is favored by pollination and disfavored by herbivory, as a result of both direct and indirect ecological interactions (Fig. 1A.a). Stability is enhanced by herbivory and reduced by pollination, as a result of the respective feedback loops (Fig. 1A.b). It is interesting to note that a large body of empirical literature (e.g. Irwin *et al.* 2003) reports shared preferences for plant phenotypes between pollinators and herbivores that would favor balanced interactions, which appear here as an emergent property of stable plant-pollinator-herbivore communities.

A Predicted effects of interactions on



B First analytical results are in line with predictions

	Effect of pollination strength	Effect of herbivory strength
On plants	$\nearrow i.e. \frac{\partial P^*}{\partial a_{pm}} > 0$	$\searrow i.e. \frac{\partial P^*}{\partial a_{ph}} < 0$
On pollinators	$\nearrow i.e. \frac{\partial M^*}{\partial a_{pm}} > 0$	$\searrow i.e. \frac{\partial M^*}{\partial a_{ph}} < 0$ (indirect)
On herbivores	$\nearrow i.e. \frac{\partial H^*}{\partial a_{pm}} > 0$ (indirect)	Parameter-dependent if $e_m a_{pm}^2 > c_m c_p$: $\searrow i.e. \frac{\partial H^*}{\partial a_{ph}} < 0$

Figure 1: A. Predicted effects of interactions on stable coexistence. a. Predicted effects on densities. Solid (resp. dashed) arrows for direct (resp. indirect) interactions. b. Predicted effects on stability. **B. Variation of biomass densities at stable coexistence with the strength of interactions.** These first analytical results are in line with predictions (see A.a). Analytical proofs in appendix B.IV.

2. Model presentation

2.1 Ecological dynamics

We formulate the dynamics of the biomass densities of three interacting species - a plant P , a pollinator M , and a herbivore H - using ordinary differential equations:

$$\frac{dP}{dt} = P(r_p - c_p P + a_{pm} M - a_{ph} H) \quad (\text{a})$$

$$\frac{dM}{dt} = M(r_m - c_m M + e_m a_{pm} P) \quad (\text{b})$$

$$\frac{dH}{dt} = H(r_h - c_h H + e_h a_{ph} P) \quad (\text{c})$$

Plants have a positive intrinsic growth rate ($r_p > 0$, autotrophs), while both pollinators ($r_m < 0$) and herbivores ($r_h < 0$) have a negative one (heterotrophs). As in previous models (e.g. Sauve *et al.* 2014), we thus assume the plant-animal interaction to be obligate for animals and facultative for the plant. Intraspecific competition is accounted for. The animal competition rates (c_m, c_h) correspond to interference while, for the plant species (c_p), this rate essentially captures the competition for resources such as light, water, and nutrients (Craine and Dybzinski, 2013). Interspecific interactions, whose strength is a_{pm} for pollination and a_{ph} for herbivory, affect population growths proportionally to biomass densities. The use of a linear functional response for mutualism exposes the model to unbounded population growths (May, 1981). It, however, enables testing whether this behavior could be top-down controlled by herbivory, placing our work in the line of research tackling how the community context could explain the stability of mutualisms in nature (e.g. Ringel *et al.* 1996). Finally, e_m and e_h are the conversion efficiencies from plants to animals. Parameter details are given in table 1.

Table 1: List of all model parameters and variables with their biological significance, value, and dimension (M for mass, L for length, and t for time).

Variables and parameters		Biological meaning	Value	Dimension
<i>Variables</i>	P	Plant biomass density		$M \cdot L^{-2}$
	M	Pollinator biomass density		$M \cdot L^{-2}$

	H	Herbivore biomass density		$M \cdot L^{-2}$
<i>Interaction strength</i>	a_{pm}	Strength of pollination (i.e. per capita effect of pollinators on plant population growth)	[0,3]	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	a_{ph}	Strength of herbivory (i.e. per capita effect of herbivores on plant population growth)	[0,3]	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
<i>Other ecological parameters</i>	r_p	Plant intrinsic growth rate	10	t^{-1}
	r_m	Pollinator intrinsic growth rate	[-5, -1]	t^{-1}
	r_h	Herbivore intrinsic growth rate	[-5, -1]	t^{-1}
	c_p	Plant intra-specific competition rate	0.6	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	c_m	Pollinator intra-specific competition rate	[0.2,0.6]	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	c_h	Herbivore intra-specific competition rate	[0.2,0.6]	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	e_m	Plant to pollinator conversion efficiency	[0.1,0.3]	Dimensionless
	e_h	Plant to herbivore conversion efficiency	[0.1,0.3]	Dimensionless

2.2 Ecological equilibria

When the three population growth rates vanish (equations (a b c) are null), we reach an ecological equilibrium (P^*, M^*, H^*). At equilibrium, each population can either be present or absent which leads to 8 potential equilibria (expressions in Appendix B.III). The present work focuses on the equilibrium in which the three species are present, hereafter “the coexistence equilibrium”. We study under which conditions of interaction strengths - (a_{pm}, a_{ph}) - this equilibrium corresponds to positive biomass densities (i.e. is feasible) and stable (i.e. is resilient to small perturbations). See Appendix B.I for detailed definitions.

2.3 Two-population subcommunities

The plant-pollinator-herbivore community is constituted of two subcommunities – plant-pollinator and plant-herbivore – sharing the same plant species. Such subcommunities

have extensively been studied in the literature (e.g. Goh 1976; Vandermeer & Boucher 1978). We briefly report here their dynamics (see Appendix B.II for details).

The plant-herbivore subcommunity is characterized by one feasible and globally stable equilibrium. Either the plant population at carrying capacity ($K_p \stackrel{\text{def}}{=} r_p/c_p$) can support the herbivore population and both coexist, or the herbivores go extinct while plants persist.

Two distinct regimes are possible for the plant-pollinator subcommunity, depending on the comparison between pollination strength and self-limiting competitions (Appendix B.II.2). (1) If the pollination positive feedback loop (destabilizing, Fig. 1A.b) is smaller than that from competition, there is one feasible and globally stable equilibrium. This equilibrium corresponds to plant-pollinator coexistence when the carrying capacity of plants is large enough to support the pollinator population. Otherwise, plants persist while pollinators go extinct. (2) If the pollination positive feedback loop is stronger than that from competition, unbounded population densities are possible. In this case, when the carrying capacity of plants is sufficient to make pollinators viable, populations unboundedly grow irrespective of initial densities. Otherwise, unbounded growth is observed if initial densities are large enough while only plants persist if it is not the case.

3. Results

At the coexistence equilibrium when feasible and stable, all biomass densities increase with the strength of pollination (Fig. 1B). On the contrary, both plant and pollinator densities decrease as herbivory gets stronger, while herbivore density can either increase or decrease (Fig. 1B). Matching our predictions (Fig. 1A.a), these dynamics are illustrated in Fig. 2, which shows how densities depend on herbivory for three pollination levels (Fig. 2a-b-c), and on pollination for three herbivory levels (Fig. 2d-e-f). Fig. 2 especially demonstrates that population dynamics are determined by both pollination and herbivory interactively. For instance, the decline of herbivore density with the strength of herbivory is observed when pollination is strong (Fig. 1B & 2c), which we interpret as a consequence of the strong indirect antagonism with pollinators (Fig. 1A.a). Another example is that the strength of one interaction affects the level the other interaction has to reach in order for the focal animal to persist in the community. As pollination increases, the minimal level of herbivory allowing herbivores to persist gets lower (Fig. 2a vs 2b). Pollination favors the feasibility of coexistence. On the

contrary, herbivory disfavors the feasibility of coexistence. As herbivory gets stronger, the minimal level of pollination allowing pollinators to persist gets higher (Fig. 2d&e vs 2f).

In line with our predictions (Fig. 1A.b), stability displays opposite patterns: it is favored by herbivory and disfavored by pollination. For a given level of herbivory, populations display unstable dynamics for high pollination strengths (Fig. 2 d-e-f, blue background). This instability captures the unbounded growth of biomass densities driven by the mutualism. As herbivory gets stronger, higher pollination levels are needed for unbounded growth to happen (Fig. 2d vs 2e vs 2f). Herbivory can indeed restore stability (Fig. 2c): starting from an initially unbounded situation, increasing herbivory restores finite densities.

The strength of pollination contributes positively to the feasibility of coexistence and negatively to its stability. It is the opposite for herbivory. Although presented for a given parameter set (Fig. 2), these two main results are general as they derive from the analytical relationships governing stable coexistence (table 2). They imply that stable coexistence requires a balance between the strengths of pollination and herbivory to achieve both feasibility and stability. Such a balance can be observed in Fig. 2: as one interaction gets stronger, the range of the other interaction intensities allowing stable coexistence shifts toward larger values (orange background, Fig. 2b vs 2c, Fig. 2e vs 2f).

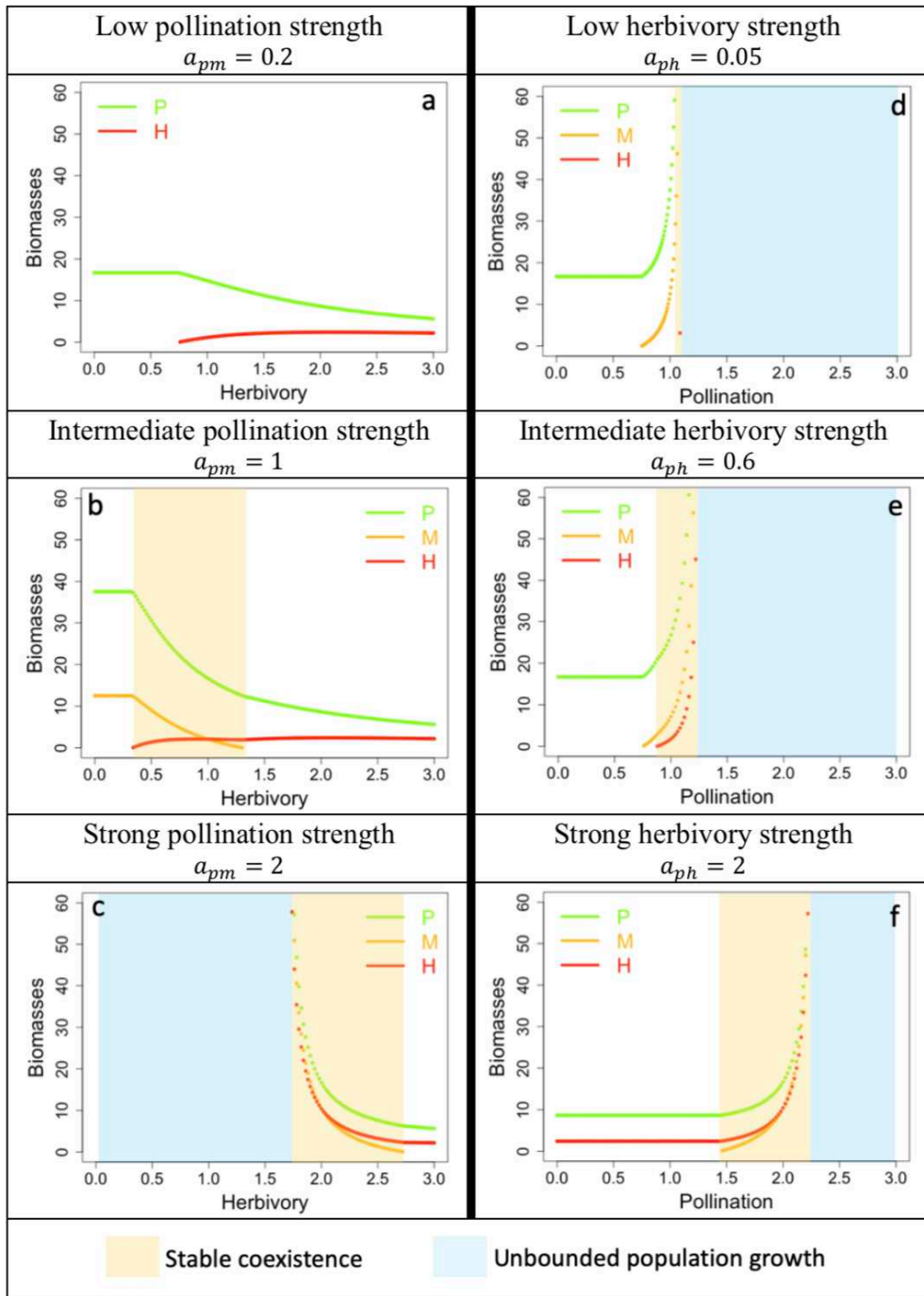


Figure 2: Biomass densities at equilibrium depend interactively on pollination and herbivory strengths. The curves are determined analytically (see appendix B.III). **a-b-c** Dependence of densities on herbivory for three pollination levels. In **a**, pollination intensity is too low for pollinators to persist. **d-e-f** Dependence of densities on pollination for three herbivory levels. Parameter set: $r_p = 10, r_m = r_h = -2.5, c_p = 0.6, c_m = c_h = 0.4, e_m = e_h = 0.2$.

3.1 Relationships governing stable coexistence

Positive animal densities necessarily imply a positive plant density because animals are obligate plant-interactors (Appendix C.I.1). In other words, the coexistence equilibrium is feasible if, and only if, both animal species have positive densities, which leads to two inequalities. It is stable if, and only if, all three eigenvalues of the Jacobian matrix (Appendix B.III.1) calculated at the coexistence equilibrium have a negative real part, which is equivalent to the three Routh-Hurwitz inequalities (Appendix B.III.3). One of these inequalities is satisfied if feasibility is assumed. Therefore, there are four relationships (i.e. inequalities) that are necessary and sufficient for the stable coexistence of plants, pollinators, and herbivores (Appendix C.II). These relationships, as well as their biological interpretations, are presented in Table 2. We illustrate the biological implications underlying them using Fig. 3, which indicates the community composition depending on the strengths of pollination and herbivory.

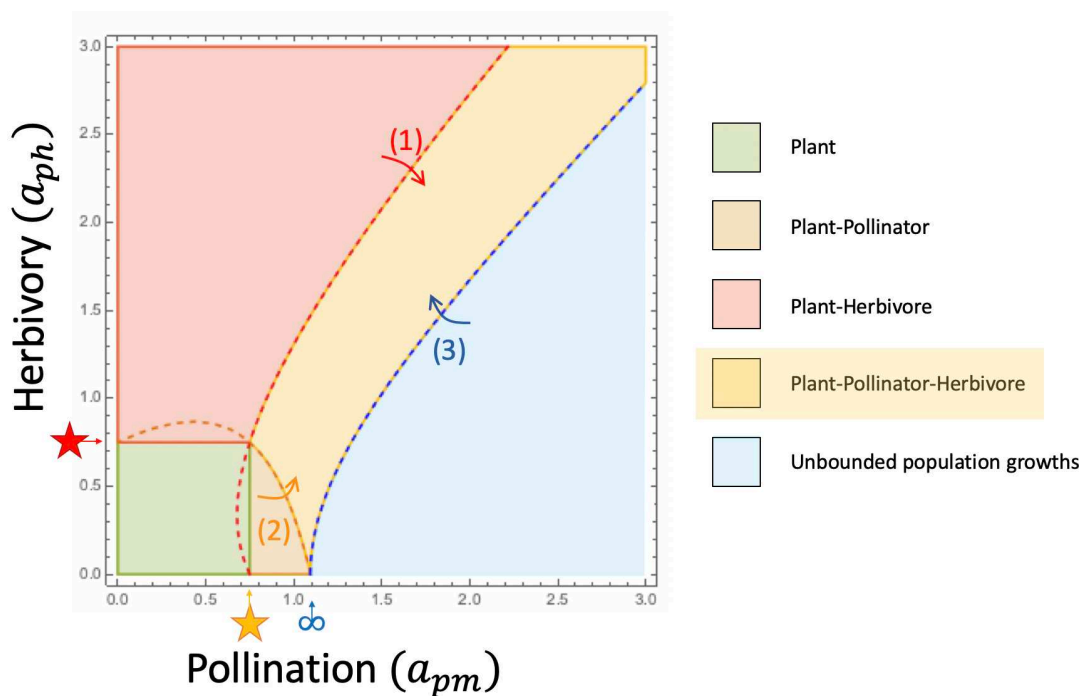


Fig. 3: Stable coexistence requires balanced pollination vs. herbivory strengths. Given the strength of pollination (a_{pm}) and herbivory (a_{ph}), the stable equilibria are determined and the point of the graph is colored accordingly. In blue, no equilibrium is stable so densities grow unboundedly. Arrows (1), (2), and (3) indicate the transitions enabling the satisfaction of relationships (1), (2), and (3) (Table 2), indicated by the dashed red, orange, and blue curve, respectively. These three relationships are sufficient to achieve stable coexistence given the parameter set (as in Fig. 2), indicating that relationship (4) is

less constraining here. The orange (resp. red) star indicates the level of pollination (resp. herbivory) that makes pollinators (resp. herbivores) viable when only plants are present (hence at carrying capacity). Unbounded growth is possible in the plant-pollinator subcommunity when the strength of pollination is higher than the level figured by an infinity symbol. Note that stable coexistence (yellow area) requires the two interactions to be of similar magnitude.

Assuming stability (relationship (3) actually), coexistence is feasible if and only if relationships (1) and (2) are satisfied.

Relationship (1) indicates that the per capita growth rate of pollinators, when low in density and within a plant-herbivore community at ecological equilibrium, is positive (Appendix C.II.1). Pollinators are thus able to invade the plant-herbivore community so that this relationship governs the transition (red dotted curve, arrow (1)) between the plant-herbivore equilibrium (red) and the coexistence equilibrium (yellow) in Fig. 3. Besides, the plant density within the plant-herbivore community (P_{PH}^*) decreases when herbivory (a_{ph}) intensifies (Appendix C.II.1). In such a situation, pollination (a_{pm}) has to get stronger as well in order for pollinators to invade the plant-herbivore community (relationship (1')).

$$\underbrace{\frac{-r_m}{e_m P_{PH}^*}}_{\substack{\text{increasing} \\ \text{with } a_{ph}}} \leq a_{pm} \quad (1')$$

The interpretation of the second relationship depends on whether unbounded population growth is possible or not within the plant-pollinator community, i.e. on the competition loop ($c_p c_m$) being weaker or stronger than the pollination feedback loop ($e_m a_{pm}^2$).

If unbounded growth is not possible, the relationship indicates that the per capita growth rate of herbivores, when low in density and within a plant-pollinator community at ecological equilibrium, is positive. In this case, the relationship governs the transition (orange dotted curve, arrow (2)) between the plant-pollinator equilibrium (orange) and the coexistence equilibrium (yellow) in Fig. 3. We mathematically demonstrate that in such a case, the feasibility of coexistence implies its global stability (Appendix B.IV). Relationships (1) and (2) are thus necessary and sufficient for stable coexistence (Fig. 3, left side of ∞). Furthermore, stronger pollination (a_{pm}) makes herbivores viable at lower predation intensities (a_{ph}) (relationship (2'a)) due to a higher plant density within the plant-pollinator community (P_{PM}^*) (Appendix C.II.2).

If unbounded growth is possible, the relationship sets an upper limit to the strength of herbivory (relationship (2'b)), which we interpret as a condition for herbivores to not exclude

pollinators by reducing plant biomass too strongly. In fact, relationship (2'b) (feasibility of H^*) is critical for a parameter configuration over which the persistence of herbivores is due to the presence of pollinators (Appendix C.II.2, Fig. S3). In such parameter instances, P_{PM}^* loses its biological meaning (as the plant-pollinator equilibrium is unstable) and decreases with pollination (a_{pm}), and alternative stable states are possible (Fig. S3). Note that no transition corresponds to relationship (2'b) in Fig. 3 as relationship (2) is only constraining at the left of the infinity symbol (∞) for the given parameter set.

$$\begin{cases} e_m a_{pm}^2 \leq c_p c_m \\ \frac{-r_h}{e_h P_{PM}^*} \leq a_{ph} \\ \text{decreasing} \\ \text{with } a_{pm} \end{cases} \quad (2'a)$$

$$\begin{cases} c_p c_m \leq e_m a_{pm}^2 \\ a_{ph} \leq \frac{-r_h}{e_h P_{PM}^*} \\ \text{increasing} \\ \text{with } a_{pm} \end{cases} \quad (2'b)$$

Relationships (1') and (2') clearly show that pollination favors the feasibility of coexistence while herbivory disfavors it. Both relationships indeed tend to be satisfied when pollination strengthens or herbivory weakens.

Assuming feasibility, coexistence is stable if and only if relationships (3) and (4) are satisfied.

Relationship (3) corresponds to the total feedback at level 3 (i.e. summation of the strengths of all three-element combinations of non-overlapping feedback loops, details in Appendix C.II.3) being negative. Pollination disfavors stability by contributing positively to this feedback, while it is the opposite for herbivory. Stability requires the competitive and the herbivory feedback loops to overcome the pollination feedback loop. Relationship (3') emphasizes the consecutive constraint limiting pollination. It governs the transition (blue dotted curve, arrow (3)) from unbounded growth (blue) to stable coexistence (yellow) in Fig. 3.

$$a_{pm} < \underbrace{\sqrt{\frac{c_h c_m c_p + c_m e_h a_{ph}^2}{e_m}}}_{\text{increasing with } a_{ph}} \quad (3')$$

Relationship (4) is harder to interpret. Given that relationships (3) and (4) imply that the feedback at each level is negative, relationship (4) could be interpreted as proposed by Levins

(1974): the negative feedback with long time lags (level 3) is weaker than the shorter-loop negative feedback (level 1 & 2) (details in Appendix C.II.4). Also, the constraints imposed by this relationship on interaction strengths are not analytically tractable, due to the effect of interactions on equilibrium densities.

Table 2: Analytical relationships governing stable coexistence. The fourth column indicates how each relationship is affected by the strength of interactions (favored +, disfavored -). Note that the third and fourth columns present a simplified summary of our analysis (see subsequent text and Appendix C, especially tables S3 & S4). Notations: P_{PM}^* plant density at plant-pollinator equilibrium; P_{PH}^* plant density at plant-herbivore equilibrium; “num” numerator; “den” denominator. Finally, the interplay between pollination and herbivory is difficult to disentangle in relationship (2), which led us to distinguish two cases (inequality (2'a) for (a) and (2'b) for (b) below). An increase in pollination (a_{pm}) makes the relationship shift from (a) to (b). In (b), P_{PM}^* loses its biological significance as the plant-pollinator subcommunity grows unboundedly. P_{PM}^* is, in this case, a mathematical function (as defined in Appendix C.II.2), which explains its counterintuitive behavior with the variation of pollination strength*.

Relationship	Mathematical meaning	Biological interpretation	Effect of interaction strengths
(1) $r_m + e_m a_{pm} P_{PH}^* \geq 0$	Feasibility (num(M^*) ≥ 0)	Pollinators can invade the plant-herbivore community	$a_{pm} +$ (direct) $a_{ph} - (P_{PH}^* \searrow)$
(2) $(c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*) \geq 0$	Feasibility (num(H^*) ≥ 0)	(a) Stable plant-pollinator dynamics with herbivores able to invade the plant-pollinator community <u>OR</u> (b) Plant-pollinator orgy with bounded herbivory	(a) $a_{pm} + (P_{PM}^* \nearrow)$ $a_{ph} +$ (direct) (b) $a_{pm} + (P_{PM}^* \searrow)^*$ $a_{ph} -$ (direct)
(3) $c_h e_m a_{pm}^2 - c_p c_m c_h - c_m e_h a_{ph}^2 < 0$	Feasibility (den(M^*, H^*) ≥ 0) Stability	Total feedback at level 3 is negative	$a_{pm} -$ $a_{ph} +$ (feedback loops, Fig. 1b)

<p>(4)</p> $(c_p P^* + c_m M^* + c_h H^*)(P^* M^* (c_p c_m - e_m a_{pm}^2) + P^* H^* (c_p c_h + e_h a_{ph}^2) + M^* H^* c_m c_h) - P^* M^* H^* (c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) > 0$	Stability	Negative feedback at level 3 is weaker than the product of negative feedback at lower levels (1 & 2)	Undetermined
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By combining relationships (1') and (3'), we obtain a necessary condition for stable coexistence (relationship (5)) which implies a positive correlation between pollination and herbivory. Stable coexistence within plant-pollinator-herbivore communities requires a balance between the strengths of pollination and herbivory. Stable coexistence in Fig. 3 (yellow) therefore happens around the first diagonal, where pollination and herbivory are of similar magnitudes.

$$\underbrace{\frac{-r_m}{e_m P_{PH}^*}}_{\text{increasing with } a_{ph}} \leq a_{pm} < \underbrace{\sqrt{\frac{c_h c_m c_p + c_m e_h a_{ph}^2}{e_m}}}_{\text{increasing with } a_{ph}} \quad (5)$$

3.2 Other ecological parameters also affect stable coexistence

In addition to the per capita effect of plant-animal interactions (i.e. interaction strength), stable coexistence depends on the densities of animal species, which in turn depend on their intrinsic growth and competition rates, as well as their conversion efficiencies. We consequently study the effect of animal growth rates (r_m vs. r_h , Fig. 4A & Fig. S4, appendix D), animal competition rates (c_m vs. c_h , Fig. 4B & Fig. S5, appendix D) and conversion efficiencies (e_m vs. e_h , Fig. S6, appendix D) on community composition. This investigation also constitutes a robustness check as we vary the parameters that were fixed hitherto.

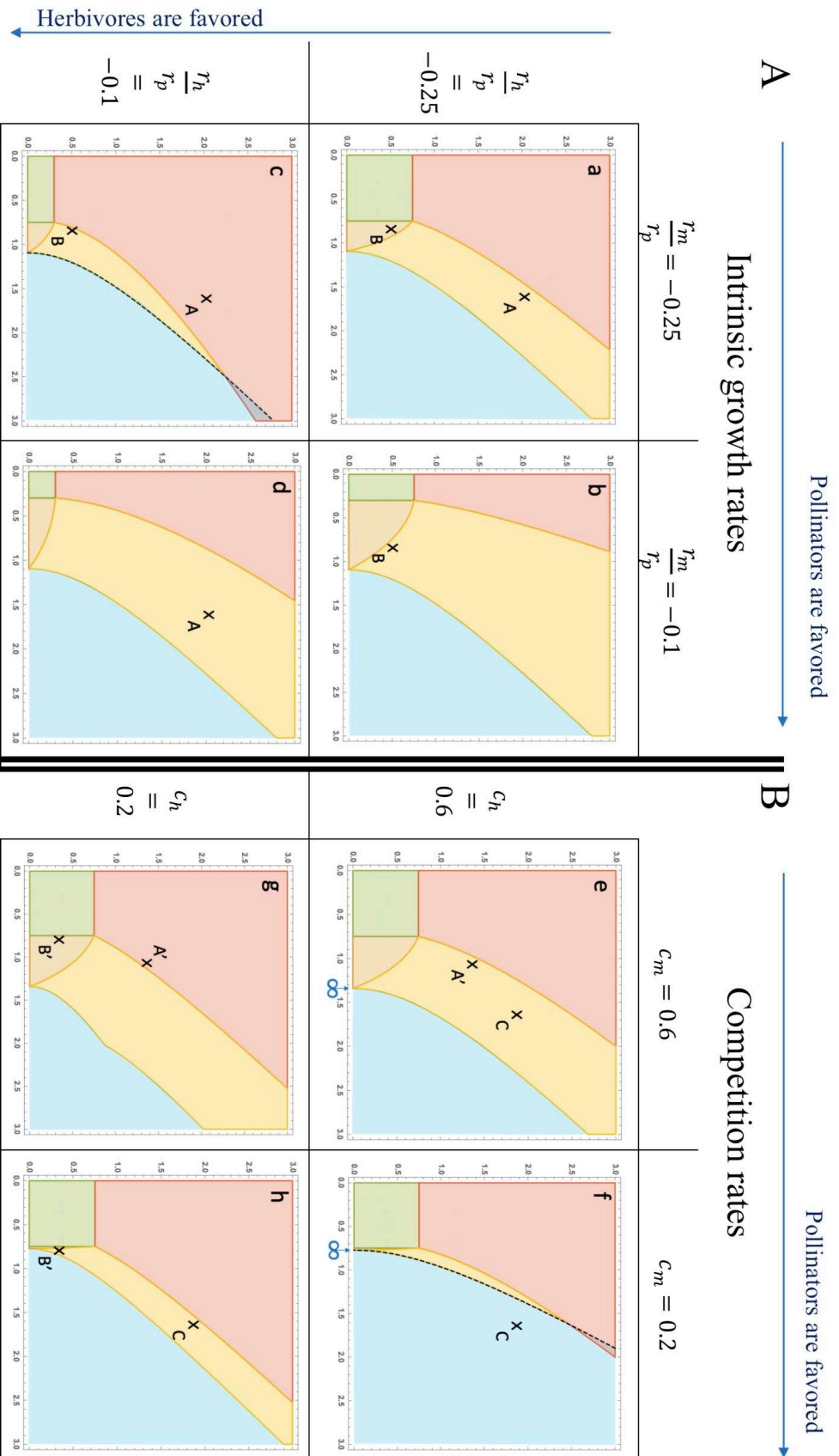


Fig. 4: Stable coexistence also depends on animal intrinsic growth rates (A) and competition rates (B). X-axis: Pollination (a_{pm}); Y-axis: Herbivory (a_{ph})

Color legend: Green: Plant, Brown: Plant-Pollinator, Red: Plant-Herbivore, Yellow: stable coexistence, Light blue: unbounded population density. In c & f, alternative states are observed (red and blue overlap): if plant and pollinator densities are initially above a given threshold (dependent on initial herbivore density), populations grow unboundedly; otherwise, pollinators are excluded. Parameters: $r_p = 10, c_p = 0.6, e_m = e_h = 0.2$; (A) $c_m = c_h = 0.4$; (B) $r_m = r_h = -2.5$. Note that Fig. S4 and S5 extend the results of 4A and 4B, respectively.

First of all, when stable coexistence is possible, it happens when the strengths of pollination and herbivory are approximately of the same magnitude (yellow area, Fig. 4 and S4 & S5 & S6 in Appendix D), as analyzed above (relationship (5)).

Stable coexistence is facilitated when the pollinator intrinsic growth rate is higher than the herbivore one. The range of pollination and herbivory strengths allowing stable coexistence indeed gets wider on the upper right of Fig. 4A. The explanation relies on two points: the feasibility of coexistence is favored by pollination and disfavored by herbivory; intrinsic growth rates play a major part in the feasibility of coexistence (relationships (1)&(2)), but only a minor part in its stability (no effect on relationship (3)). Analytical details are available in Appendix D. I. An increase in the pollinator growth rate makes it easier for pollinators to invade the plant-herbivore community (Fig. 4c vs 4d, point A). Due to a higher plant density, herbivores can also invade the plant-pollinator community more easily (Fig. 4a vs 4b, point B). Likewise, a higher herbivore growth rate enables an easier invasion of the plant-pollinator community by herbivores (Fig. 4a vs 4c, point B). It, however, makes the invasion of the plant-herbivore community by pollinators harder due to the reduction of plant density (Fig. 4a vs 4c, point A). Note finally that despite similar growth rates, the community is endangered when these growth rates are too low (Fig. S4, Appendix D).

Stable coexistence is facilitated when competition is stronger among pollinators than among herbivores. The range of pollination and herbivory strengths allowing stable coexistence indeed gets wider in the lower-left of Fig. 4B. Such a pattern is due to the effect of competition rates on stability (relationship (3)), which is much stronger than their effect on feasibility (relationships (1) & (2)). Analytical details are available in Appendix D.II. As competition among herbivores gets stronger, the plant density within the plant-herbivore community increases as a result of predation release. It becomes easier for pollinators to invade (Fig. 4g vs 4e, point A'). Unbounded dynamics are, however, facilitated (Fig. 4h vs 4f, point C) because the positive destabilizing loop increases more than the negative stabilizing loops (relationship (3)). In the plant-pollinator community, a lower pollinator density ensuing from a stronger competition rate is responsible for a lower plant density. It thus becomes harder for herbivores to invade (Fig. 4h vs 4g, point B'). Stability is, however, enhanced due to the stronger control of the pollination positive feedback in both the plant-pollinator subcommunity (Fig. 4f vs 4e, infinity symbol) and the three-species community (Fig. 4f vs 4e, point C).

To summarize, the results obtained from studying the effect of these other parameters support our main results, i.e. pollination favors feasibility at the expense of stability while it is

the opposite for herbivory. Indeed, any parameter variation that benefits pollinators (higher growth rate r_m , weaker competition c_m or higher conversion efficiency e_m (Appendix D.III)) favors feasibility, disfavors stability or both. Likewise, any parameter variation that benefits herbivores (higher growth rate r_h , weaker competition c_h or higher conversion efficiency e_h (Appendix D.III)) disfavors feasibility, favors stability, or both.

4. Discussion

At the core of community ecology, understanding the mechanisms that support the maintenance of species coexistence is of primary importance in a time of major threats to biodiversity due to global changes (Barnosky et al., 2011). In food webs, it has been shown that the coupling of weak and strong trophic interactions was among such mechanisms (McCann et al., 1998; Neutel et al., 2002). Because weak links can dampen the oscillatory dynamics ensuing from strong links, this unbalanced interaction pattern promotes stable coexistence. In contrast, we suggest that in mutualistic-antagonistic communities, a balance between the strengths of the two interaction types is required to achieve stable coexistence. This main result of our study is in agreement with the findings of several previous theoretical investigations on mutualistic-antagonistic communities, both at the module (Holland et al., 2013; Sauve et al., 2016a) and the network (Mougi and Kondoh, 2012) scale.

The balance between pollination and herbivory is driven by the opposite effects each type of interaction has on coexistence (i.e. feasibility) and stability.

In line with theoretical findings (Georgelin and Loeuille, 2014; Mougi and Kondoh, 2014b; Sauve et al., 2016a), we show that pollination increases herbivore density by enhancing plant density, while the effect of herbivory on pollinators is utterly opposite. This remains true when mutualism is modeled as a modified consumer-resource interaction, thus accounting for exploitative competition between animal species (Holland *et al.* 2013). Congruent direct effects on plant densities have been confirmed by several field experiments (Herrera, 2000; Herrera et al., 2002; Sutter and Albrecht, 2016), but empirical documentation of the consecutive indirect ecological effects between herbivore and pollinator species remains weak (e.g. Gómez 2005).

In contrast with feasibility, we find stability to be favored by herbivory and disfavored by pollination, in line with the theory on feedback loops (relationship (3), Levins 1974). Several

studies have indeed shown that pollination networks are prone to display unstable dynamics, such as sudden collapses consecutive to the crossing of tipping points (Dakos and Bascompte, 2014; Kaiser-Bunbury et al., 2010; Lever et al., 2014), as positive feedbacks amplify and propagate disturbances. The important role of predation (herbivorous here) in stabilizing population dynamics, on the other hand, has early been identified (Menge and Sutherland, 1976; Nicholson, 1954; Oksanen et al., 1981). Our results confirm that the consecutive negative feedback can stabilize the dynamics of mutualistic-antagonistic communities. It is important to note, however, that the effects of each interaction type on the stability of such communities are inconsistent across models (Georgelin and Loeuille, 2014; Holland et al., 2013; Sauve et al., 2016a). The different assumptions on the variation of the animal intake rates with plant density (i.e. functional responses) largely explain such contrasting results. It is nonetheless frequent to observe that the stability of the whole community is driven by the subcommunity displaying stable dynamics when considered in isolation. Yet, unstable dynamics are possible when merging two stable subcommunities as shown by Mougi & Kondoh (2014b). In their work, cycling densities are reported, driven by a delayed plant recovery after its exploitation by herbivores. The delay ensues from the fact that most of the productivity gain from pollination is captured by herbivores, which might be particularly problematic in an agricultural context, especially given that it has been reported in empirical studies several times (Gómez, 2005; Herrera et al., 2002). Integrative management of pollination and biological control can, fortunately, enable synergetic interactions between ecosystem services (Sutter and Albrecht, 2016).

It is important to highlight that instability, in our model, encompasses two behaviors whose biological implications are utterly different: (1) the loss of one or several species (Fig. 3, red-brown-green areas) vs. (2) the unbounded growth of population densities (Fig. 3, blue area) driven by an “orgy of mutual benefaction” (May, 1981). While coexistence is not maintained in the first case, it is in the second case. Another notion of stability – permanence (Hutson and Schmitt, 1992) - enables the distinction between these two cases: a biological community is said to be permanent if the densities of all species are always above a minimal threshold. Unbounded population growth is thus a case of “permanent coexistence” (Hutson and Law, 1985), a concept that captures the diversity of population dynamics that permit the coexistence of species in real biological communities. The orgy of mutual benefaction is, however, seldom observed in nature in spite of mutualisms being widespread (Bronstein, 1994). This indicates that the assumptions of simple models of mutualism are likely violated in real

biological systems. The functional response, which we assume linear for both interactions in order to gain analytical tractability, could saturate at high pollination levels when the handling time becomes limiting (e.g. Soberon & Martinez Del Rio 1981). The community context can also impede unrealistic population growth (Freedman et al., 1987; Heithaus et al., 1980; Ringel et al., 1996). While intraspecific competitions prevent this behavior up to a given level of pollination (Holland et al., 2002), we show here that the presence of a third species – the herbivore – allows for even stronger pollination levels to be compatible with biologically relevant finite population densities (relationship (3)). It is thus not surprising that orgies of mutual benefaction are not observed in nature as any two-species mutualism displaying such dynamics would accumulate enemies until restoring the balance required for stable coexistence. Several mechanisms could underlie this community assembly process. Firstly, as the plant biomass is booming, more and more herbivore species are becoming viable in the focal patch (e.g. relationship (2'a)). Because the plant population defines the threshold beyond which herbivore species can invade, as the plant density grows, the filter existing on the possible herbivore community weakens, and more herbivores species are susceptible to come and control the dynamics. Secondly, existing trophic links would likely strengthen as a result of adaptive foraging on the booming plant species in response to its abundance increase relative to other available resources. Adaptive foraging has notably been proposed as an important stabilizing process within complex trophic networks (Kondoh, 2003). In particular, Mougi & Kondoh (2014a) show how the interplay between adaptive foraging, pollination, and herbivory can support the maintenance of stable coexistence in plant-pollinator-herbivore communities.

Empirical evidence suggesting a balance between pollination and herbivory in natural communities does exist. At the module scale, several experimental studies manipulating the presence of animal species find the effects of pollination and herbivory on plant fecundity to be roughly of the same magnitude, approximately canceling each other (Gómez, 2005; Herrera, 2000; Herrera et al., 2002; Sutter and Albrecht, 2016). At the network scale, Melián *et al.* (2009) show that most strong interactions, mutualistic and antagonistic, are concentrated in the same few plant species of the Doñana Biological Reserve (Spain). Sauve *et al.* (2016b) exhibit a positive correlation between the number of pollinators and herbivores that interact with a given plant of the Norwood farm (UK). In line with our results, this correlation contributes positively to the stability of the community. Our results also imply that cascades of extinctions may be expected within plant-pollinator-herbivore networks as a result of the current global pollinator decline (Potts et al., 2010), given the weakening of pollination relative to herbivory.

Empirical evidence linked to species traits also supports the idea of a balanced interaction pattern. Indeed, a large number of studies documents shared preferences for plant phenotypes between pollinators and herbivores. Favoring balanced pollination vs. herbivory, shared preferences have been reported for a large number of plant traits, including flower color (Irwin et al., 2003), floral display (Cariveau et al., 2004; Gómez, 2003), chemical volatiles (Andrews et al., 2007; Theis et al., 2014), nectar quantity (Adler and Bronstein, 2004) or reproductive system (Asikainen and Mutikainen, 2005). Such a pattern implies that plant species are subject to an ecological trade-off between attracting pollinators and deterring herbivores (Strauss et al., 2002, 1999). Our work indicates that this trade-off might be ubiquitous as it fosters the stable coexistence of plant-pollinator-herbivore communities, explaining why it has been reported across a broad diversity of plant taxa. Traits of plant species might be subject to conflicting selection arising from such a trade-off (Strauss and Whittall, 2006), with potentially important implications in terms of diversity maintenance. In the case of the wild radish *Raphanus sativus*, for instance, it has been shown that the maintenance of a flower color dimorphism (white vs. pink) was due to both the pollinators and the herbivores interacting preferentially with white morphs (Irwin et al., 2003; McCall et al., 2013; Stanton, 1987). The question of whether such dimorphism emerged, in the first place, because of the interplay between pollination and herbivory, remains open. The study of mutualistic-antagonistic communities, plant-pollinator-herbivore in particular (Strauss and Irwin, 2004), thus offers opportunities to significantly improve our understanding of the ecological processes supporting the coexistence of species in natural systems, but also of the complex eco-evolutionary dynamics driving the maintenance of biodiversity.

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References

- Adler, L.S., Bronstein, J.L., 2004. Attracting antagonists: Does floral nectar increase leaf herbivory? *Ecology* 85, 1519–1526. <https://doi.org/10.1890/03-0409>
- Adler, L.S., Karban, R., Strauss, S.Y., 2001. Direct and indirect effects of alkaloids on plant fitness via herbivory and pollination. *Ecology* 82, 2032–2044. <https://doi.org/10.1890/0012->

9658(2001)082[2032:DAIEOA]2.0.CO;2

- Andrews, E.S., Theis, N., Adler, L.S., 2007. Pollinator and herbivore attraction to *Cucurbita* floral volatiles. *J. Chem. Ecol.* 33, 1682–1691. <https://doi.org/10.1007/s10886-007-9337-7>
- Asikainen, E., Mutikainen, P., 2005. Preferences of pollinators and herbivores in gynodioecious *Geranium sylvaticum*. *Ann. Bot.* 95, 879–886. <https://doi.org/10.1093/aob/mci094>
- Atwood, T.B., Valentine, S.A., Hammill, E., McCauley, D.J., Madin, E.M.P., Beard, K.H., Pearse, W.D., 2020. Herbivores at the highest risk of extinction among mammals, birds, and reptiles. *Sci. Adv.* 6, eabb8458.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471, 51–57. <https://doi.org/10.1038/nature09678>
- Bronstein, J.L., 1994. Our current understanding of mutualism. *Q. Rev. Biol.* 69, 31–51. <https://doi.org/10.1086/418432>
- Burns, T.P., Rose, K.A., Brenkert, A.L., 2014. Quantifying direct and indirect effects of perturbations using model ecosystems. *Ecol. Modell.* 293, 69–80. <https://doi.org/10.1016/j.ecolmodel.2013.12.017>
- Cardel, Y.J., Koptur, S., 2010. Effects of florivory on the pollination of flowers: An experimental field study with a perennial plant. *Int. J. Plant Sci.* 171, 283–292. <https://doi.org/10.1086/650154>
- Cariveau, D., Irwin, R.E., Brody, A.K., Garcia-Mayeya, L.S., Von Der Ohe, A., 2004. Direct and indirect effects of pollinators and seed predators to selection on plant and floral traits. *Oikos* 104, 15–26. <https://doi.org/10.1111/j.0030-1299.2004.12641.x>
- Craine, J.M., Dybzinski, R., 2013. Mechanisms of plant competition for nutrients, water and light. *Funct. Ecol.* 27, 833–840. <https://doi.org/10.1111/1365-2435.12081>
- Dakos, V., Bascompte, J., 2014. Critical slowing down as early warning for the onset of collapse in mutualistic communities. *Proc. Natl. Acad. Sci.* 111, 17546–17551. <https://doi.org/10.1073/pnas.1406326111>
- Fontaine, C., Guimarães Jr, P.R., Kéfi, S., Loeuille, N., Memmott, J., van der Putten, W.H., van Veen, F.J.F., Thébault, E., 2011. The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.* 14, 1170–1181. <https://doi.org/10.1111/j.1461-0248.2011.01688.x>
- Freedman, H.I., Addicott, J.F., Rai, B., 1987. Obligate mutualism with a predator: Stability and persistence of three-species models. *Theor. Popul. Biol.* 32, 157–175. [https://doi.org/10.1016/0040-5809\(87\)90045-1](https://doi.org/10.1016/0040-5809(87)90045-1)
- Georgelin, E., Loeuille, N., 2014. Dynamics of coupled mutualistic and antagonistic interactions, and their implications for ecosystem management. *J. Theor. Biol.* 346, 67–74. <https://doi.org/10.1016/j.jtbi.2013.12.012>
- Goh, B.S., 1976. Global Stability in Two Species Interactions. *J. Math. Biol.* 3, 313–318.
- Gómez, J.M., 2005. Non-additive effects of herbivores and pollinators on *Erysimum mediohispanicum* (Cruciferae) fitness. *Oecologia* 143, 412–418. <https://doi.org/10.1007/s00442-004-1809-7>
- Gómez, J.M., 2003. Herbivory reduces the strength of pollinator-mediated selection in the Mediterranean herb *Erysimum mediohispanicum*: Consequences for plant specialization. *Am. Nat.* 162, 242–256. <https://doi.org/10.1086/376574>
- Heithaus, E.R., Culver, D.C., Beattie, A.J., 1980. Models of Some Ant-Plant Mutualisms. *Am. Nat.* 116, 347–361. <https://doi.org/10.1086/283632>
- Herrera, C.M., 2000. Measuring the Effects of Pollinators and Herbivores: Evidence for Non-Additivity in a Perennial Herb. *Ecology* 81, 2170–2176. <https://doi.org/10.2307/177105>

- Herrera, C.M., Medrano, M., Rey, P.J., Sánchez-Lafuente, A.M., Garcia, M.B., Guitián, J., Manzaneda, A.J., 2002. Interaction of pollinators and herbivores on plant fitness suggests a pathway for correlated evolution of mutualism- and antagonism-related traits. *Proc. Natl. Acad. Sci.* 99, 16823–16828. <https://doi.org/10.1073/pnas.252362799>
- Holland, J.N., DeAngelis, D.L., Bronstein, J.L., 2002. Population dynamics and mutualism: Functional responses of benefits and costs. *Am. Nat.* 159, 231–244. <https://doi.org/10.1086/338510>
- Holland, J.N., Wang, Y., Sun, S., DeAngelis, D.L., 2013. Consumer-resource dynamics of indirect interactions in a mutualism-parasitism food web module. *Theor. Ecol.* 6, 475–493. <https://doi.org/10.1007/s12080-013-0181-9>
- Hutson, V., Law, R., 1985. Permanent coexistence in general models of three interacting species. *J. Math. Biol.* 21, 285–298.
- Hutson, V., Schmitt, K., 1992. Permanence and the dynamics of biological systems. *Math. Biosci.* 111, 1–71. [https://doi.org/10.1016/0025-5564\(92\)90078-B](https://doi.org/10.1016/0025-5564(92)90078-B)
- Irwin, R.E., Strauss, S.Y., Storz, S., Emerson, A., Guibert, G., 2003. The Role of Herbivores in the Maintenance of a Flower Color Polymorphism in Wild Radish. *Ecology* 84, 1733–1743.
- Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C.B., Caflisch, A., 2010. The robustness of pollination networks to the loss of species and interactions: A quantitative approach incorporating pollinator behaviour. *Ecol. Lett.* 13, 442–452. <https://doi.org/10.1111/j.1461-0248.2009.01437.x>
- Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., Boit, A., Joppa, L.N., Lafferty, K.D., Williams, R.J., Martinez, N.D., Menge, B.A., Blanchette, C.A., Iles, A.C., Brose, U., 2012. More than a meal... integrating non-feeding interactions into food webs. *Ecol. Lett.* 15, 291–300. <https://doi.org/10.1111/j.1461-0248.2011.01732.x>
- Kessler, A., Halitschke, R., Poveda, K., 2011. Herbivory-mediated pollinator limitation: Negative impacts of induced volatiles on plant-pollinator interactions. *Ecology* 92, 1769–1780. <https://doi.org/10.1890/10-1945.1>
- Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.* 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>
- Kondoh, M., 2003. Foraging Adaptation and the Relationship Between Food-Web Complexity and Stability. *Science* 299, 1388–1391.
- Lever, J.J., van Nes, E.H., Scheffér, M., Bascompte, J., 2014. The sudden collapse of pollinator communities. *Ecol. Lett.* 17, 350–359. <https://doi.org/10.1111/ele.12236>
- Levins, R., 1974. Discussion paper: the qualitative analysis of partially specified systems. *Ann. N. Y. Acad. Sci.* 231, 123–138.
- Lundin, O., Smith, H.G., Rundlöf, M., Bommarco, R., 2013. When ecosystem services interact: Crop pollination benefits depend on the level of pest control. *Proc. R. Soc. B Biol. Sci.* 280, 20122243. <https://doi.org/10.1098/rspb.2012.2243>
- May, R.M., 1981. Models for two interacting populations, in: May, R. (Ed.), *Theoretical Ecology: Principles and Applications* (2nd Edition). Blackwell: Oxford, UK, pp. 78–104.
- McCall, A.C., Murphy, S.J., Venner, C., Brown, M., 2013. Florivores prefer white versus pink petal color morphs in wild radish, *Raphanus sativus*. *Oecologia* 172, 189–195. <https://doi.org/10.1007/s00442-012-2480-z>
- McCann, K., Hastings, A., Huxel, G.R., 1998. Weak trophic interactions and the balance of nature. *Nature* 395, 794–798. <https://doi.org/10.1007/978-3-319-06257-0>

- Melián, C.J., Bascompte, J., Jordano, P., Křivan, V., 2009. Diversity in a complex ecological network with two interaction types. *Oikos* 118, 122–130. <https://doi.org/10.1111/j.1600-0706.2008.16751.x>
- Menge, B.A., 1995. Indirect effects in marine rocky intertidal interaction webs: Patterns and importance. *Ecol. Monogr.* 65, 21–74. <https://doi.org/10.2307/2937158>
- Menge, B.A., Sutherland, J.P., 1976. Species Diversity Gradients: Synthesis of the Roles of Predation, Competition, and Temporal Heterogeneity. *Am. Nat.* 110, 351–369. <https://doi.org/10.1086/283073>
- Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., Alon, U., 2002. Network motifs: Simple building blocks of complex networks. *Science* 298, 824–827. <https://doi.org/10.1126/science.298.5594.824>
- Mougi, A., Kondoh, M., 2014a. Adaptation in a hybrid world with multiple interaction types: A new mechanism for species coexistence. *Ecol. Res.* 29, 113–119. <https://doi.org/10.1007/s11284-013-1111-4>
- Mougi, A., Kondoh, M., 2014b. Instability of a hybrid module of antagonistic and mutualistic interactions. *Popul. Ecol.* 56, 257–263. <https://doi.org/10.1007/s10144-014-0430-9>
- Mougi, A., Kondoh, M., 2012. Diversity of interaction types and ecological community stability. *Science* 337, 349–351. <https://doi.org/10.1126/science.1220529>
- Neutel, A.-M., Heesterbeek, J.A.P., De Ruiter, P.C., 2002. Stability in real food webs: Weak links in long loops. *Science* 296, 1120–1123. <https://doi.org/10.1126/science.1068326>
- Neutel, A.-M., Thorne, M.A.S., 2014. Interaction strengths in balanced carbon cycles and the absence of a relation between ecosystem complexity and stability. *Ecol. Lett.* 17, 651–661. <https://doi.org/10.1111/ele.12266>
- Nicholson, A.J., 1954. An outline of the dynamics of animal populations. *Aust. J. Zool.* 2, 9–65.
- Oerke, E.C., 2006. Crop losses to pests. *J. Agric. Sci.* 144, 31–43. <https://doi.org/10.1017/S0021859605005708>
- Oksanen, L., Fretwell, S.D., Arruda, J., Niemelä, P., 1981. Exploitation Ecosystems in Gradients of Primary Productivity. *Am. Nat.* 118, 240–261. <https://doi.org/10.1086/283817>
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Pohl, N., Carvallo, G., Botto-Mahan, C., Medel, R., 2006. Nonadditive effects of flower damage and hummingbird pollination on the fecundity of *Mimulus luteus*. *Oecologia* 149, 648–655. <https://doi.org/10.1007/s00442-006-0479-z>
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: Trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Ringel, M.S., Hu, H.H., Anderson, G., 1996. The stability and persistence of mutualisms embedded in community interactions. *Theor. Popul. Biol.* 50, 281–297. <https://doi.org/10.1006/tpbi.1996.0032>
- Sauve, A.M.C., Fontaine, C., Thébault, E., 2016a. Stability of a diamond-shaped module with multiple interaction types. *Theor. Ecol.* 9, 27–37. <https://doi.org/10.1007/s12080-015-0260-1>
- Sauve, A.M.C., Fontaine, C., Thébault, E., 2014. Structure-stability relationships in networks combining mutualistic and antagonistic interactions. *Oikos* 123, 378–384. <https://doi.org/10.1111/j.1600-0706.2013.00743.x>
- Sauve, A.M.C., Thébault, E., Pocock, M.J.O., Fontaine, C., 2016b. How plants connect pollination and herbivory networks and their contribution to community stability. *Ecology* 97, 908–917. <https://doi.org/10.1890/15-0132.1>
- Soberon, J.M., Martinez Del Rio, C., 1981. The dynamics of a plant-pollinator interaction. *J. Theor. Biol.* 91, 363–

378. [https://doi.org/10.1016/0022-5193\(81\)90238-1](https://doi.org/10.1016/0022-5193(81)90238-1)

- Stanton, M.L., 1987. Reproductive biology of petal color variants in wild populations of *Raphanus sativus*. I. Pollinator response to colour morphs. *Am. J. Bot.* 74, 178–187. <https://doi.org/10.2307/2444019>
- Stouffer, D.B., Bascompte, J., 2010. Understanding food-web persistence from local to global scales. *Ecol. Lett.* 13, 154–161. <https://doi.org/10.1111/j.1461-0248.2009.01407.x>
- Strauss, S.Y., Irwin, R.E., 2004. Ecological and Evolutionary Consequences of Multispecies Plant-Animal Interactions. *Annu. Rev. Ecol. Evol. Syst.* 35, 435–466. <https://doi.org/10.1146/annurev.ecolsys.35.112202.130215>
- Strauss, S.Y., Murch, P., 2004. Towards an understanding of the mechanisms of tolerance: Compensating for herbivore damage by enhancing a mutualism. *Ecol. Entomol.* 29, 234–239. <https://doi.org/10.1111/j.0307-6946.2004.00587.x>
- Strauss, S.Y., Rudgers, J.A., Lau, J.A., Irwin, R.E., 2002. Direct and ecological costs of resistance to herbivory. *Trends Ecol. Evol.* 17, 278–285. [https://doi.org/10.1016/S0169-5347\(02\)02483-7](https://doi.org/10.1016/S0169-5347(02)02483-7)
- Strauss, S.Y., Siemsen, D.H., Decher, M.B., Mitchell-Olds, T., 1999. Ecological Costs of Plant Resistance To Herbivores in the Currency of Pollination. *Evolution (N. Y.)* 53, 1105–1113. <https://doi.org/10.1111/j.1558-5646.1999.tb04525.x>
- Strauss, S.Y., Whittall, J.B., 2006. Non-pollinator agents of selection on floral traits, in: Harder, L.D., Barrett, S.C.H. (Eds.), *Ecology and Evolution of Flowers*. Oxford University Press on Demand, New York, NY, USA, pp. 120–138.
- Sutter, L., Albrecht, M., 2016. Synergistic interactions of ecosystem services: Florivorous pest control boosts crop yield increase through insect pollination. *Proc. R. Soc. B Biol. Sci.* 283, 20152529. <https://doi.org/10.1098/rspb.2015.2529>
- Thébault, E., Fontaine, C., 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329, 853–856. <https://doi.org/10.1126/science.1188321>
- Theis, N., Barber, N.A., Gillespie, S.D., Hazzard, R. V., Adler, L.S., 2014. Attracting mutualists and antagonists: Plant trait variation explains the distribution of specialist floral herbivores and pollinators on crops and wild gourds. *Am. J. Bot.* 101, 1314–1322. <https://doi.org/10.3732/ajb.1400171>
- Vandermeer, J.H., Boucher, D.H., 1978. Varieties of mutualistic interaction in population models. *J. Theor. Biol.* 74, 549–558. [https://doi.org/10.1016/0022-5193\(78\)90241-2](https://doi.org/10.1016/0022-5193(78)90241-2)
- Wootton, J.T., 2002. Indirect effects in complex ecosystems: Recent progress and future challenges. *J. Sea Res.* 48, 157–172. [https://doi.org/10.1016/S1385-1101\(02\)00149-1](https://doi.org/10.1016/S1385-1101(02)00149-1)

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Appendix A: Nondimensionalization

In order to improve the readability of the mathematical analyses presented in the supporting information, the model can be rewritten in a nondimensionalized but equivalent way, which allows for fewer parameters. The analyses that use this reformulation are indicated by a star (*) accompanying the title of the corresponding section.

The dynamical system studied follows the equations:

$$\begin{aligned}\frac{dP}{dt} &= P(r_p - c_p P + a_{pm}M - a_{ph}H) \\ \frac{dM}{dt} &= M(r_m - c_m M + e_m a_{pm}P) \\ \frac{dH}{dt} &= H(r_h - c_h H + e_h a_{ph}P)\end{aligned}$$

It can be rewritten:

$$\begin{aligned}\frac{dP'}{dt'} &= P'(1 - P' + \alpha_{pm}M' - \alpha_{ph}H') \\ \frac{dM'}{dt'} &= M'(\rho_m - M' + \lambda_m \alpha_{pm}P') \\ \frac{dH'}{dt'} &= H'(\rho_h - H' + \lambda_h \alpha_{ph}P')\end{aligned}$$

With:

$$(P', M', H', t') = \left(\frac{c_p}{r_p} P, \frac{c_m}{r_p} M, \frac{c_h}{r_p} H, r_p t \right)$$

$$(\rho_m, \rho_h) = \left(\frac{r_m}{r_p}, \frac{r_h}{r_p} \right) < (0, 0)$$

$$(\lambda_m, \lambda_h) = \left(\frac{e_m c_m}{c_p}, \frac{e_h c_h}{c_p} \right)$$

$$(\alpha_{pm}, \alpha_{ph}) = \left(\frac{a_{pm}}{c_m}, \frac{a_{ph}}{c_h} \right)$$

Appendix B: Study of ecological dynamics

I. Preliminary definitions

1. Feasibility

Our dynamical system (equations (a, b, c)) captures the dynamics of a plant-pollinator-herbivore community as long as the variables, which are biomass densities, are positive. An ecological equilibrium is therefore biologically meaningful if it corresponds to positive densities, i.e. if it is feasible.

2. Stability

Local stability

What we call stability in this work corresponds to local stability. An equilibrium is locally stable when the population dynamics tend to return to the equilibrium following a small perturbation (resilience). Local stability is technically characterized by the fact that all eigenvalues of the Jacobian matrix at the equilibrium have a strictly negative real part, or by the equivalent Routh-Hurwitz criterion (Murray 2002). The latter consists of deriving three coefficients from the Jacobian Matrix (a_1, a_2, a_3) . The equilibrium is locally stable if and only if: $a_1 > 0$; $a_3 > 0$; $a_1 a_2 - a_3 > 0$.

Global stability

Global stability implies local stability. An equilibrium is globally stable when the population dynamics tend to return to the equilibrium following a perturbation, irrespective of its intensity. Note that perturbations that imply the extinction of one or more populations are excluded.

II. Subcommunities dynamics

1. Plant-Herbivore subcommunity

Only one equilibrium is feasible and globally stable, depending on the parameter set. If the plant population, when at carrying capacity (i.e. $\frac{r_p}{c_p}$), is sufficient for the herbivore population to have a positive growth rate when low in density (i.e. $r_h + e_h a_{ph} \left[\frac{r_p}{c_p} \right] > 0$) then stable coexistence between plants and herbivores is observed after a transient state. If not, the herbivore population goes extinct and the plant population remains at carrying capacity.

2. Plant-Pollinator subcommunity

The subcommunity can behave according to two regimes depending on the relative strength between the self-limiting competition loop ($c_p c_m$) and the positive feedback loop due to pollination ($e_m a_{pm}^2$).

If competition overcomes pollination (i.e. $c_p c_m - e_m a_{pm}^2 > 0$), population densities are always bounded. In such a case, there is exactly one feasible and globally stable equilibrium. If the plant population, when at carrying capacity ($\frac{r_p}{c_p}$), is sufficient for the pollinator population to have a positive growth rate when low in density (i.e. $r_m + e_m a_{pm} \left[\frac{r_p}{c_p} \right] > 0$) then stable coexistence between plants and pollinators is observed after a transient state. If not, the pollinator population goes extinct and the plant population remains at carrying capacity.

If not (i.e. $c_p c_m - e_m a_{pm}^2 < 0$), population sizes can become unbounded due to the positive amplifying feedback loop between plants and pollinators that is no longer controlled by intra-specific competition. In such a case, if the plant population at carrying capacity is sufficient for the pollinator population to have a positive growth rate when low in density, then populations grow unbounded (mathematically converging toward infinity) irrespective of initial conditions. If not, the equilibrium where only plants are present is locally stable but populations grow unbounded if initially large enough.

III. Ecological equilibria in the plant-pollinator-herbivore community

1. Dynamical system in matrix form

The dynamical system capturing population dynamics (i.e. equations (a, b, c)) can be written in matrix form as:

$$\begin{pmatrix} \frac{dP}{dt} \\ \frac{dM}{dt} \\ \frac{dH}{dt} \end{pmatrix} = \begin{pmatrix} r_p \\ r_m \\ r_h \end{pmatrix} + \begin{pmatrix} -c_p & a_{pm} & -a_{ph} \\ e_m a_{pm} & -c_m & 0 \\ e_h a_{ph} & 0 & -c_h \end{pmatrix} \begin{pmatrix} P \\ M \\ H \end{pmatrix}$$

The corresponding Jacobian matrix is written:

$$Jac = \begin{pmatrix} r_p - 2c_p P + a_{pm} M - a_{ph} H & a_{pm} P & -a_{ph} P \\ e_m a_{pm} M & r_m - 2c_m M + e_m a_{pm} P & 0 \\ e_h a_{ph} H & 0 & r_h - 2c_h H + e_h a_{ph} P \end{pmatrix}$$

2. Expressions of equilibria and feasibility

Equilibrium	Expression	Feasibility
Absence	$P^* = 0 ; M^* = 0 ; H^* = 0$	Yes
Plants	$P^* = \bar{r}_p / c_p ; M^* = 0 ; H^* = 0$	Yes
Pollinators	$P^* = 0 ; M^* = \bar{r}_m / c_m ; H^* = 0$	No
Herbivores	$P^* = 0 ; M^* = 0 ; H^* = \bar{r}_h / c_h$	No
Plants and pollinators	$P_{PM}^* = \frac{c_m \bar{r}_p + a_{pm} \bar{r}_m}{c_p c_m - e_m a_{pm}^2}$ $M_{PM}^* = \frac{e_m a_{pm} \bar{r}_p + c_p \bar{r}_m}{c_p c_m - e_m a_{pm}^2} ; H_{PM}^* = 0$	$\begin{cases} c_p c_m - e_m a_{pm}^2 \geq 0 \\ r_m + e_m a_{pm} \left[\frac{\bar{r}_p}{c_p} \right] \geq 0 \end{cases}$ <p style="text-align: center;">Or</p> $\begin{cases} c_p c_m - e_m a_{pm}^2 \leq 0 \\ r_m + e_m a_{pm} \left[\frac{\bar{r}_p}{c_p} \right] \leq 0 \end{cases}$
Plants and herbivores	$P_{PH}^* = \frac{c_h \bar{r}_p - a_{ph} \bar{r}_h}{c_p c_h + e_h a_{ph}^2}$ $M_{PH}^* = 0 ; H_{PH}^* = \frac{e_h a_{ph} \bar{r}_p + c_p \bar{r}_h}{c_p c_h + e_h a_{ph}^2}$	$r_h + e_h a_{ph} \left[\frac{\bar{r}_p}{c_p} \right] \geq 0$
Pollinators and herbivores	$P_{MH}^* = 0 ; M_{MH}^* = \bar{r}_m / c_m ; H_{MH}^* = \bar{r}_h / c_h$	No
Coexistence of plants, pollinators and herbivores	$P^* = \frac{c_h c_m \bar{r}_p + c_h a_{pm} \bar{r}_m - c_m a_{ph} \bar{r}_h}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2}$ $M^* = \frac{c_h e_m a_{pm} \bar{r}_p + (c_p c_h + e_h a_{ph}^2) \bar{r}_m - e_m a_{pm} a_{ph} \bar{r}_h}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2}$ $H^* = \frac{c_m e_h a_{ph} \bar{r}_p + e_h a_{pm} a_{ph} \bar{r}_m + (c_p c_m - e_m a_{pm}^2) \bar{r}_h}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2}$	

Table S1: Expressions of equilibria and feasibility. Reminder of our assumptions: $\bar{r}_p > 0, \bar{r}_m < 0, \bar{r}_h < 0$

3. Stability of equilibria

An equilibrium is stable if, and only if, the three eigenvalues of the Jacobian matrix, calculated at this equilibrium, have a negative real part. Such property is equivalent to the three Routh-Hurwitz inequalities, which are often easier to assess. Note that we only assess the stability of the five potentially feasible equilibria.

Equilibrium	Method	Mathematical expressions	Stability
Absence	Eigenvalues ($\lambda_1, \lambda_2, \lambda_3$)	$\lambda_1 = r_p; \lambda_2 = r_m; \lambda_3 = r_h$	No
Plants	Eigenvalues ($\lambda_1, \lambda_2, \lambda_3$)	$\lambda_1 = -r_p$ $\lambda_2 = \frac{e_m a_{pm} r_p + c_p r_m}{c_p}$ $\lambda_3 = \frac{e_h a_{ph} r_p + c_p r_h}{c_p}$	$\begin{cases} r_m + e_m a_{pm} \left[\frac{r_p}{c_p} \right] \leq 0 \\ r_h + e_h a_{ph} \left[\frac{r_p}{c_p} \right] \leq 0 \end{cases}$
Plants and pollinators	Routh-Hurwitz	$a_1 = (c_p - e_h a_{ph}) P_{PM}^* + c_m M_{PM}^* - r_h$ $a_2 = P_{PM}^* M_{PM}^* (c_p c_m - e_h c_m a_{ph} - e_m a_{pm}^2) - M_{PM}^* c_m r_h - c_p P_{PM}^* (e_h a_{ph} P_{PM}^* + r_h)$ $a_3 = P_{PM}^* M_{PM}^* (e_h a_{ph} P_{PM}^* + r_h) (e_m a_{pm}^2 - c_p c_m)$	
Plants and herbivores	Routh-Hurwitz	$a_1 = (c_p - a_{pm} e_m) P_{PH}^* + c_h H_{PH}^* - r_m$ $a_2 = P_{PH}^* H_{PH}^* (c_h c_p - a_{pm} c_h e_m + a_{ph}^2 e_h) - H_{PH}^* c_h r_m - c_p P_{PH}^* (a_{pm} e_m P_{PH}^* + r_m)$ $a_3 = -P_{PH}^* H_{PH}^* (e_m a_{pm} P_{PH}^* + r_m) (e_h a_{ph}^2 + c_h c_p)$	
Coexistence of plants, pollinators and herbivores	Routh-Hurwitz	$a_1 = c_p P^* + c_m M^* + c_h H^*$ $a_2 = P^* M^* (c_p c_m - e_m a_{pm}^2) + P^* H^* (c_p c_h + e_h a_{ph}^2) + M^* H^* c_m c_h$ $a_3 = P^* M^* H^* (c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2)$	

Table S2: Mathematical expressions of local stability. A necessary and sufficient condition for stability is either: ($\lambda_1 < 0; \lambda_2 < 0; \lambda_3 < 0$) or ($a_1 > 0; a_3 > 0; a_1 a_2 - a_3 > 0$). Reminder of our assumptions: $r_p > 0, r_m < 0, r_h < 0$

IV. First analytical results

1. Variation of biomass densities with interaction strengths

Plant density at stable coexistence increases with pollination and decreases with herbivory.

We have:

$$\begin{aligned}
 P^* &= \frac{c_h c_m r_p + c_h a_{pm} r_m - c_m a_{ph} r_h}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2} \\
 \Leftrightarrow (c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) P^* &= c_h c_m r_p + c_h a_{pm} r_m - c_m a_{ph} r_h \\
 \Rightarrow \begin{cases} -2c_h e_m a_{pm} P^* + (c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) \frac{\partial P^*}{\partial a_{pm}} = c_h r_m \\ 2c_m e_h a_{ph} P^* + (c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) \frac{\partial P^*}{\partial a_{ph}} = -c_m r_h \end{cases} \\
 \Rightarrow \begin{cases} \frac{\partial P^*}{\partial a_{pm}} = \frac{c_h (r_m + 2e_m a_{pm} P^*)}{(c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2)} \\ \frac{\partial P^*}{\partial a_{ph}} = \frac{-c_m (r_h + 2e_h a_{ph} P^*)}{(c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2)} \end{cases} \\
 \Rightarrow \begin{cases} \frac{\partial P^*}{\partial a_{pm}} = \frac{c_h (c_m M^* + e_m a_{pm} P^*)}{(c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2)} \\ \frac{\partial P^*}{\partial a_{ph}} = \frac{-c_m (c_h H^* + e_h a_{ph} P^*)}{(c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2)} \end{cases} \\
 \Rightarrow \begin{cases} \frac{\partial P^*}{\partial a_{pm}} > 0 \\ \frac{\partial P^*}{\partial a_{ph}} < 0 \end{cases}
 \end{aligned}$$

Given that $P^*, M^*, H^* > 0$ (feasibility) and $(c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) > 0$ (stability).

Moreover,

$$\begin{aligned}
 c_m M^* &= r_m + e_m a_{pm} P^* \\
 \Rightarrow \begin{cases} \frac{\partial M^*}{\partial a_{pm}} = \frac{e_m}{c_m} \left(P^* + a_{pm} \frac{\partial P^*}{\partial a_{pm}} \right) > 0 \\ \frac{\partial M^*}{\partial a_{ph}} = \frac{e_m}{c_m} a_{pm} \frac{\partial P^*}{\partial a_{ph}} > 0 \end{cases}
 \end{aligned}$$

Pollinator density at stable coexistence increases with pollination and decreases with herbivory.

And

$$c_h H^* = r_h + e_h a_{ph} P^*$$

$$\Rightarrow \begin{cases} \frac{\partial H^*}{\partial a_{pm}} = \frac{e_h}{c_h} a_{ph} \frac{\partial P^*}{\partial a_{pm}} > 0 \\ \frac{\partial H^*}{\partial a_{ph}} = \frac{e_h}{c_h} \left(P^* + a_{ph} \frac{\partial P^*}{\partial a_{ph}} \right) = e_h \frac{P^* (c_m c_p - e_m a_{pm}^2) - c_m a_{ph} H^*}{(c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2)} \end{cases}$$

Herbivore density increases with pollination. It can either increase or decrease with herbivory. It necessarily decreases if pollination is strong ($e_m a_{pm}^2 > c_m c_p$) or herbivore density (H^*) is high.

2. Global stability of the coexistence equilibrium when unbounded growth is not possible

We prove analytically that when populations cannot become unbounded in the plant-pollinator subcommunity, the feasibility of the coexistence equilibrium implies its global stability.

*Proof of the global stability of feasible coexistence in the case ($c_p c_m - e_m a_{pm}^2 > 0$)

The nondimensionalized dynamical system (Appendix A) is rewritten in matrix form:

$$\begin{pmatrix} \frac{dP}{dt} \\ \frac{dM}{dt} \\ \frac{dH}{dt} \end{pmatrix} = \begin{pmatrix} 1 \\ \rho_m \\ \rho_h \end{pmatrix} + A \begin{pmatrix} P \\ M \\ H \end{pmatrix}$$

$$A = \begin{pmatrix} -1 & \alpha_{pm} & -\alpha_{ph} \\ \lambda_m \alpha_{pm} & -1 & 0 \\ \lambda_h \alpha_{ph} & 0 & -1 \end{pmatrix}$$

Let D be the positive diagonal matrix defined as:

$$D = \begin{pmatrix} 1 & 0 & 0 \\ 0 & \frac{1}{\lambda_m} & 0 \\ 0 & 0 & \frac{1}{\lambda_h} \end{pmatrix}$$

We have:

$$D(-A) + (-A^t)D = \begin{pmatrix} 1 & -\alpha_{pm} & \alpha_{ph} \\ -\alpha_{pm} & \frac{1}{\lambda_m} & 0 \\ -\alpha_{ph} & 0 & \frac{1}{\lambda_h} \end{pmatrix} + \begin{pmatrix} 1 & -\alpha_{pm} & \alpha_{ph} \\ -\alpha_{pm} & \frac{1}{\lambda_m} & 0 \\ -\alpha_{ph} & 0 & \frac{1}{\lambda_h} \end{pmatrix} = \begin{pmatrix} 2 & -2\alpha_{pm} & 0 \\ -2\alpha_{pm} & \frac{2}{\lambda_m} & 0 \\ 0 & 0 & \frac{2}{\lambda_h} \end{pmatrix}$$

$D(-A) + (-A^t)D$ is positive definite since it satisfies the Sylvester Criterion:

$$(1) |2| = 2 > 0$$

$$(2) \begin{vmatrix} 2 & -2\alpha_{pm} \\ -2\alpha_{pm} & \frac{2}{\lambda_m} \end{vmatrix} = \frac{4}{\lambda_m} (1 - \lambda_m \alpha_{pm}^2) > 0$$

$$(3) \begin{vmatrix} 2 & -2\alpha_{pm} & 0 \\ -2\alpha_{pm} & \frac{2}{\lambda_m} & 0 \\ 0 & 0 & \frac{2}{\lambda_h} \end{vmatrix} = \frac{2}{\lambda_h} \begin{vmatrix} 2 & -2\alpha_{pm} \\ -2\alpha_{pm} & \frac{2}{\lambda_m} \end{vmatrix} = \frac{8}{\lambda_m \lambda_h} (1 - \lambda_m \alpha_{pm}^2) > 0$$

This implies that the matrix A is VL-stable (Hofbauer *et al.* 2008) and in turn, that if the coexistence equilibrium is strictly feasible ($P^* > 0, M^* > 0, H^* > 0$), it is globally stable (Logofet 2005; Hofbauer *et al.* 2008). All trajectories starting with strictly positive population densities converge toward this equilibrium.

Moreover, if the coexistence equilibrium is not strictly feasible, either the plant-pollinator or plant-herbivore equilibrium is feasible and globally stable. If not, the plant equilibrium is feasible and globally stable. The equilibrium that is feasible and globally stable attracts all solutions starting from strictly positive population densities (Hofbauer *et al.*, 2008).

References

- Hofbauer, J., Kon, R. & Saito, Y. (2008). Qualitative permanence of Lotka-Volterra equations. *J. Math. Biol.*, 57, 863–881.
- Logofet, D.O. (2005). Stronger-than-Lyapunov notions of matrix stability, or how “flowers” help solve problems in mathematical ecology. *Linear Algebra Appl.*, 398, 75–100.
- Murray, J.D. (2002). Appendix 2: Routh-Hurwitz conditions, Jury conditions, Descartes’ rule of signs and exact solutions of a cubic. In: *Mathematical Biology*. Springer-Verlag Berlin Heidelberg, pp. 702–705.

Appendix C: Relationships governing stable coexistence

I. Characterization of stable coexistence

1. Feasibility of the coexistence equilibrium

The feasibility corresponds to:

$$\begin{cases} P^* \geq 0 \\ M^* \geq 0 \\ H^* \geq 0 \end{cases}$$

However, the plant population supports the animal populations in our community ($r_m < 0, r_h < 0$) so that as long as at least one animal population is viable, the plant population is necessarily viable:

$$M^* \geq 0 \text{ or } H^* \geq 0 \Rightarrow P^* \geq 0$$

Proof:

The coexistence equilibrium satisfies:

$$\begin{cases} P^* = \frac{-r_m + c_m M^*}{e_m a_{pm}} \geq \frac{-r_m}{e_m a_{pm}} > 0 \\ P^* = \frac{-r_h + c_h H^*}{e_h a_{ph}} \geq \frac{-r_h}{e_h a_{ph}} > 0 \end{cases}$$

Hence:

$$\text{Feasibility} \Leftrightarrow \begin{cases} M^* \geq 0 \\ H^* \geq 0 \end{cases}$$

Moreover

$$\begin{aligned} M^* &= \frac{c_h e_m a_{pm} r_p + (c_p c_h + e_h a_{ph}^2) r_m - e_m a_{pm} a_{ph} r_h}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2} \\ &= \frac{(c_p c_h + e_h a_{ph}^2) (r_m + e_m a_{pm} \frac{c_h r_p - a_{ph} r_h}{c_p c_h + e_h a_{ph}^2})}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2} \\ H^* &= \frac{c_m e_h a_{ph} r_p + e_h a_{pm} a_{ph} r_m + (c_p c_m - e_m a_{pm}^2) r_h}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2} \\ &= \frac{(c_p c_m - e_m a_{pm}^2) (r_h + e_h a_{ph} \frac{c_m r_p + a_{pm} r_m}{c_p c_m - e_m a_{pm}^2})}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2} \end{aligned}$$

Given than the denominator $c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2$ can either be positive or negative, the coexistence equilibrium is feasible if and only if:

$$\begin{cases} c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2 > 0 \\ (c_p c_h + e_h a_{ph}^2)(r_m + e_m a_{pm} P_{PH}^*) \geq 0 \\ (c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*) \geq 0 \end{cases}$$

Or

$$\begin{cases} c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2 < 0 \\ (c_p c_h + e_h a_{ph}^2)(r_m + e_m a_{pm} P_{PH}^*) \leq 0 \\ (c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*) \leq 0 \end{cases}$$

2. Stability of the coexistence equilibrium

Given it is feasible, the coexistence equilibrium is stable if and only if the three Routh-Hurwitz conditions are satisfied:

$$c_p P^* + c_m M^* + c_h H^* > 0$$

$$P^* M^* H^* (c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) > 0$$

$$\begin{aligned} (c_p P^* + c_m M^* + c_h H^*) (P^* M^* (c_p c_m - e_m a_{pm}^2) + P^* H^* (c_p c_h + e_h a_{ph}^2) + M^* H^* c_m c_h) \\ - P^* M^* H^* (c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) > 0 \end{aligned}$$

The first condition is always true (feasibility). Stability is therefore characterized by the two following relationships, which correspond respectively to relationships (3) and (4) in the main text (table 2).

$$(c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) > 0$$

$$\begin{aligned} (c_p P^* + c_m M^* + c_h H^*) (P^* M^* (c_p c_m - e_m a_{pm}^2) + P^* H^* (c_p c_h + e_h a_{ph}^2) + M^* H^* c_m c_h) \\ - P^* M^* H^* (c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) > 0 \end{aligned}$$

II. Relationships governing stable coexistence

By combining the inequations characterizing feasibility and stability, we obtain a system of four inequations that are necessary and sufficient for the stable coexistence of plants, pollinators, and herbivores within our framework:

$$\left\{ \begin{array}{l} c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2 > 0 \\ (c_p c_h + e_h a_{ph}^2)(r_m + e_m a_{pm} P_{PH}^*) \geq 0 \\ (c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*) \geq 0 \\ (c_p P^* + c_m M^* + c_h H^*)(P^* M^*(c_p c_m - e_m a_{pm}^2) + P^* H^*(c_p c_h + e_h a_{ph}^2) \\ + M^* H^* c_m c_h) - P^* M^* H^*(c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) > 0 \end{array} \right.$$

$$\Leftrightarrow \left\{ \begin{array}{l} c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2 > 0 \\ r_m + e_m a_{pm} P_{PH}^* \geq 0 \\ (c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*) \geq 0 \\ (c_p P^* + c_m M^* + c_h H^*)(P^* M^*(c_p c_m - e_m a_{pm}^2) + P^* H^*(c_p c_h + e_h a_{ph}^2) \\ + M^* H^* c_m c_h) - P^* M^* H^*(c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) > 0 \end{array} \right.$$

These relationships correspond respectively to the relationships (1), (2), (3), and (4) in the main text (table 2). In what follows, we present for each relationship how its biological interpretation, as well as the influence of each type of interaction, are derived (3rd and 4th columns of table 2).

1. Relationship (1)

$r_m + e_m a_{pm} P_{PH}^* \geq 0$ $P_{PH}^* \stackrel{\text{def}}{=} \frac{c_h r_p - a_{ph} r_h}{c_p c_h + e_h a_{ph}^2}$	(1)
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Assuming that the plant-herbivore equilibrium is feasible, we have:

$$\left. \frac{1}{M} \frac{dM}{dt} \right)_{M \rightarrow 0^+} = r_m + e_m a_{pm} P_{PH}^*$$

Relationship (1) consequently means that the per capita growth rate of pollinators population, when low in density, is positive within the plant-herbivore community at ecological equilibrium. Thus, pollinators are able to invade the plant-herbivore community. This biological interpretation is valid as long as the plant-herbivore equilibrium is feasible.

Moreover, given that P_{PH}^* is always positive, relationship (1) is equivalent to relationship (1'):

$\frac{-r_m}{e_m P_{PH}^*} \leq a_{pm}$	(1')
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We can study the variations of P_{PH}^ with a_{ph} (using the nondimensionalized system for simplicity):

$$(1 + \lambda_h \alpha_{ph}^2)^2 \frac{\partial P_{PH}^*}{\partial \alpha_{ph}} = \rho_h \lambda_h \alpha_{ph}^2 - 2\lambda_h \alpha_{ph} - \rho_h$$

$$\Leftrightarrow (1 + \lambda_h \alpha_{ph}^2) \frac{\partial P_{PH}^*}{\partial \alpha_{ph}} = -\lambda_h \alpha_{ph} P_{PH}^* - H_{PH}^*$$

The latter first indicates that as long as the plant-herbivore equilibrium is feasible (i.e. $\alpha_{ph} \geq \frac{-c_p r_h}{e_h r_p}$), P_{PH}^* decreases with herbivory. Moreover, the polynomial on the right side of the first-

line equality (i.e. $\rho_h \lambda_h \alpha_{ph}^2 - 2\lambda_h \alpha_{ph} - \rho_h$) has two roots ($root1_{\pm} = \frac{1 \pm \sqrt{1 + \rho_h^2 / \lambda_h}}{\rho_h}$), only one ($root1_-$) being positive. When at this root, the polynomial switches from positive to negative indicating that P_{PH}^* is maximal. Relationship (1) can therefore never be satisfied if pollination is below a critical value:

$$\alpha_{pm} < \alpha_{pm}^{critical} \stackrel{\text{def}}{=} \frac{2\lambda_h \rho_m}{\lambda_m \rho_h^2} \left(1 - \sqrt{1 + \rho_h^2 / \lambda_h} \right)$$

The behavior of relationship (1) is now fully determined. **Table S3** recapitulates the analysis in the dimensionalized language. It notably shows that relationship (1) behaves according to biological intuition (i.e. P_{PH}^* decreases with herbivory) over the domain of feasibility of the plant-herbivore equilibrium (**green, table S3**).

Variation of P_{PH}^* with herbivory (α_{ph})	α_{ph}	0	$\frac{c_h r_p}{r_h} \left[1 - \sqrt{1 + \frac{c_p r_h^2}{e_h c_h r_p^2}} \right]$	$\frac{-c_p r_h}{e_h r_p}$	$+\infty$
	P_{PH}^*		$\frac{r_p}{c_p}$	$\max(P_{PH}^*)$	0

Table S3: Analytical study ore relationship (1). The biological interpretation of relationship (1) is valid over the domain of feasibility of the plant-herbivore equilibrium (green).

2. Relationship (2)

$(c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*) \geq 0$ $P_{PM}^* \stackrel{\text{def}}{=} \frac{c_m r_p + a_{ph} r_m}{c_p c_m - e_m a_{pm}^2}$	(2)
--	-----

Let us consider three quantities of interest here $a_{pm}^M \stackrel{\text{def}}{=} \frac{-r_m c_p}{e_m r_p}$; $a_{pm}^P \stackrel{\text{def}}{=} \frac{-c_m r_p}{r_m}$; $a_{pm}^\infty \stackrel{\text{def}}{=} \sqrt{\frac{c_p c_m}{e_m}}$:

- a_{pm}^M is the pollination level above which pollinators are able to invade the plant community when low in density; it is also the value of pollination at which the numerator of M_{PM}^* switches sign, from negative to positive
- a_{pm}^P is the value of pollination at which the numerator of P_{PM}^* switches sign, from positive to negative
- a_{pm}^∞ is the pollination level above which unbounded population growth becomes possible; it is also the value of pollination at which the denominator of P_{PM}^* and M_{PM}^* switches sign, from positive to negative

There are only two ways of ordering these three pollination levels, which are illustrated in **Fig. S1 and S2**. We invite the reader to refer to these figures in order to facilitate the comprehension of the subsequent mathematical analysis. Also note that an important distinction between the two cases is the occurrence of unbounded growth depending on initial densities in case (b), a feature enabling the occurrence of alternative stable states at the three-species community scale.

- Case (1): $a_{pm}^M < a_{pm}^\infty < a_{pm}^P$ (this case corresponds to the parameter set of Fig. 2&3)

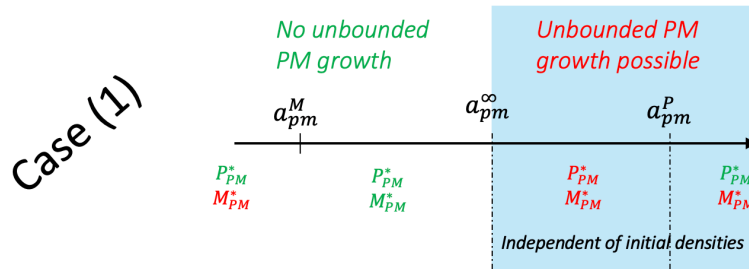


Fig. S1: Schematic representation of the parameter instance of case (1). Densities in red are negative; densities in green are positive.

- Case (2): $a_{pm}^P < a_{pm}^\infty < a_{pm}^M$ (this case corresponds to the parameter set of Fig. S3)

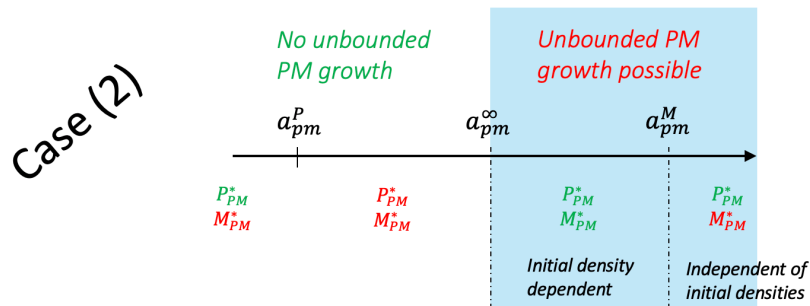


Fig. S2: Schematic representation of the parameter instance of case (2). Densities in red are negative; densities in green are positive.

P_{PM}^* is negative for pollination between $\min(a_{pm}^P, a_{pm}^\infty)$ and $\max(a_{pm}^P, a_{pm}^\infty)$. Therefore, relationship (2) is always satisfied in case (1) for pollination in the interval $[a_{pm}^\infty, a_{pm}^P]$; while it is never satisfied in case (2) for pollination in the interval $[a_{pm}^P, a_{pm}^\infty]$. When pollination is not between $\min(a_{pm}^P, a_{pm}^\infty)$ and $\max(a_{pm}^P, a_{pm}^\infty)$, because P_{PM}^* is positive, relationship (2) can take two forms according to the sign of $c_p c_m - e_m a_{pm}^2$. As in the main document, these two forms are labeled (2'a) and (2'b) (see the last row of **Table S4**).

$\begin{cases} a_{pm} \leq a_{pm}^\infty \\ \frac{-r_h}{e_h P_{PM}^*} \leq a_{ph} \end{cases}$	(2'a)
$\begin{cases} a_{pm} \geq a_{pm}^\infty \\ a_{ph} \leq \frac{-r_h}{e_h P_{PM}^*} \end{cases}$	(2'b)

Given that $\frac{-r_h}{e_h P_{PM}^*} \leq a_{ph} \Leftrightarrow (r_h + e_h a_{ph} P_{PM}^*) \stackrel{\text{def}}{=} \frac{1}{H} \frac{dH}{dt} \Big|_{H \rightarrow 0^+} \geq 0$, relationship (2'a) corresponds biologically to the herbivores being able to invade the plant-pollinator community at ecological equilibrium, when low in density and unbounded PM growth is not possible. Note that this interpretation (**Table 2, (2a)**) requires the plant-pollinator equilibrium to be feasible. Relationship (2'b) sets an upper limit to the intensity of herbivory when unbounded PM growth is possible. We interpret such a limit as follows: herbivores cannot consume the plant resource too strongly, otherwise, the plant resource density becomes too low for pollinators to persist (**Table 2, (2b)**).

Let us now study the variations of P_{PM}^* with pollination (a_{pm}). Just before that, we show that the coexistence equilibrium is not possible below the $\min(a_{pm}^P, a_{pm}^M)$ so that we can exclude the corresponding interval from our study of variations.

Proof:

When $a_{pm} \leq \min(a_{pm}^P, a_{pm}^M)$, we necessarily have that $a_{pm} \leq a_{pm}^\infty$. Consequently, the plant equilibrium is globally stable within the PM subsystem (because unbounded growth is not possible). Thus, all trajectories of the PM dynamical subsystem (population dynamics, equations (a)(b) with $a_{ph} = 0$) starting with strictly positive initial conditions converge toward the plant equilibrium.

Now assume, by the absurd, that the plant-pollinator-herbivore coexistence equilibrium is strictly feasible. Because unbounded growth is not possible, the coexistence equilibrium is globally stable: all trajectories of the dynamical system (population dynamics, equations (a)(b)(c)) starting with strictly positive initial conditions converge toward the coexistence equilibrium.

Consider such a trajectory Ψ_3 , its projection on the (P, M) space (\mathbb{R}^{+2}) (Ψ_2) and the trajectory of the PM subsystem (Ψ), that has same initial conditions as the projection. Ψ_2 is a

sub-solution of the PM dynamical system, so that we have that Ψ is always above Ψ_2 (Hulin 2020). By letting time goes toward infinity (which we can do because both Ψ and Ψ_2 converges toward finite values), we deduce that $M^* \stackrel{\text{def}}{=} \lim_{t \rightarrow +\infty} \Psi_2^{(2)} \leq \lim_{t \rightarrow +\infty} \Psi^{(2)} = 0$, which is in contradiction with the coexistence equilibrium being strictly feasible. ■

Study of the variation of P_{PM}^ with pollination a_{pm} :

By nondimensionalizing the system, we study the variations of $P_{PM}^* \stackrel{\text{def}}{=} \frac{1 + \rho_m \alpha_{pm}}{1 - \lambda_m \alpha_{pm}^2}$ with pollination (α_{pm}). We remind the reader that $P_{PM}^*(\alpha_{pm})$ is, first of all, a mathematical function. It biologically corresponds to the plant population at plant-pollinator equilibrium only with such an equilibrium is feasible ($P_{PM}^* > 0$ & $M_{PM}^* > 0$) and stable.

$$\begin{aligned} (1 - \lambda_m \alpha_{pm}^2)^2 \frac{\partial P_{PM}^*}{\partial \alpha_{pm}} &= \rho_m \lambda_m \alpha_{pm}^2 + 2\lambda_m \alpha_{pm} + \rho_m \\ \Leftrightarrow (1 - \lambda_m \alpha_{pm}^2) \frac{\partial P_{PM}^*}{\partial \alpha_{pm}} &= \lambda_m \alpha_{pm} P_{PM}^* + M_{PM}^* \end{aligned}$$

The last equation indicates that when the PM equilibrium is feasible, the plant density at this equilibrium increase with pollination below a_{pm}^∞ and decreases above a_{pm}^∞ . In the latter case, P_{PM}^* has to be regarded as a mathematical function, with no biological significance. Indeed, above a_{pm}^∞ , the model indicates that the plant biomass density is infinitely large (“orgy”, unbounded growth). In other words, biological intuition does not apply since P_{PM}^* does not correspond to the model output for plant density (but is rather a technical intermediate).

To go further, we study the polynomial that appears on the right side of the first equation (i.e. $\rho_m \lambda_m \alpha_{pm}^2 + 2\lambda_m \alpha_{pm} + \rho_m$).

- In case (2) (which implies $\rho_m^2 > \lambda_m$), this polynomial has no real roots so that it is always negative, which implies that the mathematical function (P_{PM}^*) decreases with pollination.
- In case (1) ($\rho_m^2 < \lambda_m$), this polynomial has two positive roots ($root2_\pm = \frac{(1 \pm \sqrt{(1 - \rho_m^2/\lambda_m)})}{-\rho_m}$). Plant density (P_{PM}^*) increases with pollination when the pollination intensity is between these two roots (note that $root2_+ > root2_-$). We deduce that the interval of feasibility of the plant-pollinator equilibrium in this case (2) (i.e. $[a_{pm}^M, a_{pm}^\infty]$) is included in the interval $[c_m root2_-, c_m root2_+]$ because P_{PM}^* should increase over it. Moreover, it is straightforward that $root2_+ > a_{pm}^P$ ($\stackrel{\text{def}}{=} c_m(-1/\rho_m)$).

The behavior of relationship (2) is now fully determined. **Table S4** recapitulates the analysis in the dimensionalized language.

Analytical study of relationship (2)							
Case (1)	Variation of P_{PM}^* with pollination (a_{pm})	a_{pm}	$a_{pm}^M = \frac{-r_m c_p}{e_m r_p}$	$a_{pm}^\infty = \frac{c_p c_m}{\sqrt{e_m}}$	$a_{pm}^P = \frac{-c_m r_p}{r_m}$	$root2_+ = \frac{-c_m r_p}{r_m} \left[1 + \sqrt{1 - \frac{c_p r_m^2}{e_m c_m r_p^2}} \right]$	$+\infty$
		P_{PM}^*	$\frac{r_p}{c_p}$	$+\infty$	$-\infty$	0	0
	Form of relationship (2)		(2'a)	Necessarily Satisfied		(2'b)	
Case (2)	Variation of P_{PM}^* with pollination (a_{pm})	a_{pm}	$a_{pm}^P = \frac{-c_m r_p}{r_m}$	$a_{pm}^\infty = \frac{c_p c_m}{\sqrt{e_m}}$	$a_{pm}^M = \frac{-r_m c_p}{e_m r_p}$	$+\infty$	
		P_{PM}^*	0	$-\infty$	$+\infty$	0	0
	Form of relationship (2)		Necessarily Non-Satisfied		(2'b)		

Table S4: Analytical study ore relationship (2). The domain of feasibility of the plant-pollinator equilibrium is indicated in green.

In the main document, a situation corresponding to case (1) is presented in **Fig. 3**. Here (**Fig. S2**), we present a situation corresponding to case (2).

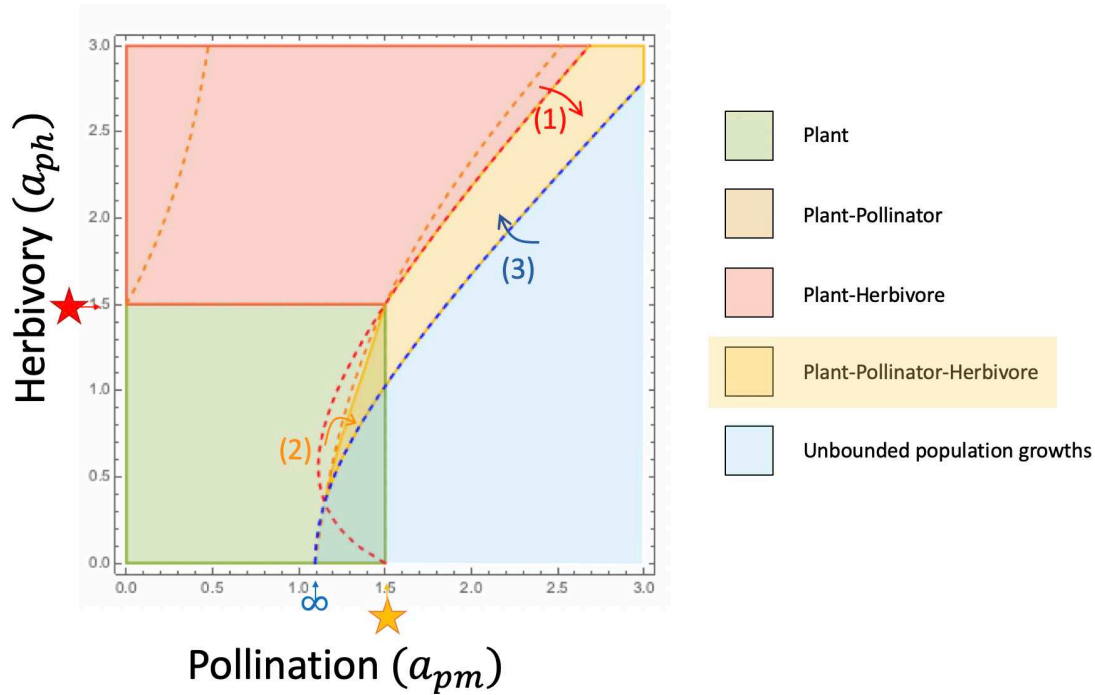


Fig. S3: Community composition according to both pollination and herbivory. In blue, no equilibrium is stable so that populations grow unboundedly. Arrows (1), (2), and (3) indicate the transitions enabling to satisfy relationships (1), (2), and (3) (**Table 2**), indicated by the dashed red, orange, and blue curve, respectively. These three relationships are not sufficient to achieve stable coexistence given the parameter set, indicating that relationship (4) is constraining here. More precisely, relationship (4) is the one that constrains the upper boundary of the stable coexistence area (yellow) between a_{pm}^{∞} (infinity symbol) and a_{pm}^M (orange star). Moreover, for such pollination levels, relationship (2) takes the form (2'b). A red star indicates the level of herbivory enabling herbivores to invade the plant community. Note that stable coexistence (yellow area) requires the two interactions to be of similar magnitude.

Fig. S3 permits to illustrate two important points:

- In case (2), the occurrence of alternative stable states is possible. Indeed, both the plant equilibrium and the coexistence equilibrium can be feasible and stable, when pollination is between a_{pm}^{∞} (symbol ∞ , **Fig. S2**) and a_{pm}^M (orange star, **Fig. S2**). The reason is that in the PM subcommunity, for such pollination levels, the plant equilibrium is locally stable but, if populations are initially large enough, they grow unboundedly. Given that the presence of herbivores can control such an unstable behavior when relationship (3) is satisfied, this leads to alternative stable states. Herbivory has nevertheless to be low enough so that the exploitation of the plant resource by herbivores does not bring the pollinator density in the catchment area of the plant equilibrium within the PM subsystem. The latter constraint corresponds to relationship (2), which sets an upper limit to the intensity of herbivory (relationship (2'b)).
- In **Fig. S3**, the upper limit of the stable coexistence area (yellow) when the strength of pollination is between a_{pm}^{∞} (symbol ∞) and a_{pm}^M (orange star) is set by relationship (4).

3. Relationship (3)

The total feedback at a given level k is a summation of the strengths of all the feedback loops of length k and that of all the combinations of disjunct (non-overlapping) feedback loops of shorter length containing k elements (Neutel & Thorne 2014). Relationship (3) corresponds to the total feedback at level 3 being negative. Here, two of these loops are stabilizing because they are negative: the self-limitation competition loop $(-c_h c_m c_p)$ and the trophic loop $(-c_m e_h a_{ph}^2)$ while the mutualistic loop is positive and hence destabilizing $(c_h e_m a_{pm}^2)$.

3. Relationship (4)

The quantity $F_1 \stackrel{\text{def}}{=} -(c_p P^* + c_m M^* + c_h H^*)$ corresponds to the feedback at level 1. The quantity $F_2 \stackrel{\text{def}}{=} -(P^* M^* (c_p c_m - e_m a_{pm}^2) + P^* H^* (c_p c_h + e_h a_{ph}^2) + M^* H^* c_m c_h)$ corresponds to the feedback at level 2. The quantity $F_3 \stackrel{\text{def}}{=} -P^* M^* H^* (c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2)$ corresponds to the feedback at level 3. Relationship (4) can be written: $F_1 F_2 + F_3 > 0$. Given that $F_1 < 0$ and assuming relationship (3) (i.e. $F_3 < 0$), relationship (4) implies that F_2 is negative. Relationships (3) and (4) together imply that the feedback at each level is negative, which is a necessary condition for stability (Levins 1974). Therefore, relationship (4) can be interpreted as the fact that the negative feedback at level 3 (long time lag) is weaker than the product of negative feedback at lower levels (1 & 2, smaller time lag) (Levins 1974).

References

Hulin, D. (2020). *Equations différentielles ordinaires : Etudes qualitatives (Cours)*.pp 56-63
Available at www.imo.universite-paris-saclay.fr/~hulin/poly-cours-EDO.pdf

Levins, R. (1974). Discussion paper: the qualitative analysis of partially specified systems.
Ann. N. Y. Acad. Sci., 231, 123–138.

Neutel, A.-M. & Thorne, M.A.S. (2014). Interaction strengths in balanced carbon cycles and the absence of a relation between ecosystem complexity and stability. *Ecol. Lett.*, 17, 651–661.

Appendix D: The effect of the other parameters on stable coexistence

I. Animal intrinsic growth rates

1. Effect on stable coexistence

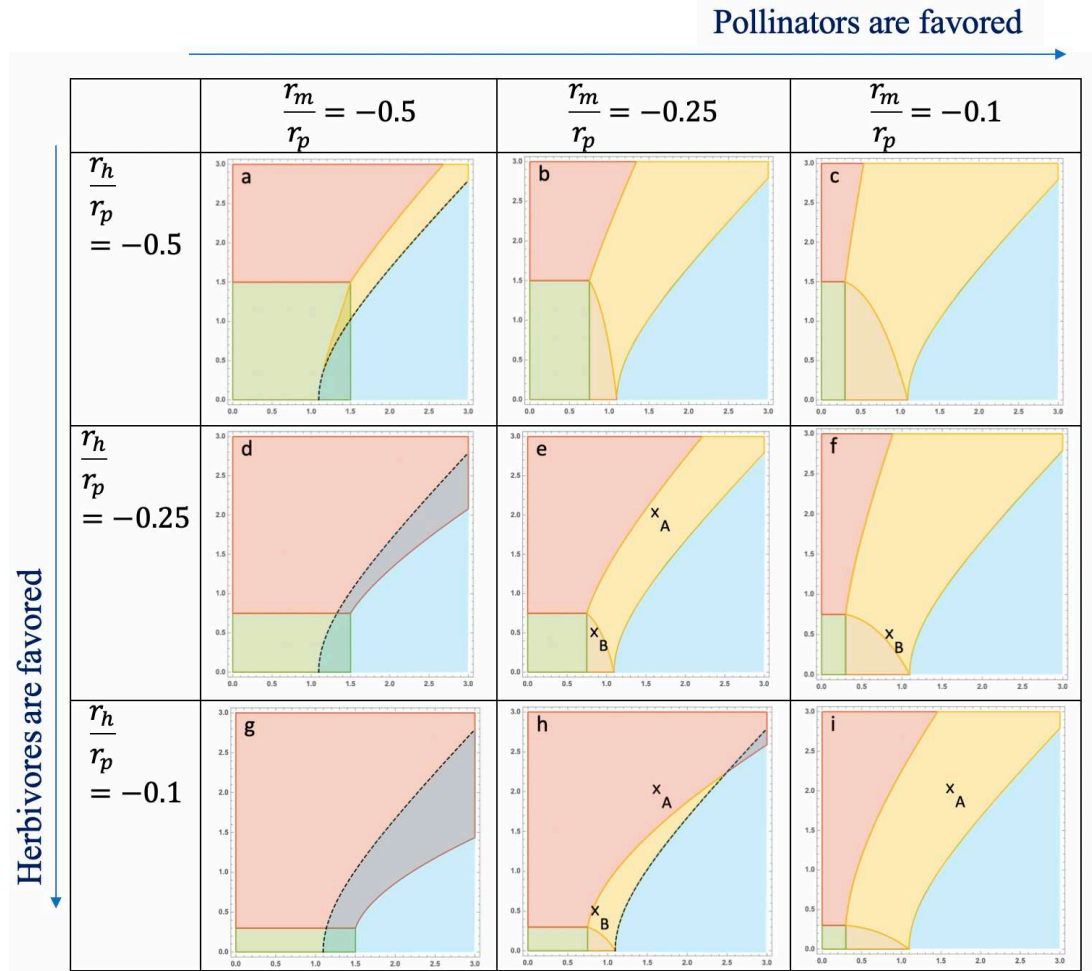


Fig. S4: Effect of animal intrinsic growth rates on stable coexistence. X-axis: Pollination (a_{pm}); Y-axis: Herbivory (a_{ph}). Colour legend: Green: Plant, Brown: Plant-Pollinator, Red: Plant-Herbivore, Yellow: stable coexistence, Light blue: unbounded population densities. In a-d-g-h, alternative (not both stable) states are observed (green and blue or red and blue overlap): if plant and pollinator densities are initially above a (herbivore-density-dependent) threshold, populations grow unboundedly; otherwise, pollinators are excluded. Note that **Fig. S4.a** corresponds to Fig. S3, characterized by the occurrence of alternative stable states (see Appendix C.II.2 for details). Parameters: $r_p = 10$, $e_m = e_h = 0.2$, $c_p = 0.6$, $c_m = c_h = 0.4$

Fig. 4A of the main document corresponds to Fig. S4 e-f-h-i. In addition to the analysis presented in the main text, we would like to highlight two points.

Firstly, stable coexistence is not possible if the pollinator intrinsic growth rate is too low in comparison with the herbivore one (Fig. S4 d&g). It is also much endangered if the intrinsic growth rates are too low, in spite of being similar (Fig. S4 a vs. i).

Secondly, for some parameter instances, unbounded population growth happens if the initial plant and pollinator densities are above a given threshold. This threshold gets higher as the initial herbivore density increases. In other words, depending on the initial control of the orgy of mutual benefaction by competition and herbivory, the community will display (or not) unbounded population dynamics. If the control is initially strong enough, pollinators are excluded. If herbivores are able to survive in the absence of pollinators, the final community consists of plants and herbivores at ecological equilibrium. If it is not the case, herbivores go extinct and only plants remain in the community.

2. Analytical grounding

Animal intrinsic growth rates affect the feasibility of coexistence as indicated by relationships (1) and (2). We determine here how these relationships vary with the growth rates r_m and r_h .

$r_m + e_m a_{pm} P_{PH}^* \geq 0$	(1)
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$$\frac{\partial(r_m + e_m a_{pm} P_{PH}^*)}{\partial r_m} = 1 > 0$$

$$\frac{\partial(r_m + e_m a_{pm} P_{PH}^*)}{\partial r_h} = e_m a_{pm} \frac{\partial P_{PH}^*}{\partial r_h} = \frac{-e_m a_{pm} a_{ph}}{c_p c_h + e_h a_{ph}^2} \leq 0$$

An increase in pollinator (resp. herbivore) growth rate facilitates (resp. impedes) the satisfaction of relationship (1).

$(c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*) \geq 0$	(2)
--	-----

$$\frac{\partial[(c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*)]}{\partial r_m} = (c_p c_m - e_m a_{pm}^2) e_h a_{ph} \frac{\partial P_{PM}^*}{\partial r_m} = e_h a_{ph} a_{pm} \geq 0$$

$$\frac{\partial[(c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*)]}{\partial r_h} = (c_p c_m - e_m a_{pm}^2)$$

An increase in pollinator growth rate makes it easier to satisfy relationship (2). An increase in herbivore growth rate makes it easier to satisfy relationship (2) when unbounded PM growth is not possible ($c_p c_m - e_m a_{pm}^2 > 0$), while it makes it harder when unbounded PM growth is possible.

II. Animal intraspecific competition rates

1. Effect on stable coexistence

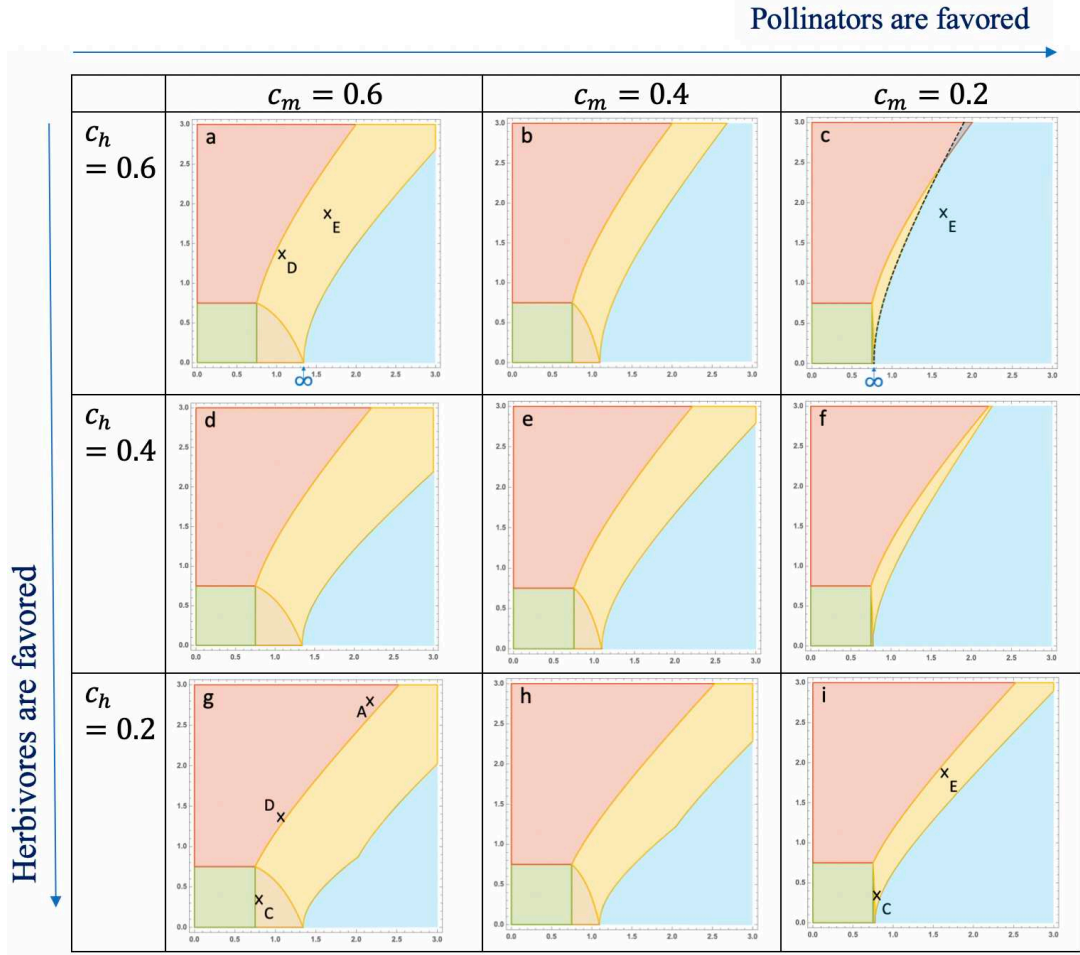


Fig. S5: Effect of animal intraspecific competition on stable coexistence. X-axis: Pollination (a_{pm}); Y-axis: Herbivory (a_{ph}) Colour legend: Green: Plant, Brown: Plant-Pollinator, Red: Plant-Herbivore, Yellow: stable coexistence, Light blue: unbounded population densities. In c, alternative states are observed (red and blue overlap): if plant and pollinator densities are initially above a (herbivore-density-dependent) threshold, populations grow unboundedly; otherwise, pollinators are excluded. In g & h, as pollination increases, the yellow-white border is first set by relationship (3) then (4), which explains the unusual shape. Parameters: $r_p = 10, r_m = r_h = -2.5, e_m = e_h = 0.2, c_p = 0.6$.

Fig. 4B of the main document corresponds to Fig. S5 a-c-g-i. In addition to the analysis presented in the main text, we would like to highlight one point. Feasibility mainly relies on the ability of a focal animal, at low population size and hence experiencing neglectable intraspecific competition, to invade the other animal-plant community (**Table 2**). As a result, the herbivore competition rate affects the pollinator ability to invade rather than its own (relationship (1)). Likewise, the pollinator competition rate affects the herbivore ability to invade rather than its own (relationship (2)).

2. Analytical grounding

Animal intraspecific competitions affect both the feasibility and stability of coexistence (relationships (1) (2) (3) (4)). We determine here how relationships (1) (2) (3) vary with competition rates c_m and c_h .

$$\frac{\partial(r_m + e_m a_{pm} P_{PH}^*)}{\partial c_m} = 0$$

$$\begin{aligned} \frac{\partial(r_m + e_m a_{pm} P_{PH}^*)}{\partial c_h} &= e_m a_{pm} \frac{\partial P_{PH}^*}{\partial c_h} = e_m a_{pm} \frac{r_p(c_p c_h + e_h a_{ph}^2) - c_p(c_h r_p - a_{ph} r_h)}{(c_p c_h + e_h a_{ph}^2)^2} \\ &= e_m a_{pm} \frac{a_{ph}(e_h a_{ph} r_p + c_p r_h)}{(c_p c_h + e_h a_{ph}^2)^2} = \frac{e_m a_{pm} a_{ph} H_{PH}^*}{c_p c_h + e_h a_{ph}^2} \end{aligned}$$

Relationship (1) is not affected by competition among pollinators. When the plant-herbivore equilibrium is feasible, biological intuition applies: an increase in competition among herbivores makes it easier for pollinators to invade the plant-herbivore community due to an increase in plant density. When it is not, relationship (1) is impeded by an increase in herbivore competition rate.

$$\frac{\partial[(c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*)]}{\partial c_m} = (c_p c_m - e_m a_{pm}^2) e_h a_{ph} \frac{\partial P_{PM}^*}{\partial c_h} = -e_h a_{pm} a_{ph} M_{PM}^*$$

$$\frac{\partial[(c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*)]}{\partial c_h} = 0$$

Relationship (2) is not affected by competition among herbivores. When the plant-pollinator equilibrium is feasible, biological intuition applies: an increase in competition among pollinators makes it harder for herbivores to invade the plant-pollinator community due to a decrease in plant density. When it is not, relationship (2) is favored by an increase in pollinator competition rate.

$c_h c_m c_p + c_m e_h a_{ph}^2 - c_h e_m a_{pm}^2 > 0$	(3)
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$$\frac{\partial(c_h c_m c_p + c_m e_h a_{ph}^2 - c_h e_m a_{pm}^2)}{\partial c_m} = c_p c_h + e_h a_{ph}^2 > 0$$

$$\frac{\partial(c_h c_m c_p + c_m e_h a_{ph}^2 - c_h e_m a_{pm}^2)}{\partial c_h} = c_p c_m - e_m a_{pm}^2 < 0$$

The last inequality ensuing from the fact that it is meaningful to consider stability only when potential instability is possible (i.e. when $c_p c_m - e_m a_{pm}^2 < 0$), we conclude that an increase in pollinator (resp. herbivore) intraspecific competition favors (resp. disfavors) stability.

Finally, we can compare the effects on feasibility and on stability by approximating their ratio when interactions are very strong (i.e. at infinity). We find that stability effects overcome feasibility effects.

$$\frac{\text{Feasibility effects}}{\text{Stability effects}} = \frac{e_m a_{pm} a_{ph} (e_h a_{ph} r_p + c_p r_h)}{(c_p c_h + e_h a_{ph}^2)^2 (c_p c_m - e_m a_{pm}^2)} \sim \frac{r_p e_m e_h a_{pm} a_{ph}^2}{-e_m e_h^2 a_{pm}^2 a_{ph}^4} \sim -\frac{r_p}{e_h a_{pm} a_{ph}^2} \xrightarrow[a_{ph} \rightarrow +\infty]{a_{pm} \rightarrow +\infty} 0$$

III. Animal conversion efficiencies

1. Effect on stable coexistence

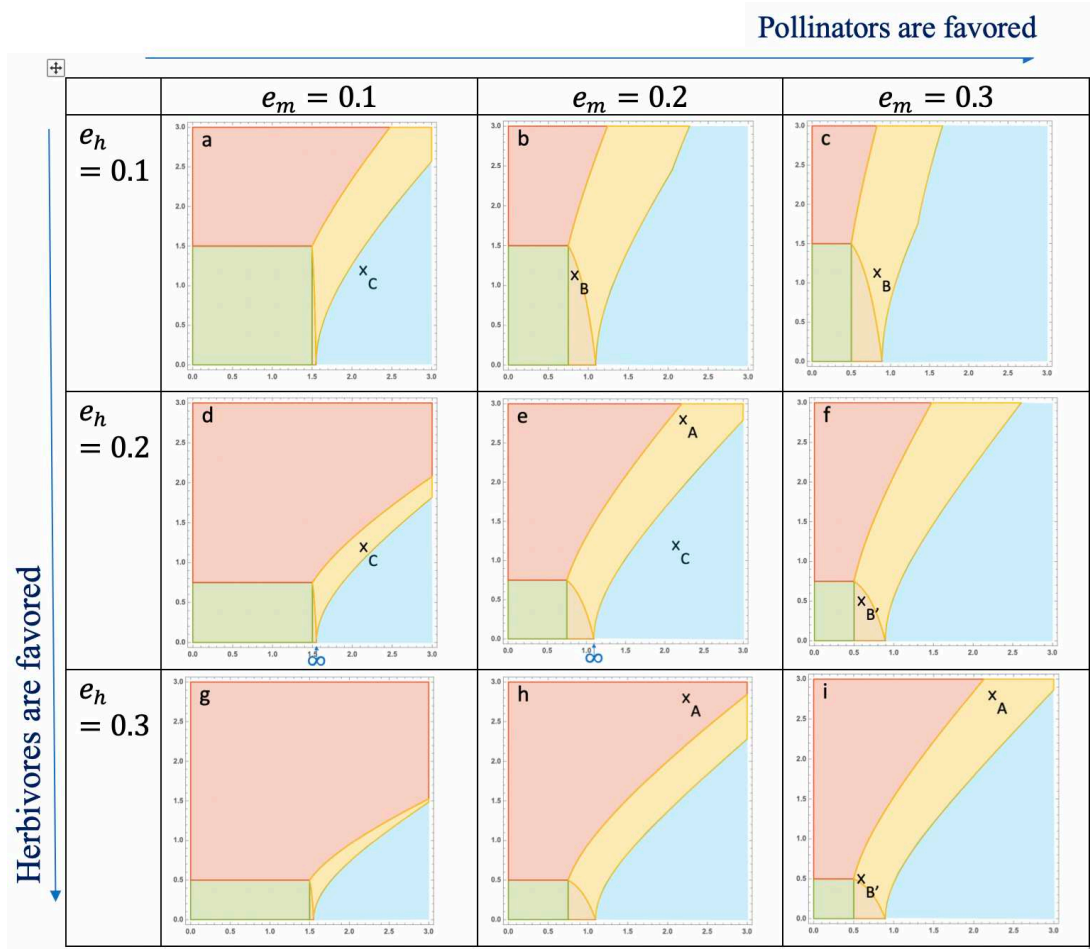


Fig. S6: Effect of conversion efficiencies on stable coexistence. X-axis: Pollination (a_{pm}); Y-axis: Herbivory (a_{ph}) Colour legend: Green: Plant, Brown: Plant-Pollinator, Red: Plant-Herbivore, Yellow: stable coexistence, Light blue: unbounded population densities. In b & c, as pollination increases, the yellow-white border is first set by relationship (3) then (4), which explains the unusual shape. Parameters: $r_p = 10, r_m = r_h = -2.5, c_p = 0.6, c_m = c_h = 0.4$.

Overall, the range of pollination and herbivory intensities allowing stable coexistence gets wider in the upper right of **Fig. S6**, when pollinators exploit the plant resource more efficiently than herbivores. This pattern suggests that the effect of conversion efficiencies on feasibility (relationships (1), (2)) is stronger than their effect on stability (relationship (3)). As pollinators get more efficient at exploiting the plant resource, it becomes easier for them to invade the plant-herbivore community (**Fig. S6h vs S6i, point A**). It also makes it easier for herbivores to invade the plant-pollinator community as a result of an increased plant density (**Fig. S6b vs S6c, point B**). The positive feedback loop driven by pollination, however, gets stronger, favoring the orgy of mutual benefaction (**Fig. S6d vs S6e, point C and infinity symbol**). The effect of herbivores getting more efficient at exploiting their plant resource is contrasted on feasibility. On the one hand, it is easier for them to invade the plant-pollinator community (**Fig. S6f vs S6i, point B'**). On the other hand, an increased herbivore density leads to less plant biomass in the plant-herbivore community, which in turn makes it more difficult for pollinators to invade (**Fig. S6e vs S6h, point A**). Finally, an increase in the herbivore conversion efficiency strengthens the related negative feedback loop, favoring stable dynamics (**Fig. S6a vs S6d, point C**).

2. Analytical grounding

Animal conversion efficiencies affect both the feasibility and stability of coexistence (relationships (1) (2) (3) (4)). We determine here how relationships (1) (2) (3) vary with conversion efficiencies e_m and e_h .

$$\frac{\partial(r_m + e_m a_{pm} P_{PH}^*)}{\partial e_m} = a_{pm} P_{PH}^* \geq 0$$

An increase in their conversion efficiency makes pollinators able to invade the plant-herbivore community more easily.

$$\begin{aligned} \frac{\partial(r_m + e_m a_{pm} P_{PH}^*)}{\partial e_h} &= e_m a_{pm} \frac{\partial P_{PH}^*}{\partial e_h} = \frac{-e_m a_{pm} a_{ph}^2 P_{PH}^*}{c_p c_h + e_h a_{ph}^2} \leq 0 \\ \frac{\partial H_{PH}^*}{\partial e_h} &= \frac{a_{ph} r_p (c_p c_h + e_h a_{ph}^2) - (e_h a_{ph} r_p + c_p r_h) a_{ph}^2}{(c_p c_h + e_h a_{ph}^2)^2} = \frac{a_{ph} c_p (c_h r_p - a_{ph} r_h)}{(c_p c_h + e_h a_{ph}^2)^2} \\ &= \frac{a_{ph} c_p P_{PH}^*}{c_p c_h + e_h a_{ph}^2} \geq 0 \end{aligned}$$

At the plant-herbivore equilibrium, the plant population gets smaller as a result of an increased herbivore density when herbivores are more efficient at exploiting their resource. It thus becomes harder for pollinators to invade the plant-herbivore community.

$$\frac{\partial[(c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*)]}{\partial e_m} = e_h a_{ph} \frac{\partial P_{PM}^*}{\partial e_m} = e_h a_{ph} a_{pm}^2 P_{PM}^* \geq 0$$

$$\frac{\partial M_{PM}^*}{\partial e_m} = \frac{c_p a_{pm} P_{PM}^*}{c_p c_m - e_m a_{pm}^2}$$

Relationship (2) is favored by an increase in the pollinator conversion efficiency (when $P_{PM}^* \leq 0$, relationship (2) is either always true or false (**Table S5**) so that we do not consider such cases here). This ensues from an increase in both plant and pollinator densities when the pollination intensity is too low to trigger unbounded growth (relationship (2'a)). It then becomes easier for herbivores to invade the sub-community. When pollination is strong enough for an orgy to occur in the plant-pollinator sub-community (relationship (2'b)), the relationship satisfaction is also favored by increasing e_m , although not mediated by the same positive effect on pollinator density.

$$\frac{\partial[(c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*)]}{\partial e_h} = (c_p c_m - e_m a_{pm}^2) a_{ph} P_{PM}^*$$

Relationship (2) is favored (resp. disfavored) by an increase in the herbivore conversion efficiency when unbounded PM growth is not possible (resp. possible) (see relationship (2'a) vs. (2'b)).

$$\frac{\partial(c_h c_m c_p + c_m e_h a_{ph}^2 - c_h e_m a_{pm}^2)}{\partial e_m} = -c_h a_{pm}^2 \leq 0$$

$$\frac{\partial(c_h c_m c_p + c_m e_h a_{ph}^2 - c_h e_m a_{pm}^2)}{\partial e_h} = c_m a_{ph}^2 \geq 0$$

Stability is favored when either the herbivore conversion efficiency increases or the pollinator conversion efficiency decreases.

III.

Chaper II

Attracting pollinators vs escaping herbivores: eco-evolutionary dynamics of plants confronted with an ecological trade-off

This chapter still needs a bit of rewriting, in particular to reduce the word count. Once it is done, we are going to submit it to the journal *Ecology Letters*.

Attracting pollinators vs escaping herbivores: eco-evolutionary dynamics of plants confronted with an ecological trade-off

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Abstract

A large number of plant traits, involved in both interactions, are subject to an ecological trade-off between attracting pollinators and escaping herbivores. Accumulating empirical evidence supports a non-linear interactive effect of plant-animal interactions on their evolution. Here, we investigate the eco-evolutionary dynamics of a plant-pollinator-herbivore community in which plant-animal interactions depend on the trait-matching between plant and animal phenotypes. We determine the type of selection arising from the interplay of pollination and herbivory, as well as the consequences in terms of interactions pattern and multispecies coexistence. By combining analytical outputs from adaptive dynamics with numerical Monte-Carlo experiments, we aim at providing a robust analysis of the eco-evolutionary dynamics of such a community. Our results show that these dynamics qualitatively differ depending on the relative strength of pollination vs. herbivory. Stabilizing selection fostering the maintenance of coexistence is favored by strong pollination, runaway selection threatening the maintenance of coexistence is favored by strong herbivory. Our results also demonstrate that the strength of the ecological trade-off – attracting pollinators vs. escaping herbivores – is a key determinant of eco-evolutionary dynamics. We notably show that disruptive selection is possible when the trade-off is strong. While the interplay of pollination and herbivory has been shown to support the maintenance of plant polymorphism in several cases, our results suggest that it might also have fueled the diversification process itself.

Keywords

Disruptive selection, pollination, herbivory, plant evolution, interaction pattern, Stabilizing selection, Runaway selection, multispecies coexistence

I. Introduction

Flowering plants (i.e. angiosperms), which need to be pollinated in order to reproduce, are the most diverse and successful plant clade in terrestrial ecosystems, representing almost 90% of the species described (Hernández-Hernández & Wiens 2020). Most of them rely on animals for pollination (Ollerton *et al.* 2011). Because animal pollination can favor reproductive isolation, it has early been proposed as an important diversity driver among angiosperms (Grant 1949). Alternatively, plant-herbivore interactions have also been identified as potentially fostering diversification due to the ensuing evolutionary arms race between interacting antagonists (Ehrlich & Raven 1964). These two non-mutually exclusive hypotheses are supported by several phylogenetic investigations, which notably emphasize the role of plant-pollinator coevolution in explaining the higher diversification rates within angiosperms (Hodges & Arnold 1995; Sargent 2004; Hernández-Hernández & Wiens 2020), and also demonstrate the role of plant-herbivore coevolution in spurring plant diversification as a result of defensive innovations (Farrell *et al.* 1991; Becerra *et al.* 2009). But plant phylogenies also reveal that plant-pollinator and plant-herbivore coevolution are very often inextricably intertwined (e.g. Armbruster 1997), which advocates for an integrative framework accounting for both interaction types (Fontaine *et al.* 2011).

A large number of plant traits are notably under conflicting selection from the interplay between pollination and herbivory (Strauss & Irwin 2004), floral traits in particular (Strauss & Whittall 2006). While the underlying mechanisms can vastly differ – herbivory-induced changes in plant chemistry reducing pollinator visitations (e.g. Kessler *et al.* 2011); plant traits involved in both interactions simultaneously (e.g. phenology Brody 2008); genetic correlation between two plant traits, each involved in one plant-animal interaction (Strauss *et al.* 2004) – the decisive consequence is that the selection pressures in the absence of either one animal species are modified, often unpredictably, in the presence of both animals (Ramos & Schiestl 2019). Conflicting selection is very often due to shared preferences for plant phenotypes between pollinators and herbivores, a pattern that is largely widespread in nature (Strauss & Whittall 2006), potentially because it promotes the stable coexistence of the community (Yacine & Loeuille 2021). This preference pattern indicates that plant species are subject to an ecological trade-off between attracting pollinators and escaping herbivores (Strauss *et al.* 2002). This trade-off has interestingly been shown to support the maintenance of a flower-color

polymorphism in the wild radish *Raphanus sativus* (Irwin *et al.* 2003), which suggests that the interplay between pollination and herbivory could play a key role in explaining the striking diversity of flowering plants.

Conflicting selection arises because pollination and herbivory exert opposite pressures on plant traits (Thompson 2009), with especially contrasting implications in terms of diversification potential (Yoder & Nuismer 2010).

As stronger mutualism increases fitness, plants are selected to better match their pollinator phenotype (e.g. spur length and pollinator tongue, Whittall & Hodges 2007). When the matching is perfect, theory indicates selection should be stabilizing (e.g. Kiestner *et al.* 1984). Pollination-induced stabilizing selection has been empirically characterized several times (e.g. Parachnowitsch & Kessler 2010). It disfavors extreme phenotypes, thus reducing the potential for disruptive selection (Kopp & Gavrillets 2006; Yoder & Nuismer 2010; Maliet *et al.* 2020). Note, however, that this does not imply that mutualism cannot promote diversification, but rather that additional processes are required, many of which are presented in the review by Chomicki *et al.* (2019). For instance, as a result of increased densities, mutualism can exacerbate intraspecific competition, which in turn favors disruptive selection (Bolnick 2004; Yoder & Nuismer 2010).

In contrast with mutualism, predation reduces prey fitness which implies that plants are selected to increasingly mismatch their herbivore phenotype (e.g. chemical defenses and herbivore tolerance, Becerra *et al.* 2009). Such arms races dynamics (Ehrlich & Raven 1964; Dawkins & Krebs 1979) expose the plant species to runaway selection, which has been measured several times in empirical systems (e.g. Mauricio & Rausher 1997). Because apparent competition (Holt 1977) imposes a cost on phenotype matching between conspecific plants, herbivory also favors increased plant phenotypic divergence and hence disruptive selection (Kopp & Gavrillets 2006; Yoder & Nuismer 2010; Maliet *et al.* 2020).

The ecological implications of such conflicting selection are also of major interest. In particular, several studies emphasize that the relative interaction strength - pollination vs. herbivory - plays a decisive role in the maintenance of coexistence within plant-pollinator-herbivore communities (Mougi & Kondoh 2014; Sauve *et al.* 2016a; Yacine & Loeuille 2021). Because interaction strengths are the result of plant-animal coevolution, the evolution of plant traits under conflicting selection has potentially important consequences for multispecies coexistence.

In the present paper, our goal is (1) to determine how the interplay between pollination and herbivory drives the evolution of plant traits involved in both interactions, (2) to understand the consequences in terms of interaction strengths and multispecies coexistence, as well as (3) to assess the potential for disruptive selection to arise from the trade-off between attracting pollinators and escaping herbivores. We consider a community – a plant species interacting simultaneously with a pollinator and a herbivore species - in which plant-animal interactions depend on a single plant trait involved in both interactions. Each interaction gets stronger as the matching between the plant phenotype and the respective animal phenotype improves. Examples of such traits include flower color (Irwin *et al.* 2003), flower display (Galen & Cuba 2001), chemical volatiles (Theis *et al.* 2014) and the corresponding animal preferences. Phenological traits (e.g. Brody 2008) also fit well within this category as plant-animal interactions require interacting species to cooccur in time. Using the framework of adaptive dynamics (Metz *et al.* 1992; Dieckmann & Law 1996), we determine how the evolutionary dynamics of the plant phenotype vary with the intensities of pollination and herbivory. In particular, we modulate the strength of the trade-off – attracting pollinators vs. escaping herbivores – by modifying the dissimilarity between animal phenotypes (x-axis in **Fig. 1a**). At weak trade-off (i.e. large dissimilarity), we expect the occurrence of runaway selection in the vicinity of the herbivore phenotype (**top right-hand corner, Fig. 1a**), leading to the disruption of plant-pollinator-herbivore coexistence (**Fig. 1b.1**). In contrast, at weak trade-off but in the vicinity of the pollinator phenotype (**bottom right-hand corner, Fig. 1a**), selection should be stabilizing, enabling the maintenance of multispecies coexistence (**Fig. 1b.2**). Our results provide strong support for this contrasting effect of pollination vs. herbivory on the eco-evolutionary dynamics of plant traits. Especially, we show that disruptive selection is possible and requires a strong ecological trade-off between attracting pollinators and escaping herbivores. Our results also show that when multispecies coexistence is maintained, the interaction pattern becomes biased toward stronger pollination than herbivory as the trade-off gets weaker.

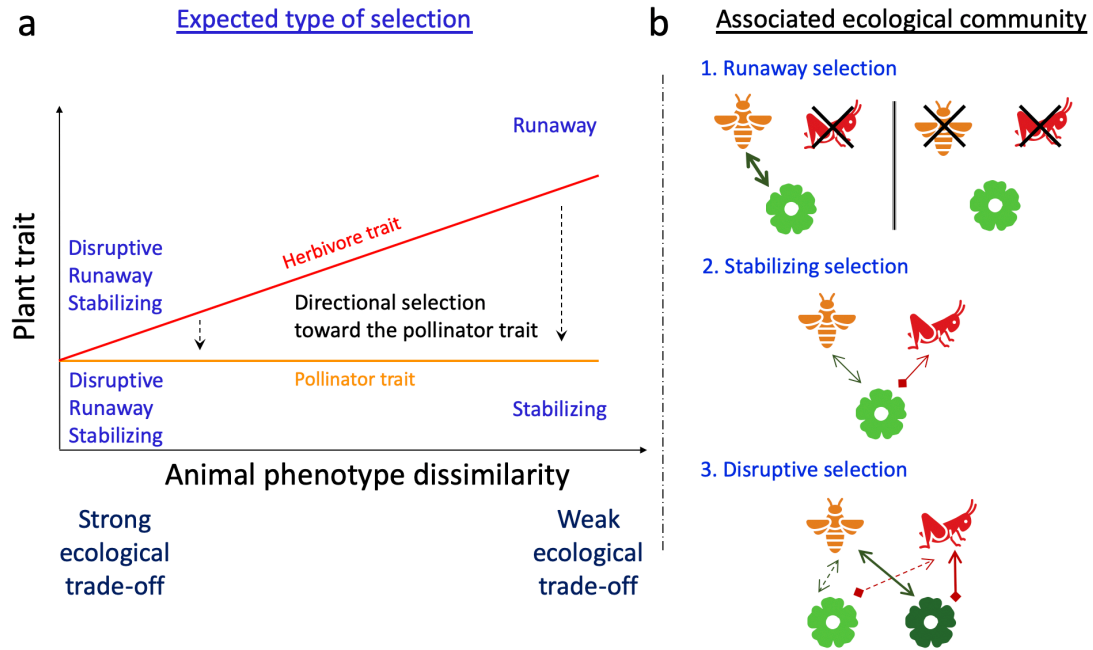


Fig. 1: Expected eco-evolutionary dynamics within the plant-pollinator-herbivore community. **a.** The type of selection should depend on the dissimilarity between animal phenotypes, which is a proxy for the strength of the trade-off between attracting pollinators and escaping herbivores. **b.** Each type of selection should lead, in the long-term, to contrasting community compositions. Note that we assume the occurrence of a given type of selection in a region of the phenotypic space characterized by the three species coexistence. (1) In the case of runaway selection, one animal should go extinct first as the plant phenotype diverges. If it is the pollinator species, runaway selection continues until the herbivore species also goes extinct. In contrast, if herbivores disappear first, evolutionary dynamics lead to a plant-pollinator community with perfect phenotype matching under stabilizing selection. (2) In the case of stabilizing selection, coexistence is maintained, with potential variations in the interaction pattern (i.e. relative strengths of interactions). (3) In the case of disruptive selection, the plant population should be dimorphic, at least temporarily.

II. Model & Methods

II.1. Model

II.1.1 Population dynamics

The biomass densities of three interacting species – a plant P , a pollinator M , and a herbivore H – follow the dynamics set by three ordinary differential equations:

$\frac{dP}{dt} = P(r_p - c_p P + a_{pm} M - a_{ph} H)$	(1)
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$\frac{dM}{dt} = M(r_m - c_m M + e_m a_{pm} P)$	(2)
$\frac{dH}{dt} = H(r_h - c_h H + e_h a_{ph} P)$	(3)

Plants are assumed to have a positive intrinsic growth rate ($r_p > 0$, autotrophs), while both pollinator ($r_m < 0$) and herbivore growth rates ($r_h < 0$) are assumed negative (heterotrophs). Plants (c_p), pollinators (c_m), and herbivores (c_h) undergo intraspecific competition. The strength of interspecific interactions is given by a_{pm} for pollination and a_{ph} for herbivory. e_m and e_h are the conversion efficiencies from plants to animals. See **table 1** for details.

A previous detailed study of these ecological dynamics (Yacine & Loeuille 2021) showed that stable coexistence requires a balance between the strengths of pollination and herbivory. The analytical expressions of the coexistence equilibrium (P^*, M^*, H^*) are given in **Appendix A.I**. Here, we want to investigate how plant evolution can modify the interaction pattern (i.e. pollination vs. herbivory), and impact multispecies coexistence.

II.1. 2 Plant-animal interactions depend on trait-matching

We assume plant-animal interactions to intensify as the matching between the plant phenotype (t_p) and the corresponding animal phenotype – pollinator (t_m) or herbivore (t_h) – increases. The considered plant trait thus corresponds to any trait affecting pollination and herbivory in such a way (equations (4&5)).

$a_{pm}(t_p) = \frac{a_{pm0}}{\sqrt{2\pi\sigma_{Pol}^2}} \exp\left[-\frac{(t_p - t_m)^2}{2\sigma_{Pol}^2}\right]$	(4)
$a_{ph}(t_p) = \frac{a_{ph0}}{\sqrt{2\pi\sigma_{Her}^2}} \exp\left[-\frac{(t_p - t_h)^2}{2\sigma_{Her}^2}\right]$	(5)

As σ_{Pol} controls how quickly the strength of pollination decreases with plant-pollinator phenotype dissimilarity, it corresponds to the pollination-niche width, which is a result of both plant and pollinator degrees of generalism. Likewise, σ_{Her} is the herbivory-niche width. a_{pm0} and a_{ph0} are scaling factors. See **table 1** for details.

Table 1: List of all model parameters and variables with their biological significance, value and dimension (**M** for mass, **L** for length and **t** for time). At the core of this work, parameters directly affecting plant-animal (i.e. interspecific) interactions vary independently and within interval range. The other ecological parameters are fixed, but we tested the robustness of our results by varying some of these parameters (in brackets). Details motivating our choice of parameter values are provided in **Appendix B.I**.

Variables and parameters		Biological significance	Value	Dimension
<i>Variables</i>	P	Plant biomass density		$M \cdot L^{-2}$
	M	Pollinator biomass density		$M \cdot L^{-2}$
	H	Herbivore biomass density		$M \cdot L^{-2}$
	t_p	Plant phenotype		Dimensionless
<i>Interspecific interaction parameters</i>	a_{pm0}	Per capita maximum pollination rate	[3,9]	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	a_{ph0}	Per capita maximum herbivory rate	[3,9]	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	t_m	Pollinator phenotype	0	Dimensionless
	t_h	Herbivore phenotype	[0,3]	Dimensionless
	σ_{Pol}	Pollination niche width	[1.5,3]	Dimensionless
	σ_{Her}	Herbivory niche width	[1.5,3]	Dimensionless
<i>Other ecological parameters</i>	r_p	Plant intrinsic growth rate	10	t^{-1}
	r_m	Pollinator intrinsic growth rate	-1	t^{-1}
	r_h	Herbivore intrinsic growth rate	-4 (or -1)	t^{-1}
	c_p	Plant intra-specific competition rate	0.6	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	c_m	Pollinator intra-specific competition rate	0.5 (or 0.4)	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	c_h	Herbivore intra-specific competition rate	0.4	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	e_m	Plant to pollinator conversion efficiency	0.2	Dimensionless
	e_h	Plant to herbivore conversion efficiency	0.3 (or 0.2)	Dimensionless
<i>Numerical simulations</i>	μ	Mutation probability (per unit of time and plant biomass density)	$2 \cdot 10^{-7}$	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	σ	Mutation amplitude (standard deviation)	0.02	Dimensionless

	ε	Extinction threshold	$2 \cdot 10^{-6}$	$M \cdot L^{-2}$
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II.2. Methods

Animal phenotypes are fixed parameters (without loss of generality: $t_m = 0, t_h \geq t_m$) while we study the evolution of the plant phenotype (t_p) within the framework of adaptive dynamics (Metz *et al.* 1992; Dieckmann & Law 1996). Parameters directly affecting plant-animal interactions - the interspecific parameter set ($t_h - t_m, a_{pm0}, a_{ph0}, \sigma_{Pol}, \sigma_{Her}$) - are at the core of our investigation. In particular, we consider the dissimilarity between animal phenotypes ($t_h - t_m$) as a proxy of the strength of the ecological trade-off that plants are confronted with (**Fig. 1a**). Indeed, when animals are very similar ($t_m \approx t_h$), any variation of the plant phenotype (t_p) has an effect of similar magnitude and direction (both increasing or decreasing) on the strengths of pollination and herbivory, which is indicative of a strong trade-off. An important dissimilarity (i.e. $t_m \ll t_h$) implies (1) that there is a significant phenotypic region (i.e. $[t_m, t_h]$) over which the plant species experiments no trade-off as increasing pollination while decreasing herbivory is possible (**Fig. 1a**, directional selection), and (2) outside this region, plant phenotype variations affect much more one interaction than the other, depending on the closest animal phenotype. The ecological trade-off is therefore weak in such instances.

II.2.1 Adaptive dynamics

Within a monomorphic plant population with phenotype t_p (resident), we investigate whether a mutant with a new phenotype t_p' can invade. Invasion happens if the mutant fitness of invasion, computed as the expected long-term per capita growth rate of that mutant, when rare and in the environment set by the resident population (i.e. P^*, M^*, H^*), is positive $w(t_p', t_p) > 0$ (see **Appendix A.II** for details). When a mutant invades, it replaces the resident population, thus becoming the new resident. The consecutive sequences of trait substitution define the long-term evolutionary dynamics. For any phenotypic trait, and assuming small mutational steps, the expected rate of such sequences is proportional to the selection gradient (equation (6) & **Appendix A.II**), i.e. the derivative of invasion fitness with respect to the mutant's trait (Dieckmann & Law 1996). Finally, evolutionary singularities t_p^* correspond to phenotypes that nullify the selection gradient.

II.2.2 Type of selection

We want to assess the type of selection – stabilizing, disruptive or runaway – acting on the plant trait. Within the adaptive dynamics’ framework, this depends on (1) the properties of the evolutionary singularities, and (2) the position of the plant phenotype relative to these singularities. Two independent properties - convergence and invasibility – characterize evolutionary singularities (mathematical criteria in **Appendix A.II**). Convergence indicates that the trait evolves toward the singularity in its vicinity. Two types of singularities are convergent – the non-invasible continuously stable strategy (CSS, Eshel, 1983) and the invasible branching point (BP, Geritz *et al.* 1997). Invasibility specifies whether the singularity may be invaded by nearby mutants (i.e. is an ESS, Maynard Smith & Price 1973). In a CSS vicinity, evolution leads to the CSS phenotype at which selection is stabilizing due to a local fitness maximum. We thus consider selection to be stabilizing in the basin of attraction of a CSS. Plant-pollinator-herbivore coexistence is notably maintained if a CSS is reached while the three species coexist (**Fig. 1b**). In contrast, a BP yields the emergence of a stable plant dimorphism (**Fig. 1b**). In its vicinity, evolution leads to the BP phenotype at which selection is disruptive because fitness is locally minimal. Accordingly, we consider that selection is disruptive in the basin of attraction of a BP. Finally, phenotypes that are not in the basin of attraction of a convergent singularity are under runaway selection. This is possible in the presence of a non-convergent singularity, i.e. a repeller. It corresponds to a fitness valley, as selection favors phenotypes that are increasingly far from it in its vicinity. In our framework, runaway selection occurs in any repeller vicinity which is not also the vicinity of a convergent singularity. This notably implies that runaway selection always leads to the disruption of plant-pollinator-herbivore coexistence (**Fig. 1b**). An illustrated example of how we calculate the proportion of phenotypic space under each type of selection is provided in **Appendix II.1**.

II.2.3 Eco-evolutionary numerical simulations

We complement the analytical investigation with numerical simulations of the community eco-evolutionary dynamics. It notably enables the study of post-branching dynamics, which are not analytically tractable. Simulations start from a monomorphic plant population (t_p) interacting with a pollinator (t_m) and a herbivore (t_h) population. Mutations are randomly generated following a Poisson process characterized by a mutation probability per unit of time and plant biomass density $\mu = 2 \cdot 10^{-7}$ (**table 1**). Proportionally to morph abundances, a parent morph is randomly chosen at each mutation event. The mutant phenotype

is drawn from a Gaussian distribution centered around the parent phenotype with standard deviation $\sigma = 0.02$ (**table 1**). Its initial density is set to ε which also corresponds to the extinction threshold (**table 1**), taken from the parent population. The code is provided in **Appendix E**.

II.2.4 Analysis performed

We extensively investigate the effect of interspecific parameters ($t_h - t_m, a_{pm0}, a_{ph0}, \sigma_{Pol}, \sigma_{Her}$) by allowing them to vary independently and within interval ranges (**table 1**). These ranges were chosen so that a wide range of pollination and herbivory intensities are explored (**Appendix B.I**). We use Monte Carlo experiments - i.e. numerical estimations of quantities of interest from a (quasi)-random parameter sampling - to understand how plant-animal interactions shape selection, and its consequences on the interaction pattern.

Firstly, we sample 10 000 interspecific parameter sets and determine the position and nature of all evolutionary singularities occurring at stable coexistence, as well as interaction strengths and animal densities at these singularities. Using the correspondence between singularities and types of selection, we derive the distribution of the ratio of pollination to herbivory according to the type of selection (**Fig. 3A**). This distribution is then analyzed using non-parametrical statistical tests (Kruskal-Wallis & Wilcoxon-Mann-Whitney, details in **Appendix C.I**).

To disentangle the effects of the different parameters, we conduct a second set of experiments. Dividing the range of a focal interspecific parameter into six intervals of similar length, interspecific parameter sets are sampled while successively constraining the focal parameter within each of these intervals. The proportion of the phenotypic space under each type of selection is calculated at each sampling (6 x 1000 samples per parameter). We therefore estimate how selection varies with the independent effect of each interspecific parameter (**Fig. 3b & 4**).

We used the same procedure to assess, on the evolutionary time scale, how the long-term interaction pattern depends on trade-off intensity (i.e. $t_h - t_m$), when the three species coexistence is maintained. Such long-term dynamics corresponds either to CSS plant phenotypes under stabilizing selection, or to post-branching dynamics in which dimorphism is maintained. For each sampling (6 x 1000 samples), we therefore calculated the contribution of

pollination to total plant-animal interactions at the CSSs, and at the evolutionary stable dimorphic situations (**Fig. 3c**).

In contrast with interspecific parameters, two sets of values were chosen for the other ecological parameters ($r_p, r_m, r_h, c_p, c_m, c_h, e_m, e_h$). All Monte Carlo experiments were conducted twice for robustness, once with each of these sets. Additional details on the Monte Carlo experiments are provided in **Appendix B.II**.

III. Results

The community eco-evolutionary dynamics qualitatively differ depending on the strength of the ecological trade-off (**Fig. 2**), with selection being either stabilizing or runaway at weak trade-offs, while disruptive selection is only possible when the trade-off is strong or intermediate.

At strong or intermediate trade-offs ($t_h - t_m \leq 2$ in **Fig. 2a**), stabilizing selection enables the maintenance of coexistence. Depending on initial plant phenotype, such outcome arises either directly through the evolution toward a CSS (e.g. point b in **Fig. 2a, Fig. 2b**), or after a transitory dimorphic situation resulting from the evolution toward a branching point (e.g. point c **Fig. 2a, Fig. 2c**). In this latter case, disruptive selection at branching favors both upper (weaker plant-animal interactions) and lower (stronger plant-animal interactions) plant phenotypes, leading to the coexistence of two morphs that get increasingly dissimilar through time (**Fig. 2c**). The upper branch finally goes extinct due to competition between morphs, while the lower branch converges toward the CSS phenotype (**Fig. 2c**). In this example, the fitness valley arising from the presence of herbivores – i.e. the repeller separating the branching and CSS basins of attraction (grey curve in **Fig. 2a**) – can be crossed thanks to the reduction of apparent competition enabled by the emergence of dimorphism.

As the trade-off gets weaker ($t_h - t_m > 2$ in **Fig. 2a**), a new repeller appears leading to the disruption of coexistence under the action of runaway selection if the plant phenotype is initially above the repeller phenotype (e.g. point d in **Fig. 2a, Fig. 2d**). There, plant-animal interactions are getting weaker through time, which leads to the extinction of pollinators, followed by the extinction of herbivores (**Fig. 2d**). Coexistence can, however, still be maintained by stabilizing selection if the plant phenotype is initially in the CSS basin of attraction (e.g. point e in **Fig. 2a**). Such maintenance notably leads to a strong plant-pollinator trait-matching. Yet, as the trade-off gets even weaker, the CSS eventually leaves the

coexistence area and only runaway selection remains possible. In this case (e.g. point f in **Fig. 2a**), the plant-herbivore interaction is weakening alongside evolutionary dynamics, until the extinction of herbivores which leaves a perfectly matching plant-pollinator community.

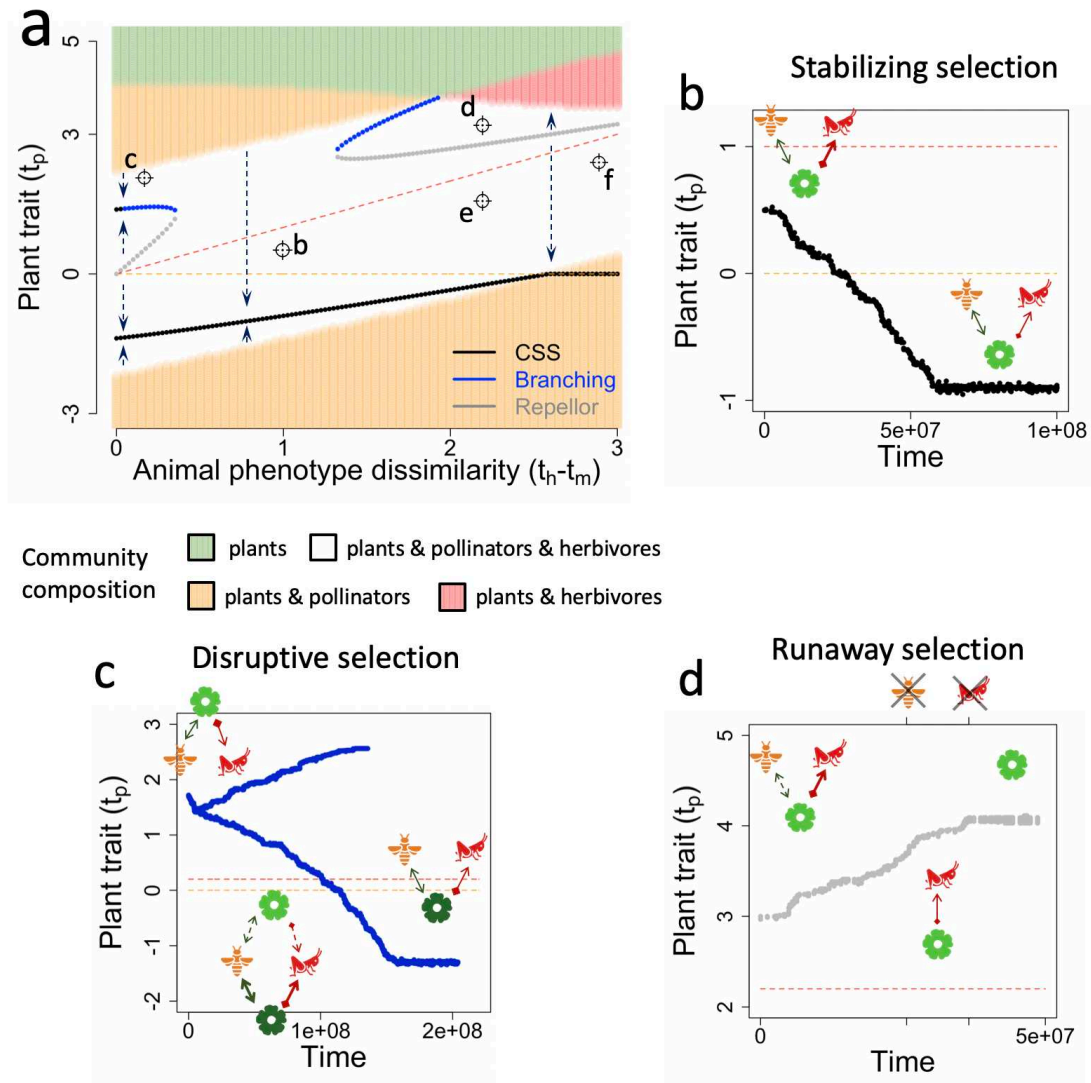


Fig. 2: Qualitative variations of community eco-evolutionary dynamics with trade-off intensity. Parameter set: ecological ($r_p = 10, r_m = -1, r_h = -4, c_p = 0.6, c_m = 0.5, c_h = 0.4, e_m = 0.2, e_h = 0.3$); interspecific ($t_m = 0, a_{pm0} = 5, a_{ph0} = 7, \sigma_{pol} = 3, \sigma_{Her} = 2.8$). **a.** The eco-evolutionary dynamics vary with the trade-off intensity. The arrows indicate the direction of evolutionary trajectories, and the background colors indicate the community composition. **b.** Simulated evolutionary dynamics under stabilizing selection. The initial plant phenotype corresponds to point b in 2.a ($t_h = 1$ i.e. intermediate trade-off). **c.** Simulated evolutionary dynamics under disruptive selection. The initial plant phenotype corresponds to point c in 2.a ($t_h = 0.2$ i.e. strong trade-off). **d.** Simulated evolutionary dynamics under runaway selection. The initial plant phenotype corresponds to point d in 2.a ($t_h = 2.2$ i.e. weak trade-off). Small pictograms depict the community composition, with arrow thickness capturing interaction strengths.

It is the ratio of pollination to herbivory that determine the nature of selection at a given evolutionary singularity (**Fig. 3a**), notably explaining (1) the emerging pattern linking selection type and trade-off intensity – i.e. stabilizing or runaway selection at weak trade-offs, disruptive selection only possible for stronger trade-offs (**Fig. 3b**) - as well as (2) the interaction pattern biased toward stronger pollination than herbivory when coexistence is maintained (**Fig. 3c**). Based on our Monte Carlo analyses on a large number of interspecific parameters sets, these key results of our study are also robust to the modification of the ecological parameter set (**Appendix C.II, Fig. S3 & table S3**).

Stabilizing, runaway and disruptive selection are characterized by contrasting – respectively large, small and balanced – pollination to herbivory ratios (i.e. $\left. \frac{a_{pm}M^*}{a_{ph}H^*} \right]_{t_p^*}$ calculated at the evolutionary singularity t_p^* , **Fig. 3a**). This ratio indeed explains around two-thirds of the variance in selection type (Kruskal-Wallis, $p_{value} < 2.10^{-16}$). Our statistical analyses (**Table S2, Appendix C.I**) also reveals that the ratios of interaction strengths $\left. \left(\frac{a_{pm}}{a_{ph}} \right) \right]_{t_p^*}$ or animal densities $\left. \left(\frac{M^*}{H^*} \right) \right]_{t_p^*}$, likely easier to measure in an empirical context, have a large and significant power in explaining the nature of selection as well. The mechanisms underlying this result appear when looking at the analytical expression of the selection gradient (equation 6), which is proportional to the temporal variation of the plant phenotype under the action of selection.

$$\frac{dt_p}{dt} \propto \underset{\text{pollination}}{\text{Selection gradient}} = - \underbrace{(t_p - t_m) \frac{a_{pm}(t_p)M^*}{\sigma_{Pol}^2}}_{\text{pollination}} + \underbrace{(t_p - t_h) \frac{a_{ph}(t_p)H^*}{\sigma_{Her}^2}}_{\text{herbivory}} \quad (6)$$

The plant phenotype is under two contrasting (i.e. opposite sign) selective forces arising from pollination and herbivory (equation 6). Opposite signs imply that, for a plant phenotype outside $[t_m, t_h]$, pollination selects for phenotypes that are closer to animal phenotypes, while herbivory selects for phenotypes that are further away from animal phenotypes. Pollination and herbivory are therefore a converging and a diverging selective force, respectively. As such, large pollination to herbivory ratios would lead to essentially converging selection (i.e. stabilizing selection), while small ratios would lead to essentially diverging selection (i.e. runaway selection). Disruptive selection requires the plant phenotype to converge toward a branching singularity at which divergent selection favors both extreme phenotypes. As a result,

balanced pollination to herbivory ratios characterize disruptive selection, which appears as an intermediate between stabilizing and runaway selection (**Fig. 3a**).

Such balanced ratios are only possible when the plant phenotype is approximately equidistant from animal phenotypes. Disruptive selection can thus occur either for similar animal phenotypes, or in between animal phenotypes (i.e. in $[t_m, t_h]$) when these phenotypes are significantly dissimilar. Over this phenotypic interval $[t_m, t_h]$, however, lower plant phenotypes improving the trait-matching with pollinators while decreasing the one with herbivores are always selected (no ecological trade-off). In other words, the selective gradient is strictly negative (equation 6) so that no evolutionary singularity is possible, branching in particular. Disruptive selection is therefore only possible for nearly similar animal phenotypes, which correspond to a strong or intermediate trade-off (**Fig. 3b**). When animals have very dissimilar phenotypes, the ratio of pollination to herbivory is either large or small outside $[t_m, t_h]$, depending on which animal phenotype is closer to the plant phenotype. As a result, selection is either stabilizing or runaway when the trade-off between pollination and herbivory is weak (**Fig. 3b**).

Finally, when coexistence is maintained, the long-term interaction pattern is biased toward stronger pollination than herbivory (**Fig. 3c**) because it is stabilizing selection, characterized by large pollination to herbivory ratios (**Fig. 3a**), which almost always support the maintenance of coexistence (more than 99% of the cases where coexistence was maintained in our Monte Carlo experiment, see **appendix B.II.4**). Disruptive selection, indeed, could only support coexistence - i.e. evolutionary stable maintenance of plant dimorphism (e.g. **Fig. S6**) - at very strong trade-offs (i.e. $t_h - t_m \leq 0.5$), and very rarely ($\approx 3\%$ of coexistence maintenance at such trade-off, see **appendix B.II.4**). Moreover, the bias toward a stronger-pollination-than-herbivory long-term interaction pattern is only minor at very strong trade-offs, but gets sharper as the trade-off is weakening (**Fig. 3c**), which implies that the coexistence maintained gets increasingly fragile. Herbivores are indeed likely closer to extinction owing to a weak plant-herbivore interaction, while the stability of population dynamics is threatened (Yacine & Loeuille 2021). As the trade-off gets weaker, coexistence is also less frequently maintained as runaway selection gets more frequent at the expense of stabilizing selection (**Fig. 3b**). Note that the opposite scenario - more frequent stabilizing selection at the expense of runaway selection as the trade-off is weakening - is observed with our second ecological parameter set (**Fig. S3b, Appendix C.II**). Although more frequent, the maintained coexistence continues to be increasingly fragile with the weakening trade-off (**Fig. S3c**).

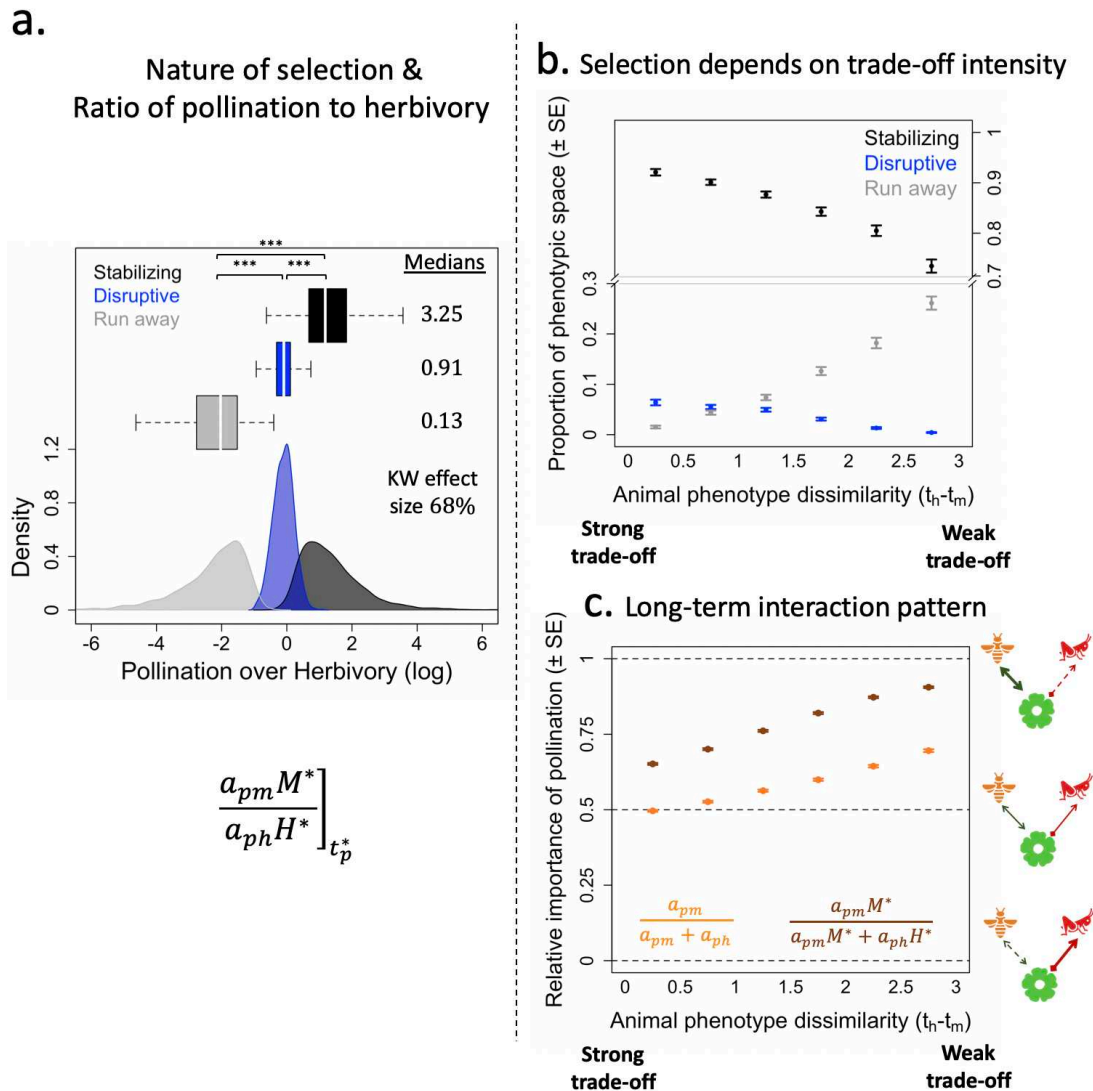


Fig. 3: The ratio of pollination to herbivory explains the nature of selection, with consequences on the link between selection, long-term interaction pattern and trade-off intensity. a. Distribution of pollination to herbivory ratio according to the type of selection. The ratio is measured at the CSS for stabilizing selection, at the branching for disruptive selection, and at the repellor for runaway selection. The medians indicated correspond to absolute values (no log). The effect size of the Kruskal-Wallis test ($p_{value} < 2 \cdot 10^{-16}$) is also indicated. The stars indicate the significance level for the pairwise comparisons (Wilcoxon test): $*** < 10^{-4}$. **b. Relative importance of each type of selection according to trade-off intensity.** The relative importance is measured as the proportion of the phenotypic space allowing stable coexistence over which a given type of selection is observed (see Fig. S2). **c. Long-term (i.e. evolutionary stable) interaction pattern when coexistence is maintained.** The cases where coexistence is maintained are under stabilizing selection (representing the vast majority of such cases), or in a dimorphic situation (extremely rare) resulting from disruptive selection. Coexistence is always disrupted under runaway selection. The results presented in this figure are from Monte-Carlo experiments (details in Appendix B.II). Interspecific parameter sets sampled: (a) 10000, (b) 1000. Ecological parameter set: ($r_p =$

10, $r_m = -1$, $r_h = -4$, $c_p = 0.6$, $c_m = 0.5$, $c_h = 0.4$, $e_m = 0.2$, $e_h = 0.3$). See Fig. S3 (Appendix C) for robustness.

In addition to the ecological trade-off (i.e. $t_h - t_m$), the other interspecific parameters also affect the ratio of pollination to herbivory, and hence the nature of selection. We isolate their effect on selection at strong and intermediate trade-offs (**Fig. 4**), and compare their impact on the community eco-evolutionary dynamics (a_{pm0} vs. a_{ph0} in **Fig. 5**, σ_{Pol} vs. σ_{Her} in **Fig. S5, appendix D**). This analysis emphasizes the opposite eco-evolutionary effect of plant-animal interactions.

The opposite effect of plant-animal interactions on selection

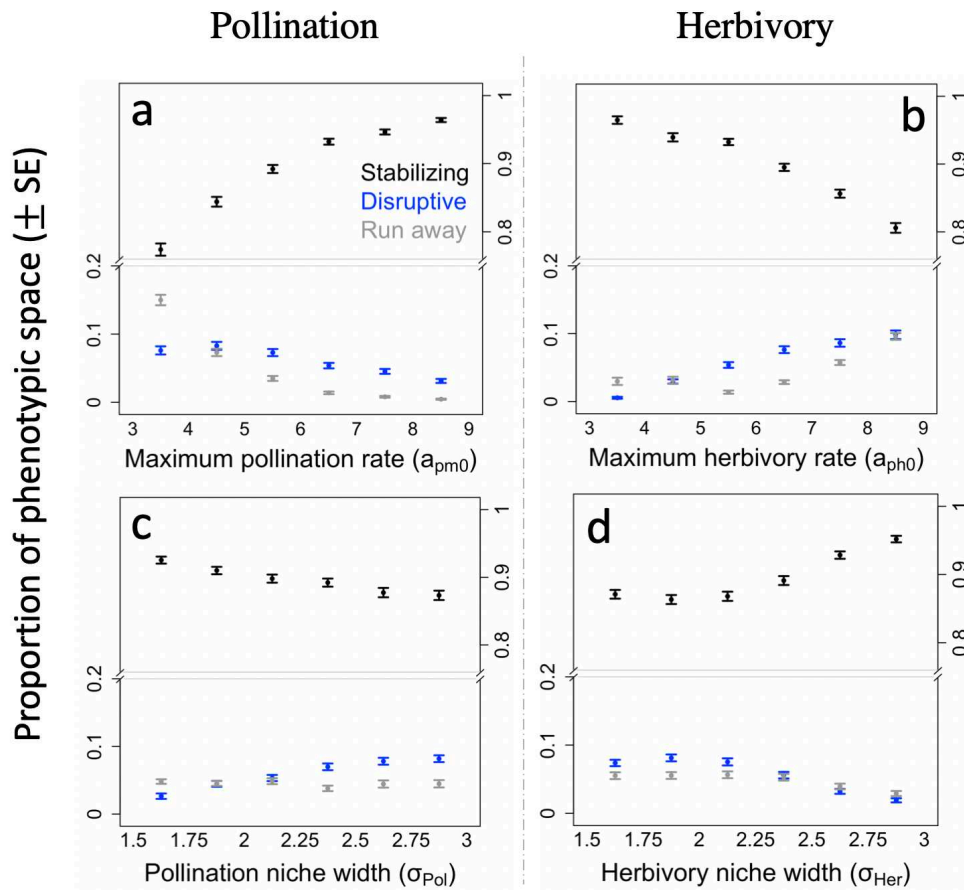


Fig. 4: The opposite effect of pollination and herbivory on selection. a. Effect of per capita maximum pollination rate. b. Effect of per capita maximum herbivory rate. c. Effect of pollination niche width. d. Effect of herbivory niche width. The results are from Monte-Carlo experiments (1000 sampled sets at each point, details in Appendix B.II). Ecological parameter set: ($r_p = 10$, $r_m = -1$, $r_h = -4$, $c_p = 0.6$, $c_m = 0.5$, $c_h = 0.4$, $e_m = 0.2$, $e_h = 0.3$). See Fig. S5 (Appendix D.I) for robustness.

Increasing the maximum rate of pollination (a_{pm0}) makes stabilizing selection more frequent at the expense of disruptive and runaway selection (**Fig. 4a**, e.g. **Fig. 5a vs. 5b**). On the contrary, a bigger maximum rate of herbivory (a_{ph0}) makes disruptive and runaway selection more frequent at the expense of stabilizing selection (**Fig. 4b**, e.g. **Fig. 5a vs. 5c**). The same pattern is observed (**Fig. 4d**, e.g. **Fig. S5b vs. S5d**) as the herbivory niche width (σ_{Her}) gets narrower. In contrast, a narrower pollination niche width (σ_{Pol}) increases the prevalence of stabilizing selection at the expense of disruptive selection, while runaway selection remains roughly unaffected (**Fig. 4c**, e.g. **Fig. S5a vs. S5b**). These patterns are, however, much less pronounced (**Fig. 4**) in the case of niche widths (σ) than interaction rates (a_0). Moreover, only in the case of interaction rates are these patterns robust to the variation of the ecological parameter set (**Fig. S4, Appendix D**).

The opposite impact of plant-animal interactions on selection implies opposite consequences for the maintenance of coexistence: plant-animal coexistence is favored by strong pollination ($a_{pm0} \nearrow, \sigma_{Pol} \searrow$) and threatened by strong herbivory ($a_{ph0} \nearrow, \sigma_{Her} \searrow$). Strong pollination, indeed, makes the evolutionary maintenance of coexistence more frequent as stabilizing selection gets more prevalent (**Fig. 4a&c, Fig. S4a**). In contrast, strong herbivory, by making runaway selection more frequent (**Fig. 4b&d, Fig. S4b**), favors evolutionary dynamics leading to the extinction of at least one animal species, very often both (**Fig. 5&S5**). Moreover, strong herbivory displaces the CSS phenotypes closer to animal extinction thresholds (e.g. **Fig. 5a vs. 5c, Fig. S5b vs. S5d**), which implies the maintenance of a fragile coexistence. Because it is characterized by weak plant-animal trait-matchings and small animal densities, such coexistence is indeed vulnerable to perturbations or stochasticity. Strong pollination, in contrast, displaces the CSS phenotypes away from extinction boundaries (e.g. **Fig. 5c vs. 5d, S5a vs. S5b**). Note, however, that strong pollination also favors the evolutionary emergence of unstable population dynamics, especially at weak trade-offs (orgies in **Fig. 5b&d vs 5a&c**). In such a state, which is characterized by the dominance of positive ecological feedback loops (Yacine & Loeuille 2021), the community is prone to exhibit sudden regime shifts (e.g. abrupt collapse).

The diversification of plant phenotype through disruptive selection is fostered by strong herbivory (**Fig. 4b&d, Fig. S4b**), and restricted by strong pollination (**Fig. 4a&c, Fig. S4a**). Such a pattern is in line with balanced pollination to herbivory ratios (**Fig. 3a**), given that the ecological parameter set favors the densities of pollinators over herbivores ($r_m \gg r_h$, but disruptive selection is actually extremely rare for our more balanced ecological parameter set,

Fig. S3b). Plant dimorphism is most often temporary (e.g. **Fig. 2c**): approximately 5% of the branching events encountered in our Monte Carlo experiment led to a maintained dimorphism (**Appendix D.III**), all occurring at very strong trade-offs (i.e. $t_h - t_m \leq 0.5$). They, nevertheless, represent around 22% of the branchings at such strong trade-offs. Post-branching dynamics always led to two morphs with qualitatively contrasting strategies, i.e. strong vs. weak plant-animal interactions (e.g. **Fig. S6**).

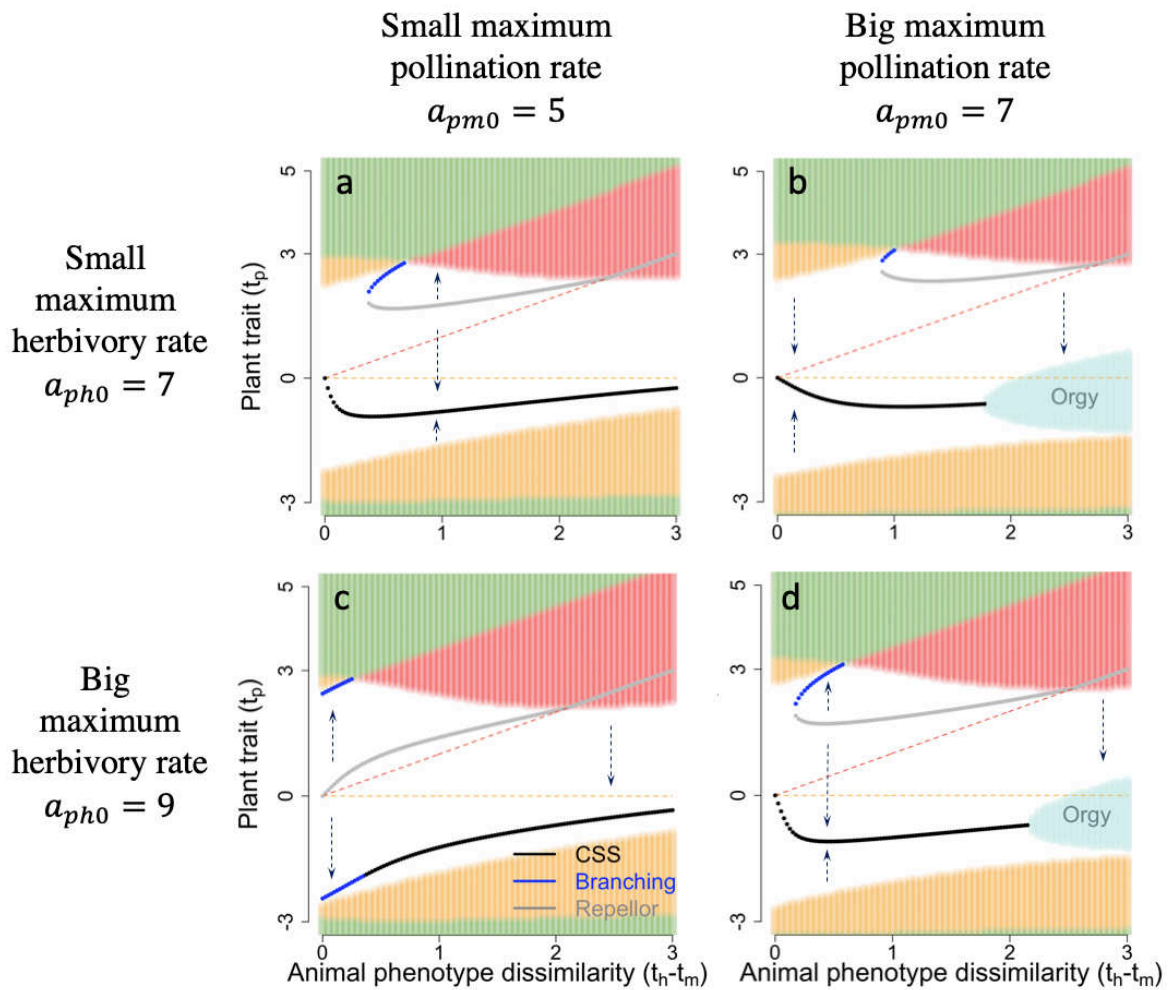


Fig. 5: Per capita maximum pollination vs. herbivory rates affect the community eco-evolutionary dynamics. Arrows indicate evolutionary trajectories and background colors indicate community composition (as in **Fig. 2a**): green for plants, orange for plant-pollinator, red for plant-herbivore and white for stable coexistence. Light blue indicates unstable population dynamics. Evolutionary singularities: CSS (black curve, convergent, non-invasible), Branching (blue curve, convergent, invasible) and repellor (grey curve, non-convergent, invasible). Arrows indicates Ecological parameter set: ($r_p = 10, r_m = -1, r_h = -4, c_p = 0.6, c_m = 0.5, c_h = 0.4, e_m = 0.2, e_h = 0.3$). Interaction niche widths: $\sigma_{pol} = 1.7, \sigma_{Her} = 2$.

IV. Discussion

In the present paper, we demonstrate the contrasting impact of pollination vs. herbivory on the eco-evolutionary dynamics of a plant-pollinator-herbivore community in which the strength of plant-animal interactions depends on the matching of a single evolving plant trait with the phenotypes of animal species. Stronger pollination makes stabilizing selection more prevalent, thus fostering the maintenance of coexistence. Stronger herbivory, in contrast, increases the prevalence of runaway selection, and hence favors the disruption of coexistence. Importantly, disruptive selection can arise from the interplay of plant-animal interactions, leading to the diversification of the plant phenotype. It requires the plant species to be subject to a strong ecological trade-off between attracting pollinators and escaping herbivores (i.e. similar animal phenotypes in our framework). Trade-off intensity indeed appears as a key determinant of the community eco-evolutionary dynamics, with notably the evolutionary emergence of an interaction pattern biased toward stronger pollination than herbivory as the trade-off is weakening. This implies, in particular, the maintenance of an increasingly fragile plant-pollinator-herbivore coexistence.

In line with our predictions (**Fig. 1a**), the plant trait involved in both interactions is subject to opposite selective pressures: pollination fosters the convergence toward the pollinator phenotype – i.e. stabilizing selection – while herbivory favors the divergence from the herbivore phenotype – i.e. runaway selection. Accordingly, such conflicting selection has notably been found acting on flower color (Irwin *et al.* 2003; Frey 2004), shape (Galen & Cuba 2001) or display (Gómez 2003), nectar quantity (Adler & Bronstein 2004) and flowering phenology (Brody 2008; Ehrlén & Münzbergová 2009). Conceptually, all traits influencing the likelihood for a plant species to be discovered by its interacting species (persistence, relative abundance, size, fragrance, attractiveness...) – i.e. its “apparency” (Feeny 1976) – are likely to experiment such conflicting selection, often characterized by the deviation of plant traits from optima favored by pollinators (Strauss & Whittall 2006, see CSSs in Fig. 5). Using experimental evolution, Ramos & Schiestl (2019) offer compelling evidence of such deviation. They show that the plants that evolved in the presence of both animals were less attractive to pollinators than those that evolved in the sole presence of pollinators, but that they were still more attractive than the plants that evolved with hand-pollination, with or without herbivores.

Short generation plant species (e.g. *Brassica rapa*, Ramos & Schiestl 2019) offer a promising avenue to investigate real-time evolutionary trajectories of plant traits subject to the ecological trade-off between attracting pollinators and escaping herbivores. This trade-off, which we find to play a key role in the community eco-evolutionary dynamics in line with the empirical evidence so far (Strauss *et al.* 2002; Strauss & Irwin 2004), could be experimentally manipulated by using different animal species as selective agents (i.e. different efficiencies of pollination and herbivory), or by varying animal densities. It would, for instance, allow testing the increasing trait deviation from pollination optimum with a strengthening trade-off that we report (i.e. CSSs displacement with trade-off intensity in **Fig. 5& S5**).

Our work also reveals the evolutionary emergence of a relatively well-balanced interaction pattern at very strong trade-offs, but that interactions become biased toward stronger pollination than herbivory as the trade-off gets weaker. In natural communities, however, the interaction pattern results from plant-animal coevolution rather than from the sole plant evolution (Thompson 2009), so that our result has to be taken cautiously. In particular, animals are selected to increasingly match their resource (i.e. plant) phenotype, leading to a strong ecological trade-off for the plant species, which would favor well-balanced interaction patterns according to our result. We hypothesize that the commonness of shared preferences between pollinators and herbivores in natural communities (Strauss & Whittall 2006) is partly driven by such coevolutionary dynamics.

Similar animal preferences would presumably foster a balanced pattern of pollination vs. herbivory strengths, which has been suggested as promoting stable multispecies coexistence (Mougi & Kondoh 2012; Sauve *et al.* 2016a; Yacine & Loeuille 2021). As a result, the maintained coexistence at weak trade-offs, characterized by strong pollination and weak herbivory (**Fig. 3c**), appears fragile. The underpinning arguments are (1) a low herbivore population vulnerable to extinction (e.g. demographic stochasticity), and (2) the potential for unstable dynamics owing to the dominance of pollination-induced positive ecological feedback over negative feedback (Yacine & Loeuille 2021). While the former is debatable as it critically depends on our assumption of a negative herbivore intrinsic growth rate (i.e. $r_h < 0$), the latter is much more robust as it relies on strong theoretical arguments independent of our particular model assumptions (Levins 1974; Neutel & Thorne 2014). Accordingly, several studies emphasize the vulnerability of pollination networks due to their inherent positive feedback which propagate and amplify disturbances (Kaiser-Bunbury *et al.* 2010; Lever *et al.* 2014), potentially explaining, in part, the decline of pollinators worldwide (Potts *et al.* 2010).

Our assumption of animals being obligate plant interactors (i.e. $r_m, r_h < 0$) might legitimately reduce the scope of our work as animal species often interact with several plant species within plant-pollinator-herbivore networks. Yet, the critical basis of our results is the conflicting selective pressures – convergent and divergent (equation 6) – arising from pollination and herbivory, which do not qualitatively depend on animal intrinsic growth rates. They indeed depend on the structural opposite effect of each plant-animal interaction on plant growth rate, which is positive for the mutualism and negative for the antagonism (population dynamics, equations 1, 2, 3).

Perhaps the most important result of our study is that disruptive selection can arise from the interplay of pollination and herbivory. Such an interplay has been shown to support the maintenance of intraspecific plant diversity in at least three cases: flower color polymorphism in both *Raphanus sativus* (Irwin *et al.* 2003) and *Claytonia virginica* (Frey 2004), and floral display dimorphism in *Primula farinosa* (Ehrlén *et al.* 2002). We show that this interplay could have fueled the diversification process itself, and that such dynamics might be common in nature owing to the strong ecological trade-off required for disruptive selection being relatively widespread. The two contrasting plant strategies – strong vs. weak plant-animal interactions – emerging in our framework, moreover, agree well with the described empirical pattern both at the three-species scale (Ehrlén *et al.* 2002; Irwin *et al.* 2003; Frey 2004), and at the network scale (Melián *et al.* 2009; Sauve *et al.* 2016b). Finally and in line with most previous theoretical works (Kopp & Gavrillets 2006; Yoder & Nuismer 2010; Maliet *et al.* 2020), our results emphasize the decisive role of herbivory in the emergence of disruptive selection (**Fig. 4**).

Dimorphism is, however, most often temporary in our framework owing to competitive exclusion, which indicates that additional processes are required for diversity to be maintained. In particular, any process reducing the strength of intraspecific competition as the two morphs get increasingly dissimilar - i.e. niche-overlap competition dependent on our focal trait t_p - would favor the maintenance of dimorphism. This is likely common in natural communities owing to potential competition for pollinators between plants (e.g. Campbell 1985), or plant traits involved in both competitive and plant-animal interactions (e.g. phenological traits, Schwinning & Kelly 2013), but also genetic correlations between such traits (e.g. plant size, Carmona *et al.* 2011). If niche-overlap competition allows maintaining dimorphism, reproductive isolation may then evolve as the morph that interacts weakly with animal species acquires new pollinators species (Baack *et al.* 2015), or evolves self-fertilization (Bodbyl Roels & Kelly 2011). Our findings – i.e. the potential for disruptive selection from the interplay of

pollination and herbivory - are therefore a first step toward modelling the evolutionary emergence of plant-pollinator-herbivore networks, which would allow new insights into the eco-evolutionary processes supporting the diversity of natural communities.

References

- Adler, L.S. & Bronstein, J.L. (2004). Attracting antagonists: Does floral nectar increase leaf herbivory? *Ecology*, 85, 1519–1526.
- Armbruster, W.S. (1997). Exaptations Link Evolution of Plant-Herbivore and Plant-Pollinator Interactions: A Phylogenetic Inquiry. *Ecology*, 78, 1661.
- Baack, E., Melo, M.C., Rieseberg, L.H. & Ortiz-Barrientos, D. (2015). The origins of reproductive isolation in plants. *New Phytol.*, 207, 968–984.
- Becerra, J.X., Noge, K. & Venable, D.L. (2009). Macroevolutionary chemical escalation in an ancient plant-herbivore arms race. *Proc. Natl. Acad. Sci. U. S. A.*, 106, 18062–18066.
- Bodbyl Roels, S.A. & Kelly, J.K. (2011). Rapid evolution caused by pollinator loss in *Mimulus guttatus*. *Evolution (N. Y.)*, 65, 2541–2552.
- Bolnick, D.I. (2004). Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution (N. Y.)*, 58, 608–618.
- Brody, A.K. (2008). Effects of Pollinators, Herbivores, and Seed Predators on Flowering Phenology. *Ecology*, 78, 1624–1631.
- Campbell, D.R. (1985). Pollinator Sharing and Seed Set of *Stellaria pubera*: Competition for Pollination. *Ecology*, 66, 544–553.
- Carmona, D., Lajeunesse, M.J. & Johnson, M.T.J. (2011). Plant traits that predict resistance to herbivores. *Funct. Ecol.*, 25, 358–367.
- Chomicki, G., Weber, M., Antonelli, A., Bascompte, J. & Kiers, E.T. (2019). The Impact of Mutualisms on Species Richness. *Trends Ecol. Evol.*, 34, 698–711.
- Dawkins, R. & Krebs, J.R. (1979). Arms races between and within species. *Proc. R. Soc. B Biol. Sci.*, 205, 489–511.
- Dieckmann, U. & Law, R. (1996). The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.*, 34, 579–612.
- Ehrlén, J., Käck, S. & Ågren, J. (2002). Pollen limitation, seed predation and scape length in *Primula farinosa*. *Oikos*, 97, 45–51.
- Ehrlén, J. & Münzbergová, Z. (2009). Timing of flowering: Opposed selection on different fitness components and trait covariation. *Am. Nat.*, 173, 819–830.
- Ehrlich, P.R. & Raven, P.H. (1964). Butterflies and Plants: A Study in Coevolution. *Evolution (N. Y.)*, 18, 586.
- Eshel, I. (1983). Evolutionary and continuous stability. *J. Theor. Biol.*, 103, 99–111.
- Farrell, B.D., Dussourd, D.E. & Mitter, C. (1991). Escalation of plant defense: do latex and resin canals spur plant diversification? *Am. Nat.*, 138, 881–900.
- Feeny, P. (1976). Chapter One. In: *Plant apparency and chemical defense*. pp. 1–40.
- Fontaine, C., Guimarães Jr, P.R., Kéfi, S., Loeuille, N., Memmott, J., van der Putten, W.H., *et al.* (2011). The

- ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.*, 14, 1170–1181.
- Frey, F.M. (2004). Opposing natural selection from herbivores and pathogens may maintain floral-color variation in *Claytonia virginica* (Portulacaceae). *Evolution (N. Y.)*, 58, 2426–2437.
- Galen, C. & Cuba, J. (2001). Down the tube: Pollinators, predators, and the evolution of flower shape in the alpine skypilot, *Polemonium viscosum*. *Evolution (N. Y.)*, 55, 1963–1971.
- Geritz, S.A.H., Metz, J.A.J., Kisdi, É. & Meszéna, G. (1997). Dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.*, 78, 2024–2027.
- Gómez, J.M. (2003). Herbivory reduces the strength of pollinator-mediated selection in the Mediterranean herb *Erysimum mediohispanicum*: Consequences for plant specialization. *Am. Nat.*, 162, 242–256.
- Grant, V. (1949). Pollination Systems as Isolating Mechanisms in Angiosperms. *Evolution (N. Y.)*, 3, 82–97.
- Hernández-Hernández, T. & Wiens, J.J. (2020). Why are there so many flowering plants? A multiscale analysis of plant diversification. *Am. Nat.*, 195, 948–963.
- Hodges, S.A. & Arnold, M.L. (1995). Spurring plant diversification: Are floral nectar spurs a key innovation? *Proc. R. Soc. B Biol. Sci.*, 262, 343–348.
- Holt, R.D. (1977). Predation, apparent competition, and the structure of prey communities. *Theor. Popul. Biol.*, 12, 197–229.
- Irwin, R.E., Strauss, S.Y., Storz, S., Emerson, A. & Guibert, G. (2003). The Role of Herbivores in the Maintenance of a Flower Color Polymorphism in Wild Radish. *Ecology*, 84, 1733–1743.
- Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C.B. & Cafisch, A. (2010). The robustness of pollination networks to the loss of species and interactions: A quantitative approach incorporating pollinator behaviour. *Ecol. Lett.*, 13, 442–452.
- Kessler, A., Halitschke, R. & Poveda, K. (2011). Herbivory-mediated pollinator limitation: Negative impacts of induced volatiles on plant-pollinator interactions. *Ecology*, 92, 1769–1780.
- Kiester, A.R., Lande, R. & Schemske, D.W. (1984). Models of coevolution and speciation in plants and their pollinators. *Am. Nat.*, 124, 220–243.
- Kopp, M. & Gavrillets, S. (2006). Multilocus genetics and the coevolution of quantitative traits. *Evolution (N. Y.)*, 60, 1321–1336.
- Lever, J.J., van Nes, E.H., Scheffer, M. & Bascompte, J. (2014). The sudden collapse of pollinator communities. *Ecol. Lett.*, 17, 350–359.
- Levins, R. (1974). Discussion paper: the qualitative analysis of partially specified systems. *Ann. N. Y. Acad. Sci.*, 231, 123–138.
- Maliot, O., Loeuille, N. & Morlon, H. (2020). An individual-based model for the eco-evolutionary emergence of bipartite interaction networks. *Ecol. Lett.*, 23, 1623–1634.
- Mauricio, R. & Rausher, M.D. (1997). Experimental manipulation of putative selective agents provides evidence for the role of natural enemies in the evolution of plant defense. *Evolution (N. Y.)*, 51, 1435–1444.
- Maynard Smith, J. & Price, G.R. (1973). The logic of animal conflict. *Nature*, 246, 15–18.
- Melián, C.J., Bascompte, J., Jordano, P. & Křivan, V. (2009). Diversity in a complex ecological network with two interaction types. *Oikos*, 118, 122–130.
- Metz, J.A.J., Nisbet, R.M. & Geritz, S.A.H. (1992). How should we define “fitness” for general ecological scenarios? *Trends Ecol. Evol.*, 7, 198–202.

- Mougi, A. & Kondoh, M. (2012). Diversity of interaction types and ecological community stability. *Science*, 337, 349–351.
- Mougi, A. & Kondoh, M. (2014). Instability of a hybrid module of antagonistic and mutualistic interactions. *Popul. Ecol.*, 56, 257–263.
- Neutel, A.-M. & Thorne, M.A.S. (2014). Interaction strengths in balanced carbon cycles and the absence of a relation between ecosystem complexity and stability. *Ecol. Lett.*, 17, 651–661.
- Ollerton, J., Winfree, R. & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120, 321–326.
- Parachnowitsch, A.L. & Kessler, A. (2010). Pollinators exert natural selection on flower size and floral display in *Penstemon digitalis*. *New Phytol.*, 188, 393–402.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends Ecol. Evol.*, 25, 345–353.
- Ramos, S.E. & Schiestl, F.P. (2019). Rapid plant evolution driven by the interaction of pollination and herbivory. *Science*, 364, 193–196.
- Sargent, R.D. (2004). Floral symmetry affects speciation rates in angiosperms. *Proc. R. Soc. B Biol. Sci.*, 271, 603–608.
- Sauve, A.M.C., Fontaine, C. & Thébault, E. (2016a). Stability of a diamond-shaped module with multiple interaction types. *Theor. Ecol.*, 9, 27–37.
- Sauve, A.M.C., Thébault, E., Pocock, M.J.O. & Fontaine, C. (2016b). How plants connect pollination and herbivory networks and their contribution to community stability. *Ecology*, 97, 908–917.
- Schwinning, S. & Kelly, C.K. (2013). Plant competition, temporal niches and implications for productivity and adaptability to climate change in water-limited environments. *Funct. Ecol.*, 27, 886–897.
- Strauss, S.Y. & Irwin, R.E. (2004). Ecological and Evolutionary Consequences of Multispecies Plant-Animal Interactions. *Annu. Rev. Ecol. Evol. Syst.*, 35, 435–466.
- Strauss, S.Y., Irwin, R.E. & Lambrix, V.M. (2004). Optimal defence theory and flower petal colour predict variation in the secondary chemistry of wild radish. *J. Ecol.*, 92, 132–141.
- Strauss, S.Y., Rudgers, J.A., Lau, J.A. & Irwin, R.E. (2002). Direct and ecological costs of resistance to herbivory. *Trends Ecol. Evol.*, 17, 278–285.
- Strauss, S.Y. & Whittall, J.B. (2006). Non-pollinator agents of selection on floral traits. In: *Ecology and evolution of flowers* (eds. Harder, L.D. & Barrett, S.C.H.). Oxford University Press on Demand, New York, NY, USA, pp. 120–138.
- Theis, N., Barber, N.A., Gillespie, S.D., Hazzard, R. V. & Adler, L.S. (2014). Attracting mutualists and antagonists: Plant trait variation explains the distribution of specialist floral herbivores and pollinators on crops and wild gourds. *Am. J. Bot.*, 101, 1314–1322.
- Thompson, J.N. (2009). The coevolving web of life. *Am. Nat.*, 173, 125–140.
- Whittall, J.B. & Hodges, S.A. (2007). Pollinator shifts drive increasingly long nectar spurs in columbine flowers. *Nature*, 447, 706–709.
- Yacine, Y. & Loeuille, N. (2021). Stable coexistence in plant-pollinator-herbivore communities requires balanced mutualistic vs antagonistic interactions. *bioRxiv*.
- Yoder, J.B. & Nuismer, S.L. (2010). When Does Coevolution Promote Diversification? *Am. Nat.*, 176, 802–817.

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Appendix A: Analytical investigation of plant-pollinator-herbivore eco-evolutionary dynamics

I. Ecological equilibria

Population dynamics reach an ecological equilibrium when the three population growth rates vanish.

$$\begin{cases} \frac{dP}{dt} \stackrel{\text{def}}{=} P(r_p - c_p P + a_{pm}M - a_{ph}H) = 0 \\ \frac{dM}{dt} \stackrel{\text{def}}{=} M(r_m - c_m M + e_m a_{pm}P) = 0 \\ \frac{dH}{dt} \stackrel{\text{def}}{=} H(r_h - c_h H + e_h a_{ph}P) = 0 \end{cases}$$

There are eight possible equilibria as each species can either be present or absent at ecological equilibrium. The goal of the present paper being to study the evolutionary dynamics of the plant phenotype within a plant-pollinator-herbivore community, we are mostly interested in the coexistence equilibrium, i.e. the ecological equilibrium characterized by the presence of all three species at densities P^*, M^*, H^* .

$$\begin{cases} P^* = \frac{c_h c_m r_p + c_h a_{pm} r_m - c_m a_{ph} r_h}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2} \\ M^* = \frac{c_h e_m a_{pm} r_p + (c_p c_h + e_h a_{ph}^2) r_m - e_m a_{pm} a_{ph} r_h}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2} \\ H^* = \frac{c_m e_h a_{ph} r_p + e_h a_{pm} a_{ph} r_m + (c_p c_m - e_m a_{pm}^2) r_h}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2} \end{cases}$$

The analytical expressions for the other equilibria can be found elsewhere (Yacine and Loeuille 2021). Moreover, assuming coexistence is feasible (i.e. $P^*, M^*, H^* > 0$), its stability depends on the satisfaction of two inequalities (Ruth-Hurwitz):

$$(c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) > 0$$

$$\begin{aligned} & (c_p P^* + c_m M^* + c_h H^*)(P^* M^* (c_p c_m - e_m a_{pm}^2) + P^* H^* (c_p c_h + e_h a_{ph}^2) + M^* H^* c_m c_h) \\ & - P^* M^* H^* (c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) > 0 \end{aligned}$$

II. Adaptive dynamics

Within a monomorphic plant population with phenotype (t_p), we consider the appearance of a mutant with phenotype (t_p'). Assuming the mutant is initially rare so that the environment (i.e. P^*, M^*, H^*) is set by the resident phenotype (t_p), the long-term per capita growth rate of the mutant (P') corresponds to its invasion fitness $w(t_p', t_p)$.

$$w(t_p', t_p) \stackrel{\text{def}}{=} \left. \frac{dP'}{P' dt} \right|_{P' \ll P^*} = r_p - c_p P^* + a_{pm}(t_p') M^* - a_{ph}(t_p') H^*$$

$$\Leftrightarrow w(t_p', t_p) = (a_{pm}(t_p') - a_{pm}(t_p)) M^* - (a_{ph}(t_p') - a_{ph}(t_p)) H^* \quad (A)$$

The last equality ensuing from the ecological equilibrium. A positive fitness of invasion indicates that the mutant invades and replaces the resident plant population, while it goes extinct otherwise. Assuming mutations of small phenotypic amplitude, the rate of this trait substitution sequence is proportional to the selection gradient (Dieckmann and Law 1996).

$$\text{Selection gradient} \stackrel{\text{def}}{=} \left. \frac{\partial w(t_p', t_p)}{\partial t_p'} \right|_{t_p' = t_p} = -(t_p - t_m) \frac{a_{pm}(t_p) M^*}{\sigma_{Pol}^2} + (t_p - t_h) \frac{a_{ph}(t_p) H^*}{\sigma_{Her}^2} \quad (B)$$

Evolutionary singularities (t_p^*) correspond to phenotypes that nullify the selection gradient.

$$0 = -(t_p^* - t_m) \frac{a_{pm}(t_p^*) M^*}{\sigma_{Pol}^2} + (t_p^* - t_h) \frac{a_{ph}(t_p^*) H^*}{\sigma_{Her}^2}$$

$$\Leftrightarrow \frac{t_p^* - t_h}{t_p^* - t_m} = \frac{a_{pm}(t_p^*) M^* / \sigma_{Pol}^2}{a_{ph}(t_p^*) H^* / \sigma_{Her}^2} \quad (C)$$

As indicated in the main text, the position and nature of evolutionary singularities enable the full characterization of evolutionary dynamics (as long as the plant population remains monomorphic). Note that no singularity can occur in the interval $[t_m, t_p]$ as this would imply a negative ratio $\frac{t_p^* - t_h}{t_p^* - t_m}$, which would never possibly satisfy equation (C) whose right side is positive. Singularities are classified into Continuously Stable Strategies (CSS), Branching points (BP) or Repellors according to two properties: invasibility (equation D) and convergence (equation E). Invasibility specifies whether the singularity may be invaded by nearby mutants (non-invasible: CSS; invasible: BP, Repellor). Convergence indicates that the trait evolves toward the singularity in its vicinity (convergent: CSS, BP; non-convergent: Repellor).

$\left. \frac{\partial^2 w(t'_p, t_p)}{\partial t_p'^2} \right]_{t'_p=t_p=t_p^*}$ $\stackrel{\text{def}}{=} -M^* \frac{a_{pm}(t_p^*)}{\sigma_{Pol}^2} \left[1 - \frac{(t_p^* - t_m)^2}{\sigma_{Pol}^2} \right] + H^* \frac{a_{ph}(t_p^*)}{\sigma_{Her}^2} \left[1 - \frac{(t_p^* - t_h)^2}{\sigma_{Her}^2} \right]$ > 0	(D)
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$\left. \frac{\frac{\partial w(t'_p, t_p)}{\partial t_p'}}{dt_p} \right]_{t'_p=t_p}$ $\left. \right]_{t_p=t_p^*}$ $\stackrel{\text{def}}{=} -(t_p^* - t_m) \frac{a_{pm}(t_p^*)}{\sigma_{Pol}^2} \frac{dM^*}{dt_p} \Big _{t_p=t_p^*} + (t_p^* - t_h) \frac{a_{ph}(t_p^*)}{\sigma_{Her}^2} \frac{dH^*}{dt_p} \Big _{t_p=t_p^*}$ $- M^* \frac{a_{pm}(t_p^*)}{\sigma_{Pol}^2} \left[1 - \frac{(t_p^* - t_m)^2}{\sigma_{Pol}^2} \right] + H^* \frac{a_{ph}(t_p^*)}{\sigma_{Her}^2} \left[1 - \frac{(t_p^* - t_h)^2}{\sigma_{Her}^2} \right]$ < 0	(E)
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Appendix B: Setting and exploring (Monte-Carlo) the parameter space

I. Choosing parameter values

The parameters that do not directly affect plant-animal interactions are ($r_p, r_m, r_h, c_p, c_m, c_h, e_m, e_h$). Two parameter sets (**table 1**) were chosen: a focal one that maximizes the range of pollination and herbivory intensities allowing stable coexistence (**Fig. S1A.a**) and a second one for robustness (**Fig. S1A.b**). In the focal parameter set, the pollinator intrinsic growth rate is much higher than the herbivore one in order to favor positive population densities. Pollinators are, however, disfavored in terms of intraspecific competition and conversion efficiency in order to enhance stability (i.e. reducing the occurrence of unbounded population growths). In contrast, the parameter set used for checking the robustness of our results does not favor any animal species over the other.

Parameters directly affecting plant-animal interactions - the interspecific parameter set ($t_h - t_m, a_{pm0}, a_{ph0}, \sigma_{Pol}, \sigma_{Her}$) - are at the core of our investigation. They vary independently and within interval ranges (**table 1**). As shown in **figure S1B**, these ranges were chosen so that a wide range of pollination and herbivory intensities are accessible. Indeed, the vast majority of the stable coexistence area is covered when varying the interspecific parameters from one extreme configuration favoring pollination over herbivory (**Fig S1B.a**), to the other extreme favoring herbivory over pollination (**Fig. S1B.c**).

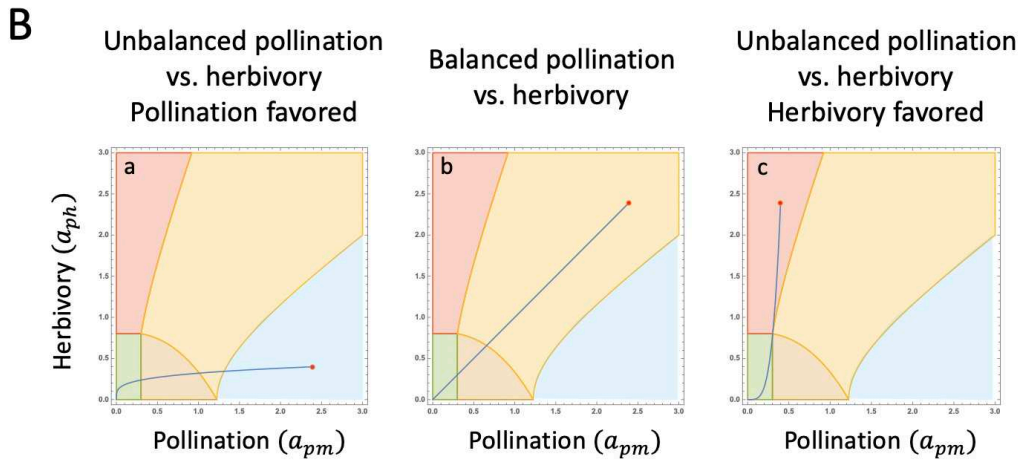
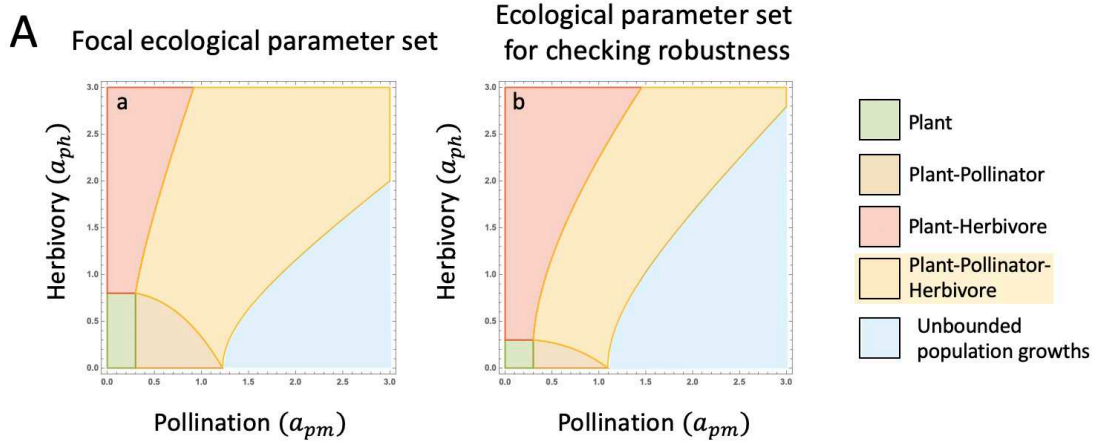


Fig. S1: Community composition according to the strengths of pollination and herbivory. A. Choosing the ecological parameter sets. a. The focal ecological parameter set maximizes the stable coexistence area. $r_p = 10, r_m = -1, r_h = -4, c_p = 0.6, c_m = 0.5, c_h = 0.4, e_m = 0.2, e_h = 0.3$. **b.** The ecological parameter set for checking robustness is symmetrical between animal species. $r_p = 10, r_m = r_h = -1, c_p = 0.6, c_m = c_h = 0.4, e_m = e_h = 0.2$. **B. The range of the interspecific parameter set was chosen to allow a wide exploration of pollination and herbivory intensities. a.** Pollination is favored over herbivory ($t_h = t_m = 0, a_{pm0} = 9, a_{ph0} = 3, \sigma_{Pol} = 1.5, \sigma_{Her} = 3$). **b.** Balanced pollination vs. herbivory ($t_h = t_m = 0, a_{pm0} = 9, a_{ph0} = 9, \sigma_{Pol} = 1.5, \sigma_{Her} = 1.5$). **c.** Herbivory is favored over pollination ($t_h = t_m = 0, a_{pm0} = 3, a_{ph0} = 9, \sigma_{Pol} = 3, \sigma_{Her} = 1.5$). The blue curve corresponds to the sets of pollination and herbivory strengths accessible (i.e. $(a_{pm}(t_p), a_{ph}(t_p))$) as the plant phenotype varies given the interspecific parameter set chosen (i.e. $(t_h - t_m, a_{pm0}, a_{ph0}, \sigma_{Pol}, \sigma_{Her})$). The red point indicates the position of t_m and t_h . The ecological parameter set is the focal one (Fig. S1A.a).

II. Monte Carlo experiments

1. Correspondence between evolutionary dynamics and types of selection.

In order to study how the interplay between pollination and herbivory affects the selection acting on the plant trait, we need to map the different types of selection into the evolutionary dynamics derived in the adaptive dynamics' framework. Here, we illustrate (Fig. S2) how the mapping presented in the Method section applies.

We decided that:

- Stabilizing selection occurs in the basin of attraction of a CSS. In **Fig. S2**, the proportion of phenotypic space corresponding to stabilizing selection is thus $\frac{Rep_1 - CSS}{t_{max} - t_{min}}$. Such quantities are summed if several CSSs occur.
- Disruptive selection occurs in the basin of attraction of a BP. In **Fig. S2**, the proportion of phenotypic space corresponding to disruptive selection is thus $\frac{Rep_2 - Rep_1}{t_{max} - t_{min}}$. Such quantities are summed if several BPs occur.
- Runaway selection occurs when neither stabilizing nor disruptive selection is occurring. This notably implies that selection is runaway when there are no evolutionary singularities. In **Fig. S2**, the proportion of phenotypic space corresponding to runaway selection is thus $\frac{t_{max} - Rep_2}{t_{max} - t_{min}}$. Such quantities are summed if runaway selection occurs multiple times.

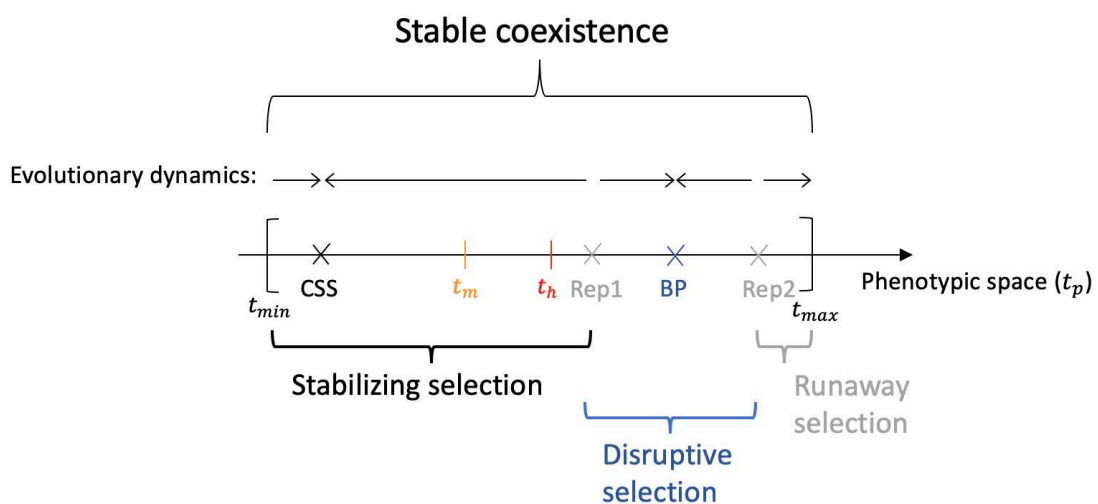


Fig. S2: Correspondence between evolutionary dynamics and types of selection. CSS, BP, and Rep stand respectively for continuously stable strategy, branching point, and repeller.

Note that the eco-evolutionary landscape can be much more complicated than the one presented in **Fig. S2**. The phenotypic space corresponding to stable coexistence can consist of several disjunct intervals. Moreover, we considered that stabilizing selection occurs in the phenotypic space where unbounded population growth is observed. In the E3 diagrams (x-axis $t_h - t_m$) where such an orgy of mutual benefaction is observed (**Fig. 5b & 5d, Fig. S5d**), a CSS always collides with the orgy area, which motivates our choice.

2. Explaining the type of selection by the relative importance of pollination and herbivory

In a first Monte Carlo experiment, we quasi-randomly sample 10 000 interspecific parameter sets. The sampling corresponds to a 5-dimensional Sobol sequence (Sobol' 1967) which enables a low-discrepancy sampling (i.e. a more homogenous coverage of the parameter space). For each parameter set, we calculate the position and nature of singularities occurring in a stable coexistence context. We also calculate plant-animal interaction strengths and animal densities at each singularity. This allows linking the ecological context (i.e. the relative importance of pollination and herbivory) to the type of selection. Consistent with the correspondence between evolutionary dynamics and types of selection introduced in the previous section, we consider that a CSS corresponds to stabilizing selection, a BP corresponds to disruptive selection, and a repeller corresponds to runaway selection. Repellers leading to the disruption of plant-pollinator-herbivore coexistence are included (e.g. Rep2 in Fig. S3), while repellers surrounded by convergent singularities (e.g. Rep1 in Fig. S3) are excluded. Three ratios of pollination over herbivory are used to describe the ecological context: the ratio of interspecific interaction strengths at the singularity t_p^* (i.e. $\frac{a_{pm}(t_p^*)}{a_{ph}(t_p^*)}$), the ratio of animal densities (i.e. $\frac{M^*}{H^*}$), and their more integrative product (i.e. $\frac{a_{pm}(t_p^*)M^*}{a_{ph}(t_p^*)H^*}$). We use non-parametric statistical tests (R-software, packages “rstatix” and “coin”) to test if, and to what extent, each ratio is able to explain the type of selection. Details of the statistical analysis performed, as well as the results obtained, are presented in **Appendix C**.

3. Isolating the effect of each interspecific parameter on selection

Given a focal parameter from the interspecific parameter set, we divide its range (table 1) into six intervals of the same length. For each interval, we then sample 1000 interspecific parameter sets (Sobol sequence), but constraining the focal parameter within the considered interval. For each sampled parameter set, we calculate the proportion of phenotypic space corresponding to each type of selection (as in **Fig. S2**). We then consider the mean (and standard error) of these proportions as a measure of the relative importance of each type of selection when the focal parameter is within the considered interval. We finally estimate the effect of the

focal parameter on selection by comparing these measures across the six intervals. The results are presented in **Fig. 3** for $t_h - t_m$, and the panel **Fig. 4** for $a_{pm0}, a_{ph0}, \sigma_{Pol}, \sigma_{Her}$.

4. Assessing the relationship between long-term interaction pattern and trade-off intensity

The range of variation of the dissimilarity between animal phenotypes (i.e. $t_h - t_m$) is divided into six intervals of similar length [0,0.5] ... [2.5,3]. We sample 1000 interspecific parameter sets while constraining animal phenotype dissimilarity in each of these intervals. This dissimilarity is a proxy for the strength of the ecological trade-off. For each parameter set, we determine the position and nature of all the singularities occurring at stable coexistence. We want to calculate the relative contribution of pollination to total plant-animal interactions when the plant trait becomes stable over time (i.e. long term on an evolutionary timescale) and when coexistence is maintained. Such dynamics are possible either when the plant phenotype is at the CSS (monomorphic) or if post-branching dynamics lead to a stable dimorphic population. We therefore (1) directly calculated the ratios $\frac{a_{pm}(t_p^*)}{a_{pm}(t_p^*)+a_{ph}(t_p^*)}$ and $\frac{a_{pm}(t_p^*)M^*}{a_{pm}(t_p^*)M^*+a_{ph}(t_p^*)H^*}$ at the CSSs (using their positions) and (2) numerically simulated the post-branching dynamics. **Table S1** indicates, for each interval of $t_h - t_m$, the type and number of singularities encountered.

Actually, for our main ecological parameter set, the number of branching points found (676 over 6000 parameter sets) was too high to simulate them all. Hopefully, preliminary work suggested that dimorphism was maintained only when **the branching point is located below t_m , or the branching is located above t_h while another branching exists below t_m (condition (A) in table S1)**. We therefore simulated the 35 branchings satisfying condition (A) (**table S1**), which were all observed when the trade-off was very strong (i.e. $t_h - t_m \leq 0.5$). After 10^9 timesteps, **dimorphism was maintained in 34 cases**. In all cases, one morph evolved toward a no interaction strategy ($t_p \nearrow$ or \searrow) while the other morph evolved to strongly interact with both animals at a stabilized phenotype. In this latter branch, the maximal variation of the plant phenotype over the last 100 mutation events was indeed lower than half of the mutation kernel standard deviation ($\sigma = 0.02$). This indicated that the local fitness landscape was flat. The ratios of pollination over total plant-animal interactions were calculated for these stabilized morphs and added to the results from the CSSs. We also simulated the post-branching dynamics following 36 randomly drawn branching events from the remaining 641 branching singularities (i.e. not satisfying condition (A), see **table S1**). In all cases, one branch went extinct while the remaining branch converged toward a CSS (as in **Fig. 2b**), supporting our assumption (i.e. condition (A)). The interaction pattern at the CSS was, by definition, already included in our dataset. We consequently assumed that dimorphism was lost following all branching points not satisfying condition (A). As a result, stabilizing selection was responsible for the maintenance of coexistence in $\frac{TotalCSS_{number}}{TotalCSS_{number}+TotalBP\ with\ maintained\ dimorphism_{number}} = \frac{4726}{4726+34} \approx 99.2\%$ of the cases (see **table S1**). Disruptive selection could maintain coexistence – i.e. evolutionary stable dimorphism – at very strong trade-offs (i.e. $t_h - t_m \leq 0.5$), in

$\frac{\text{BP with maintained dimorphism at very strong trade-off}_{\text{number}}}{\text{CSS at very strong trade-off}_{\text{number}} + \text{BP with maintained dimorphism at very strong trade-off}_{\text{number}}} = \frac{34}{1082+34} \approx 3\%$ of the cases (see **table S1**).

In the case of our robustness ecological parameter set, stabilizing selection was always responsible for the maintenance of coexistence. Indeed, 15 branchings were found (see **table S1**), no one satisfying condition (A), and simulations indicated that dimorphism was never maintained.

Ecological Parameter set	Trade-off	Number Of singularities	Repellers	CSS	Branching Points (BPs)	BPs satisfying condition (A)	BPs not satisfying condition (A)
Main ($r_p = 10, r_m = -1, r_h = -4, c_p = 0.6, c_m = 0.5, c_h = 0.4, e_m = 0.2, e_h = 0.3$)	$t_h - t_m \leq 0.5$	1604	367	1082	155	35	120
	$0.5 < t_h - t_m \leq 1$	1504	373	971	160	0	160
	$1 < t_h - t_m \leq 1.5$	1489	458	862	169	0	169
	$1.5 < t_h - t_m \leq 2$	1367	506	753	108	0	108
	$2 < t_h - t_m \leq 2.5$	1192	516	615	61	0	61
	$2.5 < t_h - t_m \leq 3$	882	416	443	23	0	23
	Total		8038	2636	4726	676	35
Robustness ($r_p = 10, r_m = r_h = -1, c_p = 0.6, c_m = c_h = 0.4, e_m = e_h = 0.2$)	$t_h - t_m \leq 0.5$	1628	876	748	4	0	4
	$0.5 < t_h - t_m \leq 1$	1658	891	762	5	0	5
	$1 < t_h - t_m \leq 1.5$	1645	895	747	3	0	3
	$1.5 < t_h - t_m \leq 2$	1534	832	699	3	0	3
	$2 < t_h - t_m \leq 2.5$	1340	698	642	0	0	0
	$2.5 < t_h - t_m \leq 3$	1072	479	593	0	0	0
	Total		8877	4671	4191	15	0

Table S1: Summary of the singularities (number and type) found in the Monte Carlo experiment aiming at determining the long-term interaction pattern when coexistence is maintained. For each line, 1000 interspecific parameter sets were sampled.

Appendix C: The ratio of pollination to herbivory explains the nature of selection

I. Statistical results

For each ratio of pollination to herbivory, we tested its power to discriminate between the three types of selection – stabilizing, disruptive and runaway – using a Kruskal-Wallis test (non-parametric ANOVA, packages “rstatix” and “coin” in R). Based on Tomczak and Tomczak (2014), the effect size (i.e. proportion of variance explained) is computed as the eta squared based on the H-statistic (i.e. $\frac{H-k+1}{n-k}$, with n and k the total number of observations and the number of groups, respectively). We complemented the analysis by comparing the distribution of ratios between each two groups (i.e. each two types of selection) using the Wilcoxon-Mann-Whitney test (Holm-Bonferroni correction for multiple comparisons). Its effect size (Tomczak and Tomczak 2014) is computed as the Z-statistic divided by the square root of the total sample size N (i.e. $\frac{Z}{\sqrt{N}}$). The tests were performed on the quasi-random (Sobol) draw of 10000 interspecific parameter sets, the ecological parameter set being fixed (focal one, see **Table 1**). Note that a given parameter set can lead to several types of selection (i.e. several evolutionary singularities), a dependence that we were not able to incorporate in the statistical model. The results of this statistical analysis are presented in the following **table S2**. All statistical tests were highly significant, with p_{value} always lower than $2 \cdot 10^{-16}$.

The ratio of pollination to herbivory that accounts for both the interaction strengths, and animal densities explains most the nature of selection (Kruskal-Wallis effect size). It is also the best to discriminate between any two types of selection (Wilcoxon effect size). This ratio, however, might be difficult to measure in an empirical context as it requires two types of information: interaction strengths, and densities. The two other ratios, requiring only one type of information, might be more suitable in an empirical context given they are also able to largely explain the nature of selection (Kruskal-Wallis effect sizes). The complementarity between them is worth mentioning (Wilcoxon effect sizes): while the ratio of interaction strengths is weaker at discriminating between disruptive and runaway selections, the ratio of animal densities is weaker at discriminating between disruptive and stabilizing selection. Overall, the ratio of interaction strengths seems better than the ratio of animal densities, but one should choose which ratio to measure according to the assumptions on the type of selection mostly occurring in the empirical system under study.

Ratio of pollination to herbivory	Expression	Median per type of selection			Kruskal-Wallis effect size	Wilcoxon effect size		
		Runaway	Disruptive	Stabilizing		D vs. RA	D vs. S	S vs. RA
Interaction strengths and animal densities	$\left. \frac{a_{pm}M^*}{a_{ph}H^*} \right]_{t_p^*}$	0.13	0.91	3.25	0.675	0.785	0.547	0.762
Interaction strengths	$\left. \frac{a_{pm}}{a_{ph}} \right]_{t_p^*}$	0.4	0.5	1.36	0.629	0.488	0.520	0.75
Animal densities	$\left. \frac{M^*}{H^*} \right]_{t_p^*}$	0.32	1.67	2.42	0.570	0.786	0.249	0.762

Table S2: Results of the statistical analysis for the three ratios of pollination to herbivory tested. The ratios are calculated at the evolutionary singularities t_p^* . Abbreviations: S for stabilizing, D for disruptive and RA for runaway. Sample size (interspecific parameter sets): 10000, which resulted in 7835 S, 2787 RA and 1137 D. Ecological parameter set: ($r_p = 10, r_m = -1, r_h = -4, c_p = 0.6, c_m = 0.5, c_h = 0.4, e_m = 0.2, e_h = 0.3$). All statistical tests were highly significant, with a p_{value} below $2 \cdot 10^{-16}$ for the Kruskal-Wallis test, and an adjusted p_{value} below 10^{-4} for the Wilcoxon tests. Correction for multiple comparisons (Wilcoxon test): Holm-Bonferroni. The interpretation of effect size commonly found in the literature is indicated by colors: small [0.1,0.3] in light red, moderate [0.3,0.5] in dark red, large [0.5,1] in black.

II. Robustness to the variation of the ecological parameter set

Here, we vary the ecological parameter set (values in parenthesis in table 1) to check the robustness of the results presented in Figure 3 and table S2.

1. Robustness of Fig. 3 to the variation of the ecological parameter set (Fig. S3)

The results presented in **Fig. 3** are robust to the variation of the ecological parameter set:

- Stabilizing selection is characterized by large pollination to herbivory ratios, while runaway selection is characterized by small pollination to herbivory ratios (**Fig. S3a**).
- Disruptive selection is characterized by balanced pollination to herbivory ratios, in between the ratios favoring the two other types of selection (**Fig. S3a**). Note, however, that in the present case, disruptive selection is extremely rare (**Fig. S3b**).
- The ratio of pollination to herbivory largely explains the nature of selection (Kruskal-Wallis effect size of 75%, **Fig. S3a**).

Changing the ecological parameter set, the most notable difference is the way in which the proportion of phenotypic space corresponding to stabilizing or runaway selection varies with the trade-off intensity. As presented in the main document, this implies that these variations depend on the ecological parameter set. When the latter favors pollinators in comparison to herbivores, stabilizing selection is more frequent at the expense of runaway selection when the trade-off intensifies (Fig. 3b). When it is not the case, the opposite pattern is observed (Fig. S3b). All else being equals, a focal animal should be favored if its growth rate or conversion efficiency is bigger, or its intraspecific competition rate smaller.

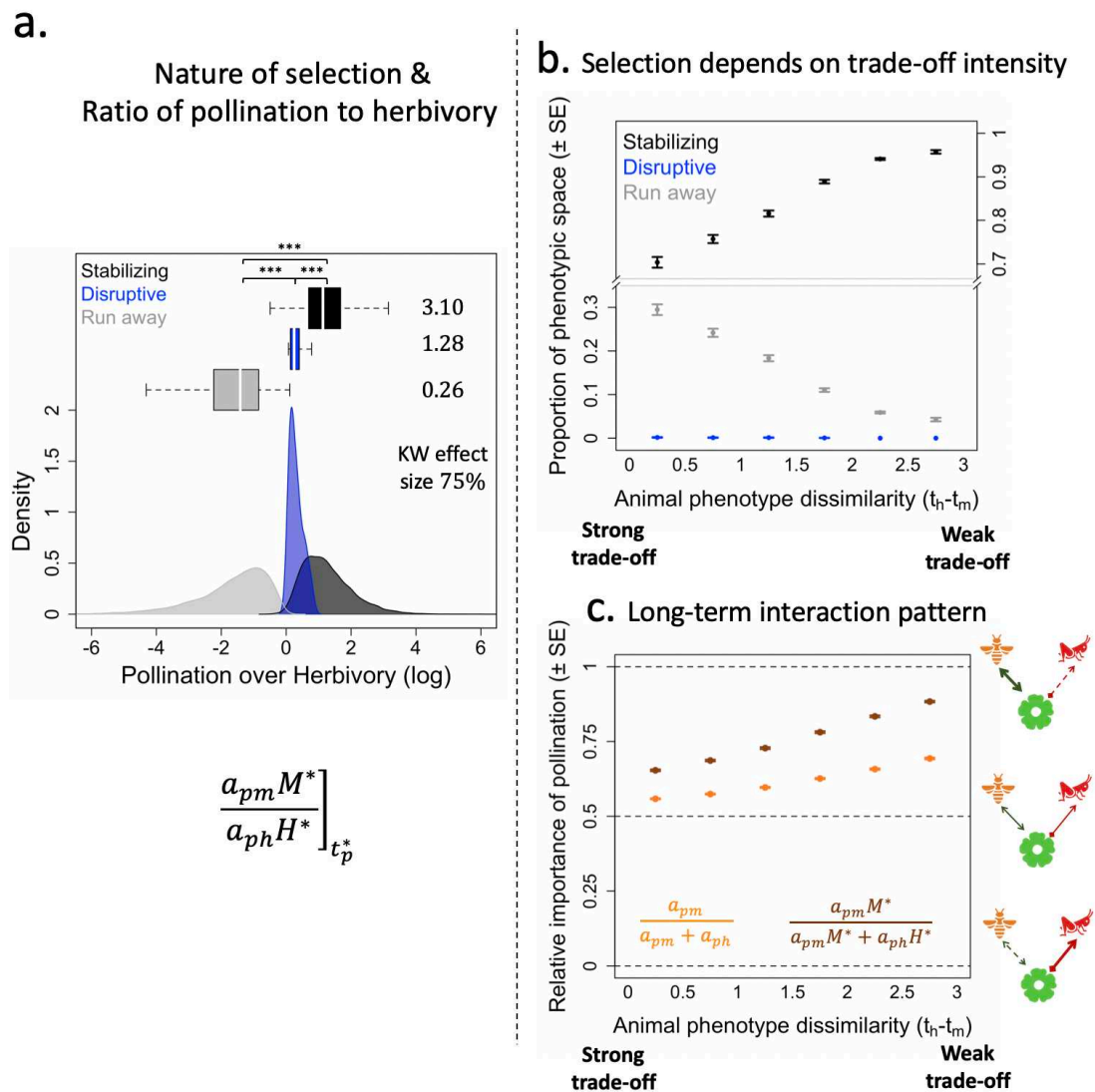


Fig. S3: The ratio of pollination to herbivory explains the nature of selection, with consequences on the link between selection, long-term interaction pattern and trade-off intensity. a. Distribution of pollination to herbivory ratio according to the type of selection. The ratio is measured at the CSS for stabilizing selection, at the branching for disruptive selection, and at the repellor for runaway selection. The medians indicated correspond to absolute values (no log). The effect size of the Kruskal-Wallis test ($p_{value} < 2 \cdot 10^{-16}$) is also indicated. The stars indicate the significance level for the pairwise comparisons (Wilcoxon test): $*** < 10^{-4}$. **b. Relative importance of each type of selection according to trade-off intensity.** The relative importance is measured as

the proportion of the phenotypic space allowing stable coexistence over which a given type of selection is observed (see Fig. S2). **c. Long-term (i.e. evolutionary stable) interaction pattern when coexistence is maintained.** The cases where coexistence is maintained are under stabilizing selection (representing the vast majority of such cases), or in a dimorphic situation (extremely rare) resulting from disruptive selection. Coexistence is always disrupted under runaway selection. The results presented in this figure are from Monte-Carlo experiments (details in Appendix B.II). Interspecific parameter sets sampled: (a) 10000, (b) 1000. Ecological parameter set: ($r_p = 10, r_m = -1, r_h = -1, c_p = 0.6, c_m = 0.4, c_h = 0.4, e_m = 0.2, e_h = 0.2$).

2. Statistical results

Overall, the variation of the ecological parameter does not change the results derived so far (Table S2). Indeed, the three ratios of pollination to herbivory still largely explain the nature of selection (Kruskal-Wallis effect size). The major difference is that their explanatory power is identical now, while it was previously a bit different. This difference is due to the fact that all ratios are now weak at discriminating between disruptive selection and other types of selection (Wilcoxon effect size). This is likely due to the very low number of observations of disruptive selection (22), and indicates the critical role of the ecological parameter set in observing disruptive selection.

Ratio of pollination to herbivory	Expression	Median per type of selection			Kruskal-Wallis effect size	Wilcoxon effect size		
		Runaway	Disruptive	Stabilizing		D vs. RA	D vs. S	S vs. RA
Interaction strengths and animal densities	$\left. \frac{a_{pm}M^*}{a_{ph}H^*} \right]_{t_p^*}$	0.26	1.28	3.10	0.747	0.091	0.08	0.864
Interaction strengths	$\left. \frac{a_{pm}}{a_{ph}} \right]_{t_p^*}$	0.67	1.07	1.52	0.745	0.091	0.073	0.863
Animal densities	$\left. \frac{M^*}{H^*} \right]_{t_p^*}$	0.38	1.22	2	0.747	0.092	0.082	0.864

Table S3: Results of the statistical analysis for the three ratios of pollination to herbivory tested. Sample size (interspecific parameter sets): 10000, which resulted in 7774 S, 7600 RA and 22 D. Ecological parameter set: ($r_p = 10, r_m = -1, r_h = -1, c_p = 0.6, c_m = 0.4, c_h = 0.4, e_m = 0.2, e_h = 0.2$). All statistical tests were highly significant, with a p_{value} below $2 \cdot 10^{-16}$ for the Kruskal-Wallis test, and an adjusted p_{value} below 10^{-4} for the Wilcoxon tests. Correction for multiple comparisons (Wilcoxon test): Holm-Bonferroni. The interpretation of effect size commonly found in the literature is indicated by colors: small [0.1,0.3] in light red, moderate [0.3,0.5] in dark red, large [0.5,1] in black.

Appendix D: Isolating the effect of interspecific parameters on community eco-evolutionary dynamics

I. Robustness of Fig. 4 to the variation of the ecological parameter set (Fig. S4)

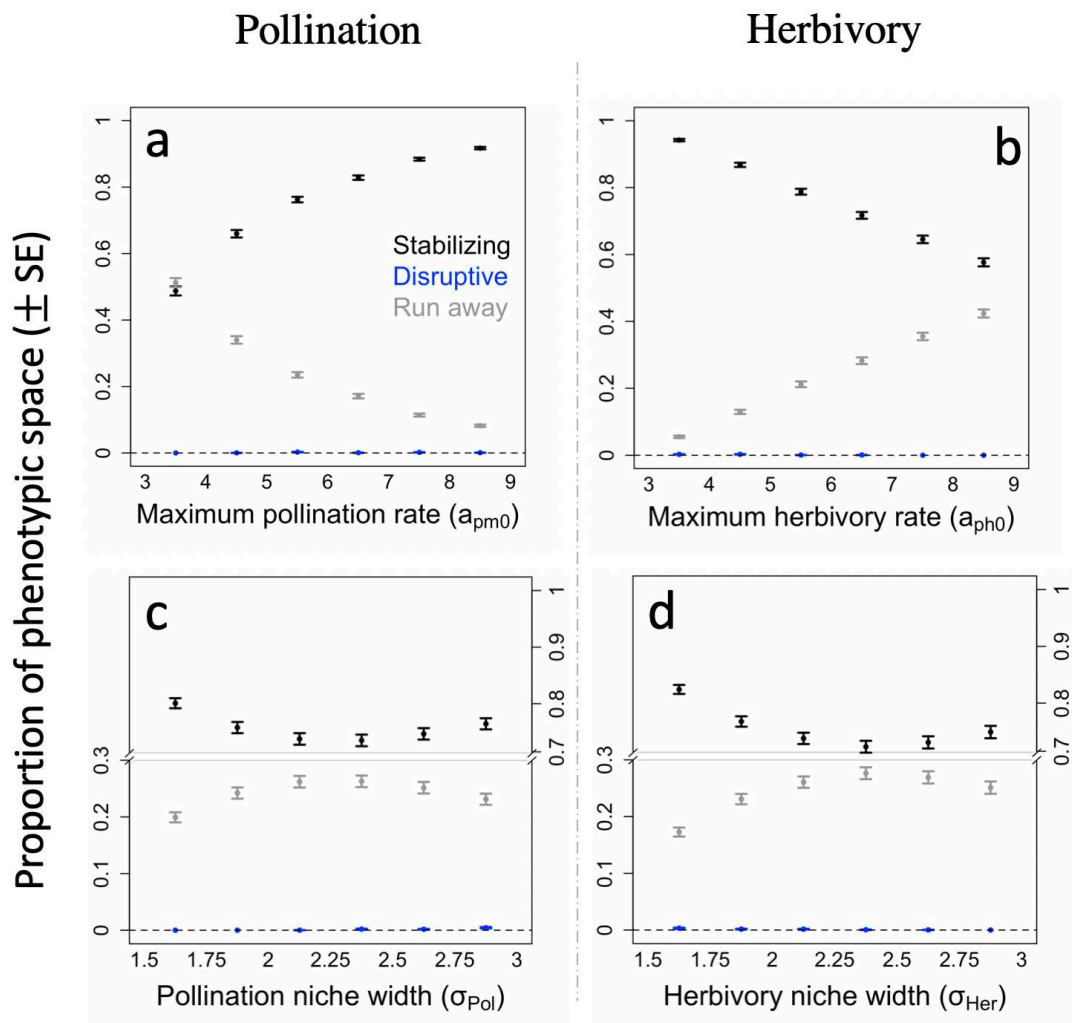


Fig. S4: The effects of interspecific parameters on selection are robust in the case of maximum interaction rates, but not in the case of interaction niche widths a. Effect of per capita maximum pollination rate. b. Effect of per capita maximum herbivory rate. c. Effect of pollination niche width. d. Effect of herbivory niche width. The results are from Monte-Carlo experiments (1000 sampled sets at each point, details in Appendix B.II). Ecological parameter set: ($r_p = 10, r_m = -1, r_h = -1, c_p = 0.6, c_m = 0.4, c_h = 0.4, e_m = 0.2, e_h = 0.2$).

The effect of scaling factors on selection seem robust to the variation of the ecological parameter set. An increase of the pollination scaling factor (a_{pm0}) makes stabilizing selection more frequent at the expense of runaway selection. The effect of the herbivory scaling (a_{ph0}) factor is utterly opposite. Finally, disruptive selection is extremely rare for this ecological parameter set.

In contrast, the effects of interaction niche widths on selection are not robust to the variation of the ecological parameter set. In particular, the niche width of both interactions seems to similarly affect selection: an intermediate niche width maximizes runaway selection and minimizes stabilizing selection. It is interesting to note that intermediate niche widths favor small and intermediate niche width asymmetries (over large asymmetries) between pollination and herbivory.

II. Effects of interaction niche widths on eco-evolutionary dynamics (Fig. S5)

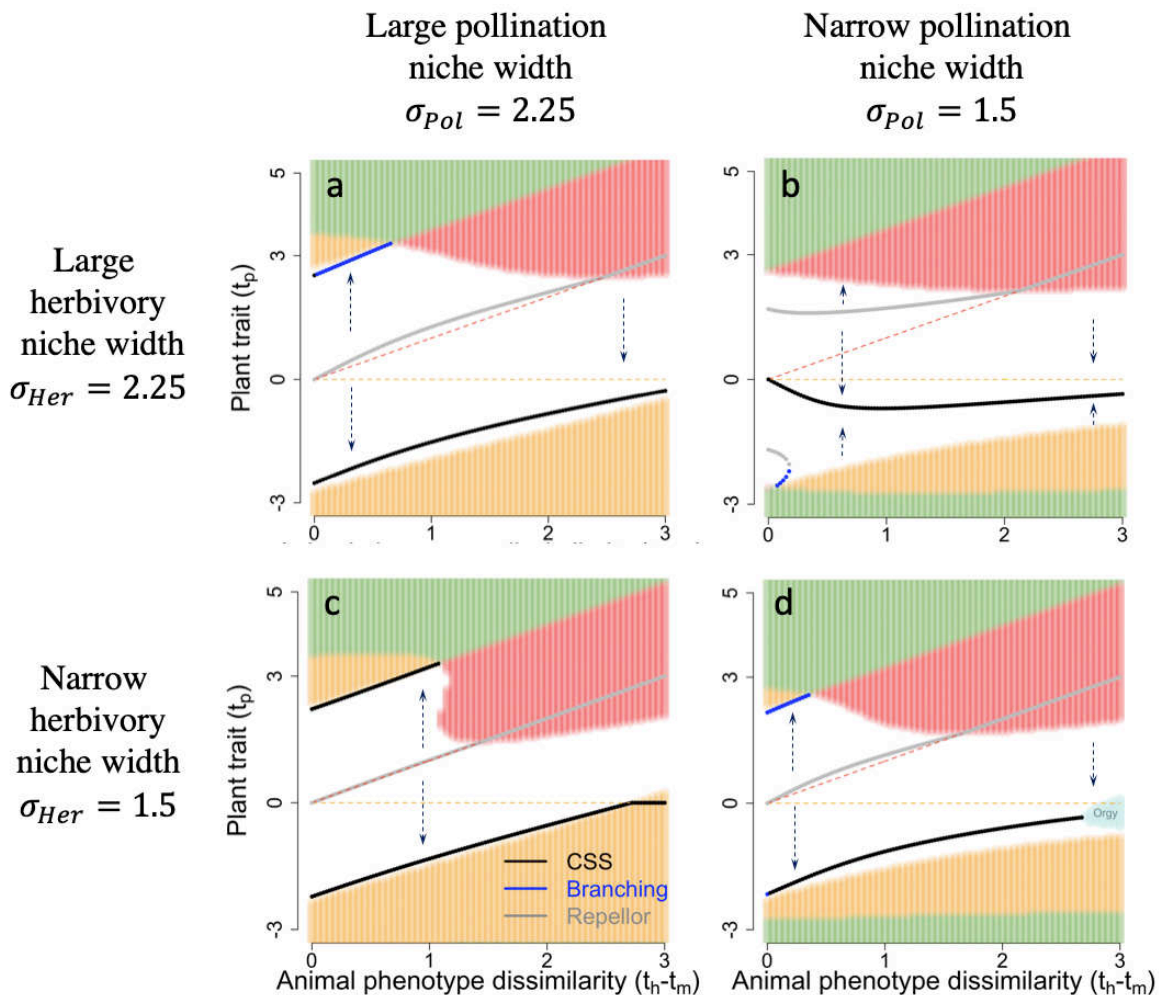


Fig. S5: Pollination vs. herbivory niche widths affect the community eco-evolutionary dynamics. Arrows indicate evolutionary trajectories and background colors indicate community composition (as in Fig.

2a): green for plants, orange for plant-pollinator, red for plant-herbivore and white for stable coexistence. Light blue indicates unbounded population growths. Evolutionary singularities are figured as colored curves: CSS (convergent, non-invasible), BP (convergent, invasible) and repellor (non-convergent, invasible). Ecological parameter set: $(r_p = 10, r_m = -1, r_h = -1, c_p = 0.6, c_m = 0.4, c_h = 0.4, e_m = 0.2, e_h = 0.2)$. Scaling factors for plant-animal interactions: $a_{pm0} = 5, a_{ph0} = 9$.

III. Long-term dynamics after branching events (i.e. disruptive selection)

Our Monte Carlo experiment aiming at quantifying the long-term interaction pattern (**Appendix B.II.4**) led us to simulate the long-term evolutionary dynamics after the encountered branchings. Among the 676 branching points encountered (**table S1 in Appendix B.II.4**), we simulated the dynamics following 71 of them. Those 71 corresponded to (1) 35 branchings satisfying condition (A) (i.e. the branching singularity occurs above t_h , or the branching singularity occurs below t_m but the fitness landscape has also a branching singularity above t_h), and (2) 36 branchings that were randomly drawn within the remaining 641 branching points not satisfying condition (A). The results strongly support the key role of condition (A): (1) 34 out of 35 branchings led to a maintained (i.e. evolutionary stable) dimorphism; (2) all 36 branchings did not maintain dimorphism in the long term. From these results, we concluded that dimorphism was maintained in $\frac{34}{676} \approx 5\%$ of the branching events encountered. These 34 cases were all observed at a very strong trade-off (i.e. $t_h - t_m \leq 0.5$), and represented $\frac{34}{155} \approx 22\%$ of the branching encountered at these strong trade-offs (**table S1**).

In addition, we simulated the branchings appearing in **Fig. 5 & S5** (8 branching points). As shown in table S4, the results regarding these simulations are in line with the previous analysis based on a large set of interspecific parameters (Monte Carlo experiment). Only when condition (A) was satisfied did the two branches maintain in the long run (i.e. BP 3, 4 & 7 in **table S4**). Condition (A) correspond to a “yes” in columns 5 or 6 of **table S4**. The potential for disruptive selection to occur when the plant-pollinator trait matching is better than the plant-herbivore one seems thus key for the maintenance of dimorphism.

Fig. S6 presents the long-term evolutionary dynamics after the branchings BP3 & BP4 (**table S4, Fig. 5c**). Note that (1) these dynamics are different, but (2) in both cases (and also for BP7, not shown), one plant morph evolves toward strong plant-animal interactions while the other morph evolves toward weak plant-animal interactions.

Designation	Figure	Animal phenotype dissimilarity (i.e. t_h , given $t_m = 0$).	Position of the branching singularity t_p^*	Is the focal branching point closer to t_m than t_h ?	Is there a branching point closer to t_m than t_h ?	Dimorphism maintained?
BP 1	Fig. 5a	0.6	$t_p^* > t_h$	No	No	No
BP 2	Fig. 5b	0.9	$t_p^* > t_h$	No	No	No
BP 3	Fig. 5c	0.1	$t_p^* > t_h$	No	Yes (BP4)	Yes
BP 4	Fig. 5c	0.1	$t_p^* < t_m$	Yes	Yes (BP4)	Yes
BP 5	Fig. 5d	0.5	$t_p^* > t_h$	No	No	No
BP 6	Fig. S5a	0.4	$t_p^* > t_h$	No	No	No
BP 7	Fig. S5b	0.15	$t_p^* < t_m$	Yes	Yes (BP7)	Yes
BP 8	Fig. S5d	0.25	$t_p^* > t_h$	No	No	No

Table S4: Dimorphism is temporary in most cases, but it can be maintained in the long term (BPs 3, 4 & 7).

Branching Point 3 (Fig. 5c, top)

Branching Point 4 (Fig. 5c, bottom)

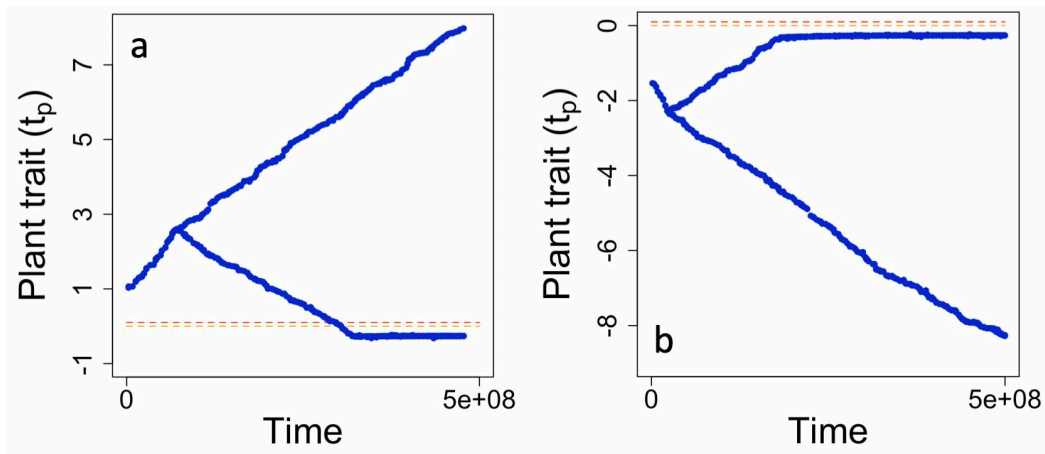


Fig. S6: Simulation of the plant phenotype long-term dynamics after a branching (a. BP3, b. BP4). The orange (resp. red) dotted line indicates the pollinator (resp. herbivore) phenotype t_m (resp. t_h).

Appendix E: Simulation code

The analytical investigation is completed by numerical simulations of the community eco-evolutionary dynamics. The code was implemented in C and the GNU Scientific library was extensively used.

In addition to the description given in the Method section, it is worth mentioning that:

- initial biomasses are set to $\varepsilon = 2 \cdot 10^{-6}$, which is also the extinction threshold below which a population is removed from the simulation
- the first mutation events take place after 1000 timesteps
- the time of any next mutation event is randomly drawn from an exponential random variable whose parameter λ is the frequency of mutation events, which corresponds to the product of total plant biomass (at the time of drawing) and the mutation probability per biomass unit ($\mu = 2 \cdot 10^{-7}$). This procedure makes the succession of mutation events correspond to a Poisson process characterized by a mutation probability per unit biomass μ .

References

- Dieckmann, U., and R. Law. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of Mathematical Biology* 34:579–612.
- Sobol', I. Y. M. 1967. On the distribution of points in a cube and the approximate evaluation of integrals. *USSR Computational Mathematics and Mathematical Physics* 7:86–112.
- Tomczak, M., and E. Tomczak. 2014. *The need to report effect size estimates revisited. An overview of some recommended measures of effect size*. Trends in Sport Sciences (Vol. 1).
- Yacine, Y., and N. Loeuille. 2021. Stable coexistence in plant-pollinator-herbivore communities requires balanced mutualistic vs antagonistic interactions. bioRxiv.

IV.

Chaper III

Pollinator and herbivore (co)-evolution within a two
plant-species floral landscape

There is still some work needed to properly finish this chapter. In particular, the study of coevolution is not complete yet. We notably have to explore stronger trade-off intensities, as preliminary results indicate qualitatively novel patterns in comparison to what we have obtained so far (see **VI. Perspectives**). In addition, the introduction and discussion are not fully written yet. Once this is done (in a few months or so), the paper will be submitted to a generalist ecology journal such as *The American Naturalist*.

Pollinator and herbivore (co)-evolution within a two plant-species floral landscape

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Abstract

Both plant-pollinator and plant-herbivore interactions are key drivers of the evolution of pollinator and herbivore species, respectively. But pollination, by modifying the floral landscape, is also responsible for indirect selective pressures on herbivore phenotypes. Conversely, herbivory may also modify the selective pressures acting on pollinator phenotypes. As such, the evolutionary dynamics of pollinators and herbivores are intimately intertwined. To shed light on such dynamics - as well as on their consequences on the coexistence of plants, pollinators and herbivores - we investigate the eco-evolutionary dynamics arising from the (co)evolution of animal phenotypes within a plant community consisting of two competing species. Using the adaptive dynamics framework, we start by comparing pollinator vs. herbivore evolution within communities of increasing ecological complexity (i.e. presence/absence of the other animal). We then use numerical simulations to investigate coevolutionary scenarios. Our results demonstrate the prevailing role of the eco-evolutionary feedback - positive for pollinators and negative for herbivores – in driving qualitatively distinct, if not opposite, eco-evolutionary dynamics. Pollinator evolution fosters the exclusion of the inferior competitor plant species, while the evolution of herbivores favors plant coexistence. Herbivores are selected toward increasing their niche overlap with pollinators, while pollinators are selected toward niche partitioning. This notably explains the occurrence of fluctuating selection leading to cycling coevolving phenotypes. Such a situation is, however, transient as coevolution always leads to similar animal phenotypes. Shared animal preferences for plant phenotypes have been frequently reported in the literature. We notably discuss how our results might help explain why such a pattern could be widespread in natural communities.

Keywords

competition, eco-evolutionary feedback, evolutionary murder, herbivory, pollination, disruptive selection, coexistence maintenance, diversity

Introduction

In the present paper, we investigate the eco-evolutionary dynamics arising from the evolution of animal phenotypes within a two-species floral landscape. We consider two animal species – a pollinator and a herbivore – that interact simultaneously with two competing plant species. Plant-animal interactions depend on a single plant trait involved in both interactions. These interactions get stronger as the matching between the respective plant and animal phenotypes increases. Examples of such traits include flower color (Irwin et al. 2003), flower display (Galen and Cuba 2001), chemical volatiles (Theis et al. 2014) and the corresponding animal preferences. Phenological traits (e.g. Brody 2008) also fit well within this category as plant-animal interactions require interacting species to co-occur in time. Animal phenotypes are allowed to evolve while plant phenotypes are fixed, and more importantly, differ. Animal species are thus subject to an ecological trade-off because increasing their trait-matching with a given plant species strengthens the focal plant-animal interaction but weakens the other one. In such a context, our overarching goal is to characterize and compare the effects of pollinator vs. herbivore evolution, as well as of their coevolution, on the diversity within the community. Before considering coevolutionary scenarios, we start by comparing pollinator vs. herbivore evolution within communities of increasing ecological complexity. First, we consider the evolution of a focal animal in the absence of the other animal species (i.e. plant-pollinator vs. plant-herbivore communities). Second, we study the evolution of each animal within the whole plant-pollinator-herbivore community, but fixing the other animal phenotype. Finally, we investigate the coevolution of animal phenotypes. In all cases, we are interested in (1) assessing the type of evolutionary dynamics – the potential for disruptive selection in particular – arising from the availability of plant resources with distinct phenotypes (i.e. ecological trade-off), and (2) determining how these dynamics affect the maintenance of plant coexistence. We use the framework of adaptive dynamics (Metz et al. 1992; Dieckmann and Law 1996) to address these questions when only one animal is evolving, while the coevolutionary scenario is studied using numerical simulations. In particular, the analytical results obtained in the lower complexity scenarios shed light on the mechanisms underlying the dynamics observed when pollinators and herbivores are coevolving. Our results emphasize the prevailing role of the eco-evolutionary feedback loops arising from each plant-animal interaction – positive for pollination and negative for herbivory – in driving opposite eco-evolutionary patterns (i.e. (1) & (2)).

Model & Methods

Model

Population dynamics

We consider two plant species, P_1 and P_2 , which interact with a pollinator M and a herbivore H . Their biomass densities follow the dynamics set by the following four ordinary differential equations (details on parameters in **table 1**).

$\frac{dP_1}{dt} = P_1(r_p - c_p P_1 - c_{p21} P_2 + a_{pm1} M - a_{ph1} H)$	(1)
$\frac{dP_2}{dt} = P_2(r_p - c_p P_2 - c_{p12} P_1 + a_{pm2} M - a_{ph2} H)$	(2)
$\frac{dM}{dt} = M(r_m - c_m M + e_m a_{pm1} P_1 + e_m a_{pm2} P_2)$	(3)
$\frac{dH}{dt} = H(r_h - c_h H + e_h a_{ph1} P_1 + e_h a_{ph2} P_2)$	(4)

Plants are assumed to have positive and identical growth rates ($r_p > 0$, autotrophs), as well as identical intraspecific competition rates (c_p). The two plant species are also competing for space, light and/or nutrients (Craine and Dybzinski 2013) as captured by the rates of interspecific competition (c_{p12}, c_{p21}). Those rates are not necessarily identical: c_{p12} captures the effect of species 1 on species 2, while c_{p21} captures the reverse effect. We are thus focusing on the effect of asymmetrical plant competitive abilities on community eco-evolutionary dynamics.

Pollinator ($r_m < 0$) and herbivore ($r_h < 0$), in contrast, have negative intrinsic growth rates (heterotrophs). They also undergo intraspecific competition (c_m, c_h). The efficiencies of biomass conversion from plants to animals are set by e_m, e_h . As indicated in **table 1**, all these parameters are assumed identical for pollinators and herbivores because we are interested in the potential differential eco-evolutionary patterns that arise as a result of the differences in plant-animal interactions. Those interactions are captured by a_{pm1} & a_{pm2} for pollination, and a_{ph1} & a_{ph2} for herbivory.

Such a dynamical system reaches an ecological equilibrium when all population growth rates vanish (i.e. right sides of equations 1-4 are null). There are 16 possible equilibria whose

analytical expressions (P_1^*, P_2^*, M^*, H^*), as well as stability, is determined in **Appendix B.V**. Instability can notably take the form of unbounded population growth driven by “an orgy of mutual benefaction” (May 1981) owing to the linear plant-pollinator interactions.

Plant-animal interactions depend on trait-matching

We assume plant-animal interactions to intensify as the matching between the plant phenotype (t_{p1} or t_{p2}) and the corresponding animal phenotype – pollinator (t_m) or herbivore (t_h) – increases. The considered plant trait thus corresponds to any trait affecting pollination (equation 5) and herbivory (equation 6) in such a way.

$a_{pm1} \stackrel{\text{def}}{=} a_{pm}(t_{p1}, t_m) = \frac{a_{pm0}}{\sqrt{2\pi\sigma_{Pol}^2}} \exp\left[-\frac{(t_{p1} - t_m)^2}{2\sigma_{Pol}^2}\right]; a_{pm2} \stackrel{\text{def}}{=} a_{pm}(t_{p2}, t_m) \quad (5)$
$a_{ph1} \stackrel{\text{def}}{=} a_{ph}(t_{p1}, t_h) = \frac{a_{ph0}}{\sqrt{2\pi\sigma_{Her}^2}} \exp\left[-\frac{(t_{p1} - t_h)^2}{2\sigma_{Her}^2}\right]; a_{ph2} \stackrel{\text{def}}{=} a_{ph}(t_{p2}, t_h) \quad (6)$

As σ_{Pol} controls how quickly the strength of plant-pollinator interactions decreases with plant-animal phenotype dissimilarities, it corresponds to the breadth of pollination niches. Niche breadth is the result of both plant and pollinator degrees of generalism. Likewise, σ_{Her} is the breadth of herbivory niches. Because it is not the focus of this work, pollinator and herbivore niche breadths are assumed equal ($\sigma_{Pol} = \sigma_{Her}$). The maximum per capita rates of plant-animal interactions are scaled by a_{pm0} for pollination, and a_{ph0} for herbivory. Finally, it is assumed that $t_{p1} < 0$ and $t_{p2} = -t_{p1}$, without any loss of generality.

In the present work, we focus on the asymmetry (P_1 vs. P_2) of plant-animal interactions arising from the sole plant phenotype dissimilarity ($t_{p1} \neq t_{p2}$), which explains why all other parameters affecting plant-animal interactions are assumed equal between the two plants. **Table 1** recapitulates our assumptions regarding the different parameters, as well as their biological meanings and dimensions.

Table 1: List of all model parameters and variables with their biological significance, value and dimension (M for mass, L for length and t for time).

Variables and parameters		Biological significance	Value	Dimension
<i>Variables</i>	P_1	Plant biomass density		$M \cdot L^{-2}$
	P_2	Plant biomass density		$M \cdot L^{-2}$
	M	Pollinator biomass density		$M \cdot L^{-2}$
	H	Herbivore biomass density		$M \cdot L^{-2}$
	t_m	Pollinator phenotype		Dimensionless
	t_h	Herbivore phenotype		Dimensionless
<i>Interspecific interaction parameters</i>	a_{pm0}	Scaling of per capita maximum pollination rate	[3,9]	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	a_{ph0}	Scaling of per capita maximum herbivory rate	[3,9]	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	c_{p12}	Interspecific competition rates Effect of P_1 on P_2	[0.35,0.77]	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	c_{p21}	Interspecific competition rate Effect of P_2 on P_1	0.35	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	$t_{p1} = -t_{p2}$	Plant phenotypes	[-2.5,0]	Dimensionless
	$\sigma_{Pol} = \sigma_{Her}$	Pollination and herbivory niche breadths	1.5	Dimensionless
<i>Other ecological parameters</i>	$r_p > 0$	Plant intrinsic growth rates	10	t^{-1}
	$r_m = r_h < 0$	Animal intrinsic growth rates	-1	t^{-1}
	$c_{p1} = c_{p2}$	Plant intra-specific competition rates	0.7	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	$c_m = c_h$	Animal intra-specific competition rates	0.5	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	$e_m = e_h$	Plant to animal conversion efficiencies	0.2	Dimensionless
<i>Numerical simulations</i>	μ	Mutation probability (per unit of time and animal biomass density)	$2 \cdot 10^{-7}$	$(M \cdot L^{-2})^{-1} \cdot t^{-1}$
	σ	Mutation amplitude (standard deviation)	0.02	Dimensionless
	ε	Extinction threshold	$2 \cdot 10^{-6}$	$M \cdot L^{-2}$

Methods

We successively investigate scenarios of increasing eco-evolutionary complexity: (A) pollinator evolution within a plant-pollinator community vs. herbivore evolution within a plant-herbivore community; (B) pollinator evolution vs. herbivore evolution within a plant-pollinator-herbivore community; and (C) pollinator and herbivore coevolution within a plant-pollinator-herbivore community. The ecological dynamics of the subcommunities considered, which are given by a subset of equations 1-4, are presented in **Appendix B.II & III**. In each scenario, we are interested in characterizing (1) the evolutionary dynamics of animal phenotypes, and (2) their consequences for plant coexistence.

In what follows, we detail the approaches – analytical and numerical respectively – used to investigate the community eco-evolutionary dynamics in the case of one animal species evolving (scenarios A & B), and in the case of animal coevolution (scenario C).

Analytical study of the evolution of one animal species (A & B)

We use the framework of adaptive dynamics (Metz et al. 1992; Dieckmann and Law 1996) to analytically study the evolutionary dynamics of animal phenotypes and their ecological consequences. The underlying rationale is illustrated here in the case of pollinator evolution.

Within a monomorphic pollinator population with phenotype t_m (resident), we investigate whether a mutant with a new phenotype t_m' can invade. Invasion happens if the mutant fitness of invasion, computed as the expected long-term per capita growth rate of that mutant, when rare and in the environment set by the resident population (i.e. P_1^*, P_2^*, M^* and, depending on the scenario, H^*), is positive $w(t_m', t_m) > 0$ (see **Appendix C.II** for details). When a mutant invades, it replaces the resident population, thus becoming the new resident. The consecutive sequences of trait substitution define the long-term evolutionary dynamics. For any phenotypic trait, and assuming rare and small mutations, the expected rate of such sequences is proportional to the selection gradient (**Appendix C.II**), i.e. the derivative of invasion fitness with respect to the mutant's trait (Dieckmann and Law 1996). Finally, evolutionary singularities t_m^* correspond to phenotypes that nullify the selection gradient.

Community eco-evolutionary dynamics are utterly determined by the position and properties – convergence and invasibility (mathematical criteria in **Appendix C.II**) – of the

evolutionary singularities. Convergence indicates that the trait evolves towards the singularity in its vicinity, while invasibility specifies whether the singularity can be invaded by nearby mutants (i.e. is an ESS, Maynard Smith & Price 1973). There are thus two types of convergent singularities: the non-invasible continuously stable strategy (CSS, Eshel, 1983) and the invasible branching point (BP, Geritz *et al.* 1997). In their vicinity, selection favors closer phenotypes until the singularity phenotype is reached. Selection then is stabilizing in the case of a CSS, while it turns disruptive in the case of BP. As such, branching points are particularly important in terms of diversity as they yield the emergence of a stable dimorphism (e.g. the coexistence of two pollinator populations, each specialized in one plant species). There are also two types of non-convergent singularities – the invasible repeller and the non-invasible garden of Eden (Nowak 1990) – which produce qualitatively similar evolutionary dynamics corresponding to runaway selection that favors phenotypes that are increasingly farther.

We start by comparing the eco-evolutionary dynamics ensuing from animal evolution in the plant-pollinator vs. plant-herbivore community (A). We thus study how evolutionary singularities depend on the trade-off between interacting preferentially with either one plant species, as previous works on the evolution of consumer preference in the presence of two resources have demonstrated it plays a critical role (Levins 1962; de Mazancourt and Dieckmann 2004; Rueffler *et al.* 2006). In our framework, trade-off strength and shape (concave vs. convex) is determined by the degree of plant phenotype dissimilarity (i.e. $t_{p2} - t_{p1}$), as detailed in **Appendix C.I**. We then compare the eco-evolutionary dynamics resulting from pollinator vs. herbivore evolution within a plant-pollinator-herbivore community (B). Here, we particularly focus on how evolutionary dynamics depend on the fixed phenotype of the non-evolving animal species (i.e. t_m or t_h).

Finally, community eco-evolutionary dynamics – the consequences of animal evolution on plant coexistence in particular – may strongly depend on the structure of the plant community in the absence of animals (details in **Appendix B.I**). As a result, we systematically investigate three cases (see **Fig. S1** in **appendix B.I**): plant coexistence under similar interspecific competitive abilities (i.e. $c_{p12} = c_{p21}$, $P_1^* = P_2^*$, **(1) in Fig. S1**); plant coexistence but one species is competitively dominant (i.e. $c_{p12} > c_{p21}$, $P_1^* > P_2^*$, **(2) in Fig. S1**); and one plant species competitively excludes the other one (i.e. $c_{p12} \gg c_{p21}$, $P_1^* > 0$, $P_2^* = 0$, **(3) in**

Fig. S1). The ecological dynamics of the plant-pollinator and plant-herbivore communities in each of these cases are described in **Fig. S2 (Appendix B. IV)**.

Numerical study of animal coevolution (C)

Animal coevolution and its effect on the maintenance of coexistence is studied by numerical simulations of community eco-evolutionary dynamics. Simulations start from monomorphic pollinator ($t_m^{initial}$) and herbivore ($t_h^{initial}$) populations interacting with the two plant-species (t_{p1}, t_{p2}). Mutations are randomly generated following a Poisson process characterized by a mutation probability per unit of time and animal biomass density $\mu = 2 \cdot 10^{-7}$ (**table 1**). Proportionally to morph abundances, a parent morph is randomly chosen at each mutation event. The mutant phenotype is drawn from a Gaussian distribution centered around the parent phenotype with standard deviation $\sigma = 0.02$ (**table 1**). Its initial density is set to ε which also corresponds to the extinction threshold (**table 1**), taken from the parent population. The parameters of the mutation process (μ & σ) were chosen to abide by the assumptions of adaptive dynamics – i.e. mutations are rare and of small amplitude – in order to make the comparison between evolutionary (A&B) and coevolutionary (C) scenarios relevant. The code used to do the simulations is provided in **Appendix E**.

We first explored the different potential coevolutionary dynamics of animal phenotypes within a plant community in which the two species have identical competitive abilities (i.e. $c_{p12} = c_{p21} = 0.35$) so that their abundances are equal in the absence of animal species. We varied the initial niche overlap between animal species (i.e. $t_h^{initial} - t_m^{initial}$) to obtain an overview of the dynamics that are possible.

Second, we studied how such coevolutionary dynamics affect the maintenance of coexistence when one plant species (P_1) is competitively dominant (i.e. $c_{p12} = 0.5, c_{p21} = 0.35, P_1^* > P_2^*$, **(2) in Fig. S1**). Based on the results from scenarios A & B, we focus on how the relative strength of pollination vs. herbivory (i.e. a_{pm0} vs. a_{ph0}) affects the community composition ensuing from the coevolution of animal phenotypes. For each combination of the parameters (a_{pm0}, a_{ph0}) within the interval range [3,9] discretized by steps of 0.25, fifty simulations were launched by varying initial animal phenotypes ($t_m^{initial}, t_h^{initial}$), which were randomly sampled within the interval $[t_{p1}, t_{p2}] = [-0.75, 0.75]$. Simulations end when stable coexistence is lost – i.e. extinction of one species unbounded growth (instability) – or after 10^9

timesteps. For each (a_{pm0}, a_{ph0}) pair, we determine the proportion of each type of outcome (details in **Appendix D.I**). In particular, we statistically analyzed how the proportion of coexistence maintenance depends on the strengths of plant-animal interactions (a_{pm0} & a_{ph0} as quantitative variables), as well as on the initial animal niche overlap ($abs(t_h^{initial} - t_m^{initial})$ as a 2-level factor, big if < 0.5 , small otherwise), using the following (equation 7). The analysis was performed using the R-software and model assumptions were visually checked.

$\begin{aligned} \text{logit}(p_{coex}) &\stackrel{\text{def}}{=} \log\left(\frac{p_{coex}}{1 - p_{coex}}\right) \\ &= \mu + \alpha_{\text{Small NicheOverlap}} + \beta_1 a_{pm0} + \beta_2 a_{ph0} + \delta a_{pm0} a_{ph0} \end{aligned}$	(7)
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Lastly and to better understand the mechanisms underlying the maintenance of coexistence, we analyzed the final plant-animal trait-matching, as well as the community structure in the cases where coexistence was maintained.

Note finally that this numerical experiment was conducted again with a stronger trade-off intensity $[t_{p1}, t_{p2}] = [-1.5, 1.5]$ to assess the robustness of our results. For comparison purposes, the ending time of this second set of simulations was set to $2 \cdot 10^9$.

Results

(A) Pollinator evolution without herbivores vs. herbivore evolution without pollinators

In the absence of the other animal, the evolutionary dynamics of pollinators and herbivores are qualitatively different, with disruptive selection in response to the availability of two plant resources being only possible in the case of herbivore evolution (**Fig. 1b vs. 1c**).

When the two plant-species are equally abundant in the absence of animals ($c_{p12} = c_{p21}$ in our framework, **Fig. 1a**), the gradient of selection vanishes when the animal phenotype similarly matches both plant phenotypes (i.e. there is an evolutionary singularity at $\frac{t_{p1}+t_{p2}}{2} \stackrel{\text{def}}{=} 0$, given $a_{pm1} = a_{pm2}$ & $P_1^* = P_2^*$, see **equations 8-9**). For both animals, when the trade-off is weak – i.e. plants have similar phenotypes $t_{p2} \approx t_{p1}$ – this singularity is a CSS so that a generalist strategy is selected and maintained by stabilizing selection (**Fig. 1b&c**, analytical proof in **Appendix C.II**). Such generalist strategy is favored over specialist strategies owing to a convex trade-off shape (**Appendix C.I**). As the trade-off intensifies ($t_{p2} - t_{p1} > 2\sigma_{Pol/Her}$, **appendix C.I**), its shape turns concave making the generalist singularity invisable. While the singularity loses its convergence at a weaker trade-off in the case of pollinator evolution, convergence is lost at a stronger trade-off in the case of herbivore evolution (analytical proof in appendix C.II.3). As a result (**Fig. 1b**), at the generalist singularity ($t_m^* = \frac{t_{p1}+t_{p2}}{2} \stackrel{\text{def}}{=} 0$), selection on pollinators turns from stabilizing to runaway (Eden and repeller), the latter leading to the emergence of alternative stable states as the pollinator specializes on the plant species whose phenotype is initially closer to his. In contrast (**Fig. 1c**), selection on herbivores turns from stabilizing to disruptive – leading to the coexistence of two specialist morphs, each preferentially consuming one plant species (e.g. **Fig. S4** in **appendix C.II.3**), before runaway dynamics are observed. Those two contrasting patterns are still observed in the case of slightly asymmetrical interspecific plant competitive abilities ($c_{p12} > c_{p21}$, **Fig. S5b vs. c**, **appendix C.III**).

Pollinator	$\text{Selection gradient} = \frac{e_m}{\sigma_{Pol}^2} [-(t_m - t_{p1})a_{pm1}P_1^* + (t_{p2} - t_m)a_{pm2}P_2^*]$	(8)
Herbivore	$\text{Selection gradient} = \frac{e_h}{\sigma_{Her}^2} [-(t_h - t_{p1})a_{ph1}P_1^* + (t_{p2} - t_h)a_{ph2}P_2^*]$	(9)

The opposite signs of the eco-evolutionary feedback loops arising from pollinator (positive) vs. herbivore (negative) evolution are responsible for such a major qualitative difference in evolutionary dynamics. When the pollinator phenotype better matches the phenotype of a focal plant species, its density increases while that of the other plant decreases because pollination is beneficial to plants. As a result, selection toward matching the focal plant phenotype is reinforced (equation 8). Because herbivory is detrimental to plants, the dynamics are reversed: a better herbivore matching with any given plant phenotype reduces subsequent selection toward increasing trait-matching with that same plant species (equation 9). It is these feedback loops that explain why, as the trade-off intensifies, the convergence of the generalist singularity is lost before becoming invisable in the case of pollinator evolution, and after in the case of herbivore evolution. In particular, in the absence of eco-evolutionary feedback (i.e. P_1^*, P_2^* held constant), convergence and non-invasibility are lost simultaneously (**appendix C.II**) as the shape of the trade-off turns from convex to concave. Note finally that in both cases, the direct ecological consequences of animal evolution are amplified by interspecific plant competition.

The opposite effect of pollination vs. herbivory on plant densities is also responsible for opposite consequences of animal evolution on the maintenance of plant coexistence (**Fig. 1d & S5d vs. 1e & S5e**).

Both animals are selected to better match the most abundant plant species (**equations 8&9**). When, in the absence of animal, plant coexistence is possible despite one plant species (P_1) being a superior competitor ($c_{p12} > c_{p21}$), its greater abundance ($P_1^* > P_2^*$) leads to animal phenotypes that are closer to its phenotype than to that of the inferior competitor (**Fig. 1d & S4e**). As stronger pollination implies larger plant abundances, such a pattern reinforces the competitive advantage of this first plant species in the case of pollinator evolution, and may lead to the competitive exclusion of the second plant species (**Fig. 1d**). The competitive advantage is, in contrast, reduced in the case of herbivore evolution as stronger herbivory implies smaller plant abundances. Herbivore evolution thus cannot provoke the competitive exclusion of the inferior competitor plant species (**Fig. S5e**).

The exact same mechanisms explain the opposite effect of animal evolution on plant coexistence when, in the absence of animals, one plant species (P_1) competitively excludes ($c_{p12} \gg c_{p21}$) the other one (P_2) (**Fig. S5d vs. 1e**). In such a scenario, the evolution of herbivores may notably maintain the coexistence of plant species (**Fig 1e**). Naturally, pollinator

evolution, which reinforces initial competitive advantages, cannot prevent the exclusion of the inferior competitor (**Fig. S5d**).

Note finally that in order for animal evolution to switch the initial pattern of plant coexistence, a minimal level of trade-off is necessary (**Fig. 1d&e**). Indeed, such dynamics require animals to have a sufficiently distinct effect on the densities of each plant species, which implies a minimal level of plant phenotype dissimilarity.

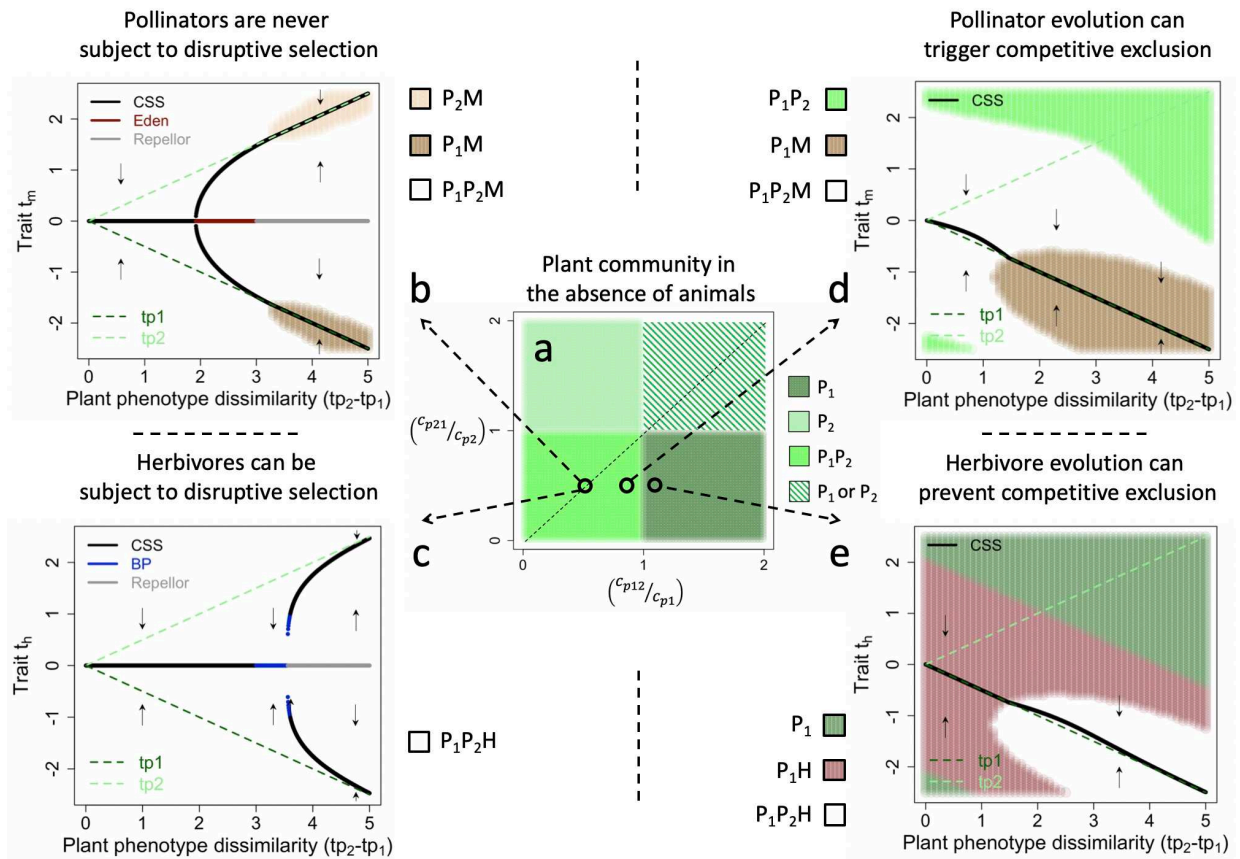


Fig. 1: Contrasting pollinator vs. herbivore eco-evolutionary dynamics within a 2-plant species community.
a. Plant community in the absence of animal species (see **Fig. S1** for details). **b.** Pollinator evolution within a plant community of similarly abundant plant species in the absence of animals. ($c_{p12} = c_{p21} = 0.35, a_{pm0} = 4$) **c.** Herbivore evolution within a plant community of similarly abundant plant species in the absence of animals. ($c_{p12} = c_{p21} = 0.35, a_{ph0} = 4$) **d.** Pollinator evolution within a plant community dominated by P_1 in the absence of animals ($c_{p12} = 0.6, c_{p21} = 0.35, a_{pm0} = 3.5$) **e.** Herbivore evolution within a plant community in which P_2 is competitively excluded in the absence of animals. Parameters: ($c_{p12} = 0.77, c_{p21} = 0.35, a_{ph0} = 3.5$) Other parameters as in **table 1**.

(B) Pollinator vs. herbivore evolution within a plant-pollinator-herbivore community

The evolutionary dynamics arising from pollinator vs. herbivore evolution within the plant-pollinator-herbivore community are, again, qualitatively contrasted. In particular, the pollinator is selected to reduce its niche overlap with the herbivore (i.e. niche partitioning, **Fig. 2 b.1 & c.1**), while the herbivore is selected to increase its niche overlap with the pollinator species (**Fig. 2 b.2 & c.2**).

When plant species have similar competitive abilities, in the case of relatively weak trade-off ($t_{p2} - t_{p1} = 1.5$, **Fig. 2b**), both animals are subject to stabilizing selection (i.e. CSS) toward a given phenotype which depends on the fixed phenotype of the non-evolving animal species. The correlation between the latter and the selected phenotype is negative in the case of pollinator evolution (**Fig. 2b.1**), and positive in the case of herbivore evolution (**Fig. 2b.2**). In other words, when pollinators have a better matching with one plant species than the other, herbivores are selected to better match the same plant species. If that focal pollinator-plant matching further increases, evolution favors a similar trait-matching increase in herbivores. In contrast, when herbivores have a better matching with a given plant species than the other, pollinators are selected to better match that other plant species. The more herbivores are matching a given plant phenotype, the more evolution leads to a better trait-matching between pollinators and that other plant species.

In the plant-pollinator-herbivore community, animals are indirectly interacting through their effect on plant densities. Herbivores, by reducing the density of plant resources, reduce pollinator density. Pollinators, on the contrary, have a positive effect on the density of herbivores as they increase the density of plant species. Because this indirect ecological interaction gets stronger as the animal niche overlap increases, pollinators are selected toward animal niche partitioning while herbivores are selected toward animal niche overlap.

These evolutionary patterns are also observed at stronger trade-offs ($t_{p2} - t_{p1} = 3$, **Fig. 2c**). In such a case, however, pollinator evolutionary dynamics are characterized by abrupt transitions from being specialist on one or the other species (**Fig. 2c.1**), as the relative strength of plant-herbivore interactions is switching. In particular, over a wide range of generalist herbivore phenotypes (Eden in **Fig. 2c.1**), community eco-evolutionary dynamics are characterized by the existence of alternative stable states with pollinators specializing in either one plant species, notably responsible for evolutionary hysteresis. Such dynamics are due to the positive eco-evolutionary feedback arising from pollinator evolution. In contrast, the

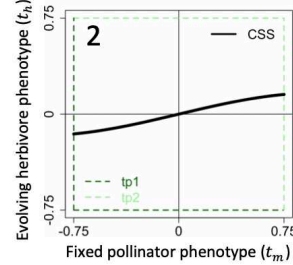
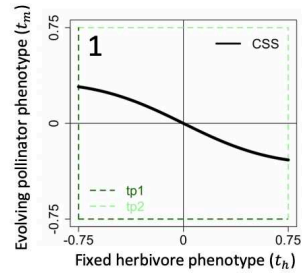
negative eco-evolutionary feedback associated with the evolution of herbivores leads to a smooth evolution of their phenotype as the relative strength of plant-pollinator interactions is switching (**Fig. 2c.2**).

The ecological consequences of pollinator vs. herbivore evolution are also opposite, in line with our previous results in the absence of either one animal species. Pollinator evolution disfavors the maintenance of plant coexistence (**Fig. 2 d.1 & e.1**), while the latter is fostered by the evolution of herbivores (**Fig. 2 d.2 & e.2**).

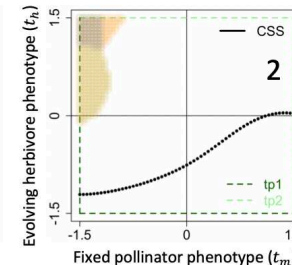
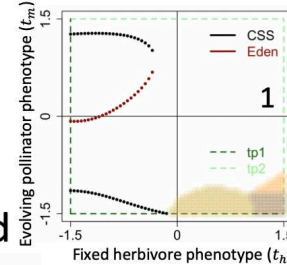
This contrasting pattern can first be observed in the case where, in the absence of animal species, plants coexist despite one (P_1) being a superior competitor (**Fig. 2d**). In such a case, herbivore evolution maintains plant coexistence, even when the superior competitor benefits from the additional advantage of stronger pollination (**Fig. 2d.2**). The herbivore selection toward animal niche overlap indeed cancels this latter advantage. In contrast, when herbivores are more strongly consuming the inferior competitor plant species, pollinators further exacerbate such disadvantage by evolving toward matching the superior competitor species because selection fosters animal niche partitioning (**Fig. 2d.2**). Pollinator evolution leads to the evolutionary murder of the inferior competitor.

These opposite effects of animal evolution on plant coexistence are even more visible in the case where one plant species (P_1) is competitively excluding the other one in the absence of animals (**Fig. 2e**). Owing to the same dynamics as in the case of a smaller trade-off, the evolution of pollinators cannot prevent competitive exclusion (**Fig. 2e.1**), while herbivore evolution can enable the maintenance of plant diversity (**Fig. 2e.2**).

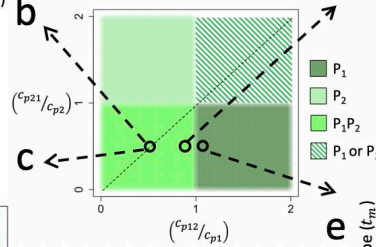
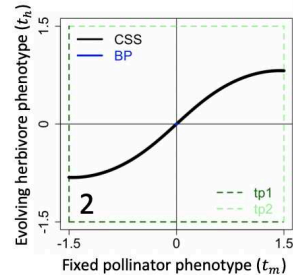
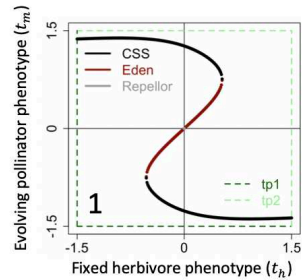
Animal niche overlap increases with herbivore evolution and decreases with pollinator evolution



Pollinator evolution disfavors the maintenance of plant coexistence
Herbivore evolution favors the maintenance of plant coexistence

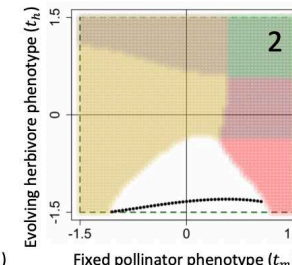
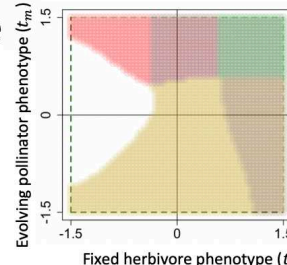


Small plant phenotype dissimilarity
 $t_{p1} = -t_{p2} = -0.75$



Plant coexistence with P_1 dominating the plant community

Important plant phenotype dissimilarity
 $t_{p1} = -t_{p2} = -1.5$



P_1 competitively excludes P_2 without animals

Fig. 2: Eco-evolutionary dynamics arising from the evolution of one animal in the presence of the other animal. **a. Plant community** in the absence of animal species (see Fig. S1 for details). **b. Focal animal evolution (1: pollinator, 2: herbivore)** depending on the other animal fixed phenotype, within a plant community characterized by dissimilar plant phenotypes ($t_{p2} = -t_{p1} = 0.75$) as well as similarly abundant plant species in the absence of animals ($c_{p12} = c_{p21} = 0.35$). **c. Focal animal evolution (1: pollinator, 2: herbivore)** depending on the other animal fixed phenotype, within a plant community characterized by very dissimilar plant phenotypes ($t_{p2} = -t_{p1} = 1.5$) as well as similarly abundant plant species in the absence of animals ($c_{p12} = c_{p21} = 0.35$). **d. Ecological consequences** of the evolution of the focal animal phenotype (1: pollinator, 2: herbivore) within a plant community characterized by very dissimilar plant phenotype ($t_{p2} = -t_{p1} = 1.5$), and plant coexistence in the absence of animals despite P_1 being a superior competitor ($c_{p12} = 0.5, c_{p21} = 0.35$). **e. Ecological consequences** of the evolution of the focal animal phenotype (1: pollinator, 2: herbivore) within a plant community characterized by very dissimilar plant phenotype ($t_{p2} = -t_{p1} = 1.5$), and the exclusion of P_2 in the absence of animal species ($c_{p12} = 0.735, c_{p21} = 0.35$). In all cases: ($a_{mno} = a_{no} = 3.5$) Other parameters as in table 1.

(C) Pollinator and herbivore coevolution within a plant-pollinator-herbivore community

First, our investigation of coevolutionary dynamics (so far) shows that they always – i.e. independent of the trade-off intensity $t_{p2} = 0.1, 0.75$ or 1.5 – lead to a perfect overlap between animal niches with both animal traits maintained at the same phenotype by stabilizing selection (i.e. CSS). Before reaching such a final state, two types of dynamics are possible (**Fig. 3**). In particular, fluctuating selection (**Fig. 3c**) characterized by cycling animal phenotypes (**Fig. 3d**) can be observed. According to our previous results (**Fig. 2 b & c**), such dynamics are likely the result of pollinator selection toward animal niche partitioning vs. herbivore selection toward animal niche overlap. These dynamics seem more frequent when plant phenotype dissimilarity is important, in line with our finding that abrupt pollinator evolutionary transitions happen at strong trade-offs (**Fig. 2c1**). Such abrupt transitions indeed indicate fast pollinator evolution potentially enabling them to escape trait-matching with herbivores, thus starting a new evolutionary race between animal species (e.g. arrow in **Fig. 4c**). Transient fluctuating selection seems also more frequent when the initial animal niche overlap is important. When it is not the case (**Fig. 3a & b**), directional selection – i.e. animal phenotypes directly converging toward the selected phenotypes – is most often observed. Note that a detailed study on the occurrence of either type of dynamics goes beyond the scope of the present paper.

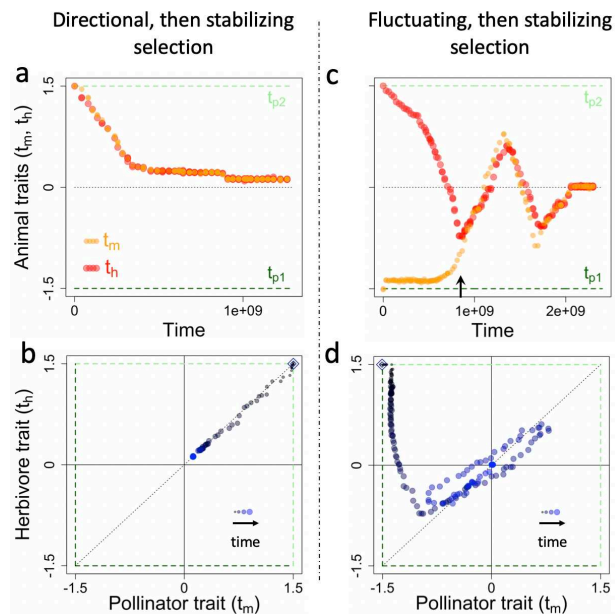


Fig. 3: The different coevolutionary dynamics observed. a/b Stabilizing selection after directional selection. a. Temporal dynamics of animal traits. **b.** Corresponding dynamics in the trait space. **c/d Stabilizing selection after fluctuating selection. c.** Temporal dynamics of animal traits. **d.** Corresponding dynamics in the trait space. Parameters: $c_{p12} = c_{p21} = 0.35$, $a_{pm0} = a_{ph0} = 3.5$, $t_{p2} = -t_{p1} = 1.5$. Others as in **table 1**.

Second, we studied in detail (**Fig. 4 & S6**) the community resulting from animal coevolution in the case where both plant species coexist in the absence of animals, but one (P_1) benefits from a competitive advantage over the other (P_2).

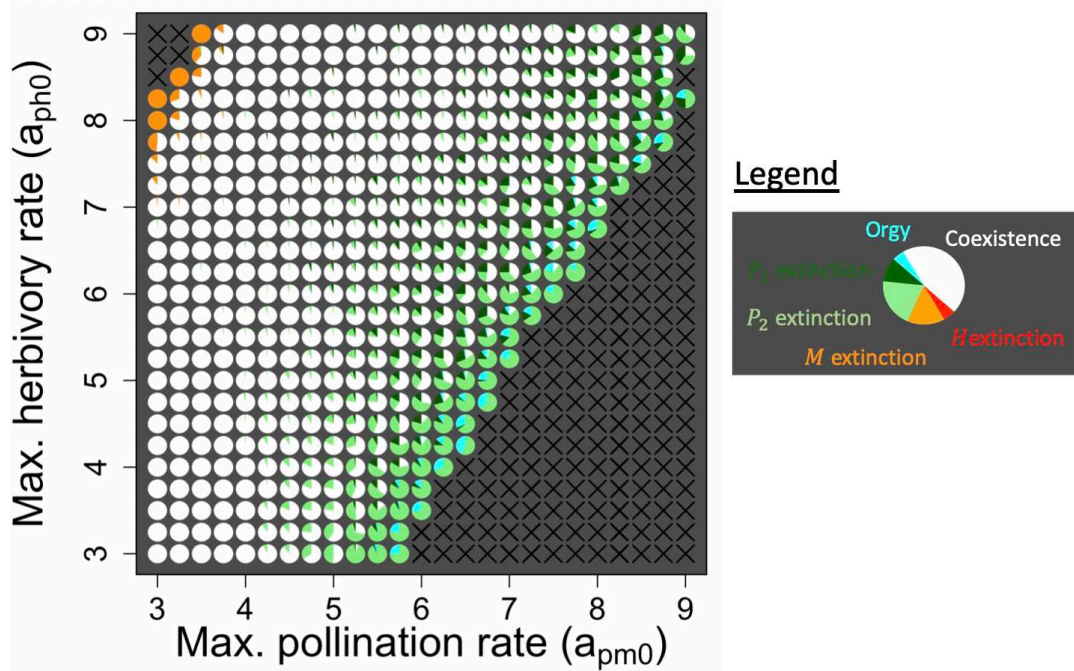


Fig. 4: Relative importance of the different simulation outcomes depending on the relative strength of pollination vs. herbivory (a_{pm0} , a_{ph0}). The different possible outcomes are indicated in the legend. These outcomes are obtained after animals coevolve during 10^9 timesteps. It is also possible that initially (i.e. first timestep), stable plant-pollinator-herbivore coexistence is not obtained. When it was the case, the simulation was excluded so that the proportions presented in this figure do not account for the simulations that crashed instantaneously. The pairs (a_{pm0}, a_{ph0}) characterized by more than two-thirds of initial crashes (over 50 simulations) are indicated by a black cross, and are ignored in our analysis. Interspecific plant competition: ($c_{p12} = 0.5, c_{p21} = 0.35$). Trade-off intensity ($t_{p2} = -t_{p1} = 0.75$). Other parameters as in **table 1**.

Our results clearly show that the maintenance of plant-pollinator-herbivore along animal coevolutionary trajectories requires herbivory to be as strong as, or moderately stronger than pollination (**Fig. 4**). This qualitative pattern is conserved stronger trade-offs (**Fig. S6 in appendix D.II**). When the maximal pollination rate is much stronger than that of herbivory, stable coexistence is frequently lost due to the extinction of one plant species (green frontier in **Fig. 4**), very often that of the inferior competitor P_2 . Such a pattern agrees with our result that pollinator evolution favors competitive exclusion among plant species (**Fig. 2d & e**). Less frequently, strong pollination makes coevolution lead to unbounded population growths (blue

in **Fig. 4**). The strength of herbivory cannot, however, totally outweigh that of pollination as such a configuration leads to the extinction of pollinators (orange frontier in **Fig. 4**). According to our previous detailed investigation of the ecological dynamics of similar communities (Yacine and Loeuille 2021), this is due to weak pollination making pollinators unable to survive in a context of reduced plant resource density resulting from strong herbivory. Note finally that when both maximal interaction rates are weak (i.e. < 4.5), stable coexistence is almost always maintained.

The statistical model fitted to explain the probability of coexistence maintenance (i.e. p_{coex}) emphasizes the described pattern (equation 10, $p_{value} < 2 \cdot 10^{-16}$ for all coefficients). This model, which explains approximately 55% of the total variance, shows that strong plant-animal interactions threaten the maintenance of coexistence (direct effects), except when both interactions are strong (interaction term). Note, however, that the deleterious effect of pollination is twice as important as that of herbivory, explaining why coexistence is maintained when herbivory is as strong, or slightly stronger than pollination. The statistical analysis additionally reveals that coexistence is more often lost when animal phenotypes are initially very dissimilar (i.e. small niche overlap, $abs(t_h^{initial} - t_m^{initial}) > 0.5$). In such cases, it is more likely that one plant species is benefiting from pollination while the other is suffering from herbivory, a situation that favors competitive exclusion among plant species. Note finally that the statistical analysis yields similar results in the case of a stronger trade-off ($t_{p2} - t_{p1} = 3$, **appendix D.II**).

$\begin{aligned} \text{logit}(p_{coex}) &\stackrel{\text{def}}{=} \log\left(\frac{p_{coex}}{1 - p_{coex}}\right) \\ &= 31.3 \quad \underbrace{-2.38}_{\text{Small NicheOverlap}} \quad - 5.67a_{pm0} - 3.32a_{ph0} + 0.63a_{pm0}a_{ph0} \end{aligned}$	(10)
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In order to unravel the mechanisms underlying the maintenance of coexistence, we study the plant-animal trait-matching arising from coevolutionary dynamics when coexistence is maintained (**Fig. 5A**), and its consequences on the structure of the community (**Fig. 5B**), as well as on the distribution of densities within such a maintained community (**Fig. 5C**).

As already indicated (see **Fig. 3**), animal traits converge toward the same phenotype (**Fig. 5A. a & b**). The selected phenotype corresponds to generalist animal species when the maximal rate of herbivory is much higher than that of pollination (top-left of **Fig. 5A. a & b**). This generalist phenotype is indeed characterized by animals interacting equally (50%) with

both plant species (top-left of **Fig. 5B. b & c**). As the maximal pollination rate gets stronger and/or the maximal herbivory rate gets weaker, animal phenotypes increasingly match the superior competitor phenotype (t_{p1}) owing to its greater abundance (below diagonal in **Fig. 5A. a & b**). Despite a strong trait-matching, the resulting animal specialization on this superior competitor (P_1) is rather weak (i.e. 60%, below diagonal in **Fig. 5B. b & c**). This indicates that a slight animal specialization toward the superior competitor is sufficient to trigger competitive exclusion among plant species. Note that the correspondence between trait-matching and specialization depends on the trade-off intensity (i.e. $t_{p2} - t_{p1}$). When plant phenotype dissimilarity is stronger ($t_{p2} = -t_{p1} = 1.5$, **Fig. S7B** in **appendix D.II**), the emerging specialization is much more pronounced, probably explaining the larger proportion of coexistence disruption as a result of competitive exclusion among plant species. Note finally that the relative importance of the interaction with each plant species is identical for both animal species (**Fig. 5B b vs. c**), as a result of identical coevolved animal phenotypes.

The evolutionary emergence of a perfect animal niche overlap is also responsible for the relative importance of pollination vs. herbivory being identical for both plant species (**Fig. 5B. a vs. d**). The realized interaction pattern directly corresponds to the ratio of maximal plant-animal interaction rates (equation 11).

$\frac{a_{pm1}}{a_{pm1} + a_{ph1}} = \frac{a_{pm2}}{a_{pm2} + a_{ph2}} = \frac{a_{pm0}}{a_{pm0} + a_{ph0}}$	(11)
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In contrast with the relative strength of animal interactions with plant species, the relative strength of plant interactions varies over a much wider range (30 – 65%), and does not depend on trade-off intensity (**Fig. S7B** in **appendix D.II**). Starting from plant interactions being biased toward much stronger herbivory (70%) than pollination (30%) when the maximum rate of herbivory is important and that of pollination weak (**top-left of Fig. 5B. a & d**), plant interactions become biased toward much stronger pollination (55-65%) than herbivory (25-35%) when the pattern of maximum plant-animal interaction rates is reversed (**below diagonal in Fig. 5B. a & d**). Note, however, that when pollination is relatively important (65%), coexistence is maintained at weak pollination levels (**bottom-left of Fig. 5B. a & d**), and much more frequently lost (**top-right of Fig. 5B. a & d**). In contrast, when herbivory is relatively important (65-70%), there is a vast region over which coexistence is maintained (**top-left of Fig. 5B. a & d**). This indicates that a rather slight increase of maximal pollination relative to maximal herbivory triggers the disruption of coexistence.

The community structure emerging from the coevolution of animal phenotypes modifies the relative abundance of plant (**Fig. 5C. a**) and animal species (**Fig. 5C. b**). In particular, when the maximal rates of pollination and herbivory are equal, animals have identical densities (white in **Fig. 5C. b**), thus canceling their respective effects on the plant community. As a result, the relative abundance of plant species is not modified by the presence of animals (i.e. $P_1^* = 0.65 * (P_1^* + P_2^*)$, blue diagonal in **Fig. 5C. a**). Stronger herbivory than pollination is responsible for more balanced densities in the plant community (**Fig. 5C. a, above diagonal**). As herbivory gets stronger and pollination weaker, balanced plant densities are smoothly recovered until almost equal densities are observed. Note that such a balanced pattern is maintained over a wide range of stronger herbivory/weaker pollination ($P_1^* \approx P_2^*$, top-left of **Fig. 5C. a**). In such instances, herbivores are much more abundant than pollinators, the latter drawing near extinction when herbivory is much stronger than pollination (top-left of **Fig. 5C. b**). In contrast, stronger pollination than herbivory exacerbates, rather abruptly, the initial imbalance in plant densities (**Fig. 5C. a, below diagonal**). This leads to the rapid competitive exclusion of the inferior competitor as pollination gets stronger and/or herbivory weaker. In such cases, pollinators slightly dominate the animal community in density (**Fig. 5C. b, below diagonal**).

In summary, coevolution (**Fig. 5A**) leads to a pattern of similar animal preference for plant phenotypes, which gets increasingly biased toward the most abundant plant species (i.e. superior competitor) as the maximum rate of pollination increases and/or that of herbivory decreases. Ultimately, the emerging community structure (**Fig. 5B**) is characterized by: (1) plant species preferentially interacting with herbivores in the context of generalist animal species at strong herbivory and weak pollination maximal rates, and (2) plant species preferentially interacting pollinators while animal species preferentially interacting with the superior plant competitor at weak herbivory and/or strong pollination. The latter community scenario leads more often to the disruption of coexistence owing to the competitive exclusion of plant species (**Fig. 5C. a**), but the first scenario can also, sometimes, provoke the extinction of pollinators (**Fig. 5C. b**). Stronger herbivory than pollination fosters the maintenance of plant-pollinator-herbivore coexistence. Similar qualitative patterns are also observed in the case of a much stronger trade-off ($t_{p2} = -t_{p1} = 1.5$, **Fig. S7 in appendix D.II**).

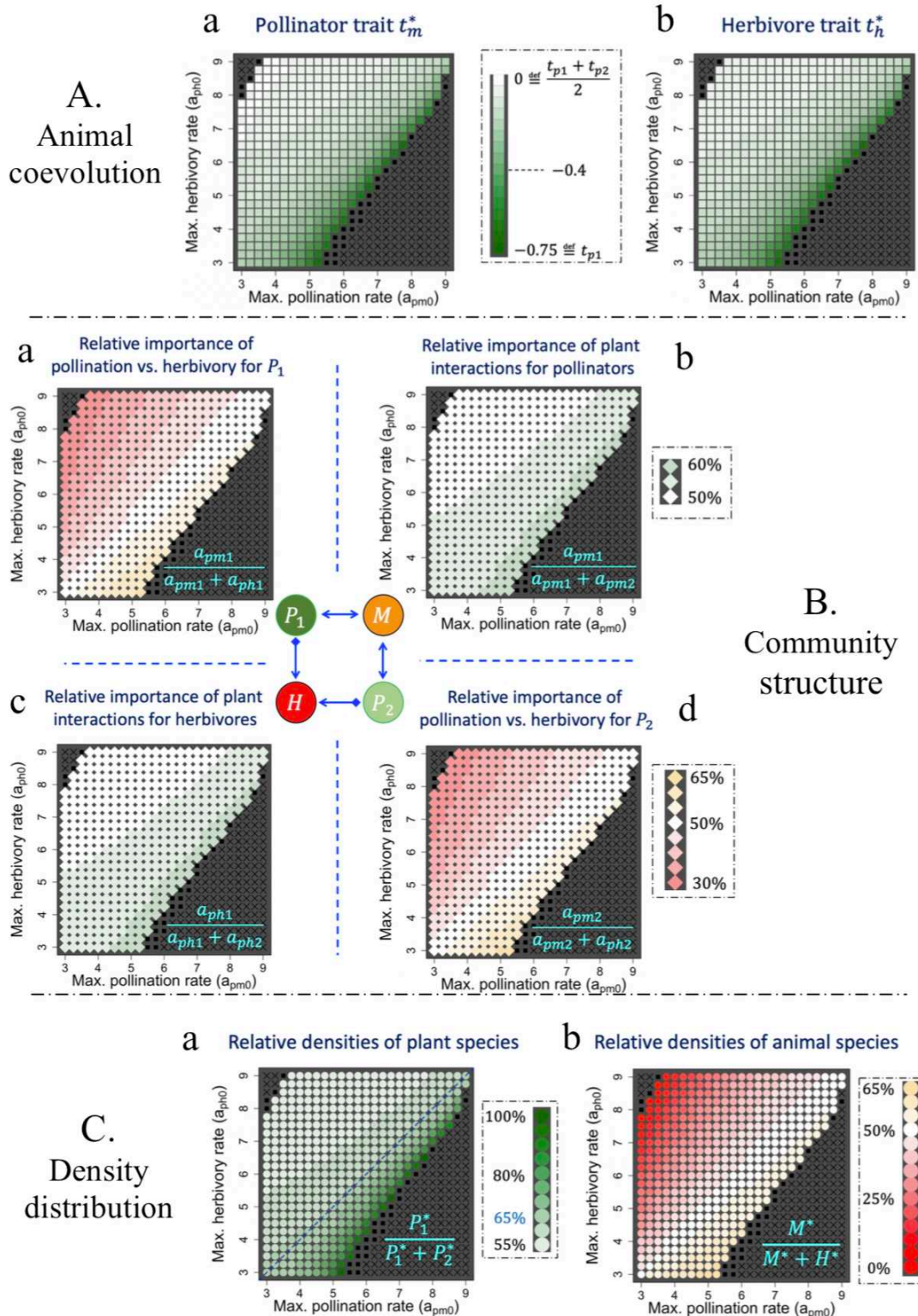


Fig. 5: Community arising from animal coevolution when coexistence is maintained, depending on the relative strength of pollination vs. herbivory. A. Plant-animal trait matching. a. Final pollinator phenotype (t_m^*) **b.** Final herbivore phenotype (t_h^*) **B. Community structure. a.** Relative importance of pollination vs.

herbivory for P_1 . **b.** Relative importance of P_1 -pollinator interaction vs. P_2 -pollinator interaction for the pollinator species. **c.** Relative importance of pollination vs. herbivory for P_2 . **d.** Relative importance of P_1 -herbivore interaction vs. P_2 -herbivore interaction for the herbivore species. **C. Distribution of densities.** **a.** Relative density of plant species. The blue line represents the relative plant densities in the absence of animal species, i.e. $P_1^* = 0.65(P_1^* + P_2^*)$ **b.** Relative densities of animal species. ($c_{p12} = 0.5, c_{p21} = 0.35$), ($t_{p2} = -t_{p1} = 0.75$). Other parameters as in **table 1**.

Discussion (beginning)

Our investigation emphasizes the contrasting eco-evolutionary dynamics arising from pollinator vs. herbivore evolution within a two plant-species floral landscape. These contrasting patterns are due to opposite eco-evolutionary feedback loops – positive in the case of pollinators, and negative in the case of herbivores. As a result, pollinator evolution disfavors the maintenance of plant coexistence, while the latter is fostered by the evolution of herbivores. Another important consequence is that animal diversification in response to the availability of two plant resources is only possible for herbivores. Last but not least, selection on pollinators fosters the partitioning of animal niches, while herbivores, in contrast, are selected toward increasing the overlap of these same niches. Our study of coevolutionary dynamics shows that this might be responsible for fluctuating selection on animal phenotypes. Such selection eventually dissipates, leading to a perfect overlap of animal niches in the long term. Such coevolutionary dynamics might notably explain why shared animal preferences for plant phenotypes have been frequently observed in natural communities.

References

- Brody, A. K. 2008. Effects of Pollinators , Herbivores , and Seed Predators on Flowering Phenology. *Ecology* 78:1624–1631.
- Craine, J. M., and R. Dybzinski. 2013. Mechanisms of plant competition for nutrients, water and light. *Functional Ecology* 27:833–840.
- de Mazancourt, C., and U. Dieckmann. 2004. Trade-Off Geometries and Frequency-Dependent Selection. *The American Naturalist* 164:765–778.
- Dieckmann, U., and R. Law. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of Mathematical Biology* 34:579–612.
- Eshel, I. 1983. Evolutionary and continuous stability. *Journal of Theoretical Biology* 103:99–111.
- Galen, C., and J. Cuba. 2001. Down the tube: Pollinators, predators, and the evolution of flower shape in the alpine sky pilot, *Polemonium viscosum*. *Evolution* 55:1963–1971.

- Geritz, S. A. H., J. A. J. Metz, É. Kisdi, and G. Meszéna. 1997. Dynamics of adaptation and evolutionary branching. *Physical Review Letters* 78:2024–2027.
- Irwin, R. E., S. Y. Strauss, S. Storz, A. Emerson, and G. Guibert. 2003. The Role of Herbivores in the Maintenance of a Flower Color Polymorphism in Wild Radish. *Ecology* 84:1733–1743.
- Levins, R. 1962. Theory of Fitness in a Heterogeneous Environment. I. The Fitness Set and Adaptive. *The American Naturalist* 96:361–373.
- May, R. M. 1981. Models for two interacting populations. Pages 78–104 in R. May, ed. *Theoretical ecology: principles and applications* (2nd edition) (2nd ed.). Blackwell: Oxford, UK.
- Maynard Smith, J., and G. R. Price. 1973. The logic of animal conflict. *Nature* 246:15–18.
- Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. How should we define “fitness” for general ecological scenarios? *Trends in Ecology and Evolution* 7:198–202.
- Nowak, M. 1990. An evolutionarily stable strategy may be inaccessible. *Journal of theoretical biology* 142:237–241.
- Rueffler, C., T. J. M. Van Dooren, and J. A. J. Metz. 2006. The evolution of resource specialization through frequency-dependant and frequency-independant mechanisms. *The American Naturalist* 167:81.
- Theis, N., N. A. Barber, S. D. Gillespie, R. V. Hazzard, and L. S. Adler. 2014. Attracting mutualists and antagonists: Plant trait variation explains the distribution of specialist floral herbivores and pollinators on crops and wild gourds. *American Journal of Botany* 101:1314–1322.
- Yacine, Y., and N. Loeuille. 2021. Stable coexistence in plant-pollinator-herbivore communities requires balanced mutualistic vs antagonistic interactions. *bioRxiv*.

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Preliminary note:

In the supporting material, we decided to consider the dynamical system defining the ecological dynamics of plant-pollinator-herbivore communities in our framework (equation 1-4 in the main document) with the most general formulation possible. As such, the parameters that are assumed equal for both plant species in the main document, are here considered to potentially differ. Practically, this means that our dynamical system is here written as:

$\frac{dP_1}{dt} = P_1(r_{p1} - c_{p1}P_1 - c_{p21}P_2 + a_{pm1}M - a_{ph1}H)$	(1')
$\frac{dP_2}{dt} = P_2(r_{p2} - c_{p2}P_2 - c_{p12}P_1 + a_{pm2}M - a_{ph2}H)$	(2')
$\frac{dM}{dt} = M(r_m - c_mM + e_{m1}a_{pm1}P_1 + e_{m2}a_{pm2}P_2)$	(3')
$\frac{dH}{dt} = H(r_h - c_hH + e_{h1}a_{ph1}P_1 + e_{h2}a_{ph2}P_2)$	(4')

Likewise, plant-animal interactions are written:

Pollination	$a_{pm1} = \frac{a_{pm01}}{\sqrt{2\pi\sigma_{Pol1}^2}} \exp\left[-\frac{(t_{p1} - t_m)^2}{2\sigma_{Pol1}^2}\right]$	(5')
	$a_{pm2} = \frac{a_{pm02}}{\sqrt{2\pi\sigma_{Pol2}^2}} \exp\left[-\frac{(t_{p2} - t_m)^2}{2\sigma_{Pol2}^2}\right]$	(5'')
Herbivory	$a_{ph1} = \frac{a_{ph01}}{\sqrt{2\pi\sigma_{Pol1}^2}} \exp\left[-\frac{(t_{p1} - t_h)^2}{2\sigma_{Pol1}^2}\right]$	(6')
	$a_{ph2} = \frac{a_{ph02}}{\sqrt{2\pi\sigma_{Her2}^2}} \exp\left[-\frac{(t_{p2} - t_h)^2}{2\sigma_{Her2}^2}\right]$	(6'')

Appendix A: Nondimensionalization

In order to improve the readability of the mathematical analyses presented in the supporting information, the model can be rewritten in a nondimensionalized but equivalent way, which allows for fewer parameters. Whenever this nondimensionalization is used, it is explicitly indicated.

The dynamical system studied (equation 1-4 in the main document) can be rewritten:

$\frac{d\tilde{P}_1}{d\tilde{t}} = \tilde{P}_1(1 - \tilde{P}_1 - \alpha_{21}\tilde{P}_2 + \alpha_{pm1}\tilde{M} - \alpha_{ph1}\tilde{H})$	(1)
$\frac{d\tilde{P}_2}{d\tilde{t}} = \tilde{P}_2(\rho_2 - \tilde{P}_2 - \alpha_{12}\tilde{P}_1 + \alpha_{pm2}\tilde{M} - \alpha_{ph2}\tilde{H})$	(2)
$\frac{d\tilde{M}}{d\tilde{t}} = \tilde{M}(\rho_m - \tilde{M} + \lambda_{m1}\alpha_{pm1}\tilde{P}_1 + \lambda_{m2}\alpha_{pm2}\tilde{P}_2)$	(3)
$\frac{d\tilde{H}}{d\tilde{t}} = \tilde{H}(\rho_h - \tilde{H} + \lambda_{h1}\alpha_{ph1}\tilde{P}_1 + \lambda_{h2}\alpha_{ph2}\tilde{P}_2)$	(4)

With the new variables:

$$(\tilde{t}, \tilde{P}_1, \tilde{P}_2, \tilde{M}, \tilde{H}) = (r_{p1}t, \frac{c_{p1}}{r_{p1}}P_1, \frac{c_{p2}}{r_{p1}}P_2, \frac{c_m}{r_{p1}}M, \frac{c_h}{r_{p1}}H)$$

And the new parameters:

$$(\rho_2, \rho_m, \rho_h) = \left(\frac{r_{p2}}{r_{p1}}, \frac{r_m}{r_{p1}}, \frac{r_h}{r_{p1}}\right)$$

$$(\alpha_{12}, \alpha_{21}) = \left(\frac{c_{p12}}{c_{p1}}, \frac{c_{p21}}{c_{p2}}\right)$$

$$(\alpha_{pm1}, \alpha_{pm2}, \alpha_{ph1}, \alpha_{ph2}) = \left(\frac{a_{pm1}}{c_m}, \frac{a_{pm2}}{c_m}, \frac{a_{ph1}}{c_h}, \frac{a_{ph2}}{c_h}\right)$$

$$(\lambda_{m1}, \lambda_{m2}, \lambda_{h1}, \lambda_{h2}) = \left(\frac{e_{m1}c_m}{c_{p1}}, \frac{e_{m2}c_m}{c_{p2}}, \frac{e_{h1}c_h}{c_{p1}}, \frac{e_{h2}c_h}{c_{p2}}\right)$$

Appendix B: Ecological dynamics of the different communities involved

I. Plant community in the absence of animal species

In the absence of animal species, the dynamics of plant species are given by

$\frac{dP_1}{dt} = P_1(r_{p1} - c_{p1}P_1 - c_{p21}P_2)$	(a)
$\frac{dP_2}{dt} = P_2(r_{p2} - c_{p2}P_2 - c_{p12}P_1)$	(b)

There are four possible ecological equilibria.

$$(P_1^*, P_2^*) = (0,0); \left(\frac{r_{p1}}{c_{p1}}, 0\right); \left(0, \frac{r_{p2}}{c_{p2}}\right); \left(\frac{c_{p2}r_{p1} - c_{p21}r_{p2}}{c_{p1}c_{p2} - c_{p12}c_{p21}}, \frac{-c_{p12}r_{p1} + c_{p1}r_{p2}}{c_{p1}c_{p2} - c_{p12}c_{p21}}\right)$$

- The null equilibrium is stable if and only if $r_{p1} \leq 0$ and $r_{p2} \leq 0$. It is thus never stable as we assume $r_{p1} > 0$ and $r_{p2} > 0$.
- The equilibrium where only species (1) is present is feasible if $r_{p1} > 0$. In addition, it is stable if and only if $c_{p12}r_{p1} + c_{p1}r_{p2} \leq 0$, as species (2) cannot invade.
- The equilibrium where only species (2) is present is feasible if $r_{p2} > 0$. In addition, it is locally stable if and only if $c_{p2}r_{p1} - c_{p21}r_{p2} \leq 0$, as species (1) cannot invade.
- The equilibrium where both species are present is feasible and stable if and only if:

$$\begin{aligned} c_{p2}r_{p1} - c_{p21}r_{p2} &> 0 \\ -c_{p12}r_{p1} + c_{p1}r_{p2} &> 0 \end{aligned}$$

These two inequalities notably imply that intraspecific competition must outweigh interspecific competition: $c_{p1}c_{p2} - c_{p12}c_{p21} > 0$.

Fig. S1 summarizes these results. In particular, alternative stable states are observed when neither species can invade the other. When both species can invade each other, stable coexistence is observed. **Fig. S1** also shows the different cases of plant community structure that are considered when investigating the eco-evolutionary dynamics in the presence of evolving animals: **(1)** plant coexistence under similar interspecific competitive abilities (i.e. $c_{p12} = c_{p21}$, $P_1^* = P_2^*$); **(2)** plant coexistence but one species is competitively dominant (i.e.

$c_{p12} \geq c_{p21}$, $P_1^* > P_2^*$); and (3) P_1 competitively excludes P_2 (i.e. $c_{p12} \gg c_{p21}$, $P_1^* > 0$, $P_2^* = 0$).

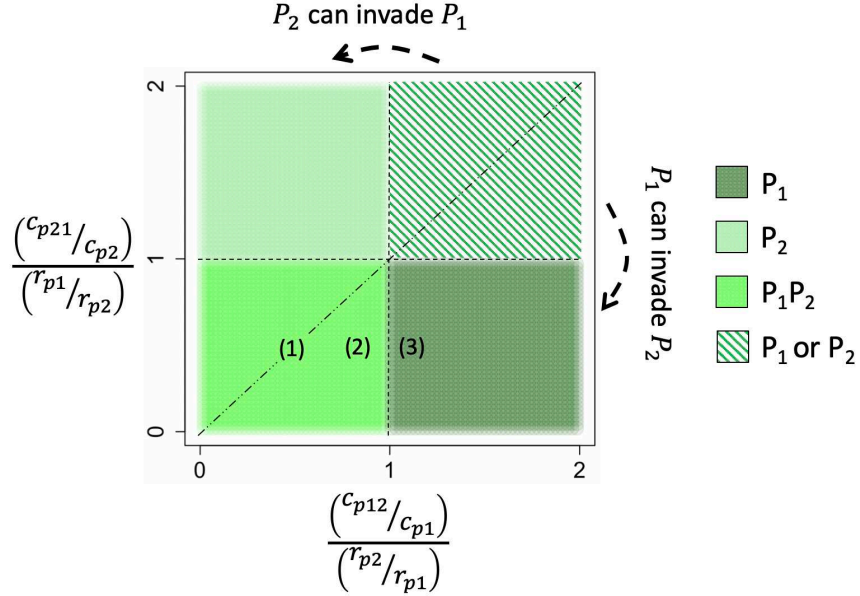


Fig S1: Stable equilibria within the plant community, in the absence of animal species.

II. Plant-pollinator community

In the absence of herbivores, the dynamics of the plant-pollinator community are given by:

$\frac{dP_1}{dt} = P_1(r_{p1} - c_{p1}P_1 - c_{p21}P_2 + a_{pm1}M)$	(a')
$\frac{dP_2}{dt} = P_2(r_{p2} - c_{p2}P_2 - c_{p12}P_1 + a_{pm2}M)$	(b')
$\frac{dM}{dt} = M(r_m - c_mM + e_{m1}a_{pm1}P_1 + e_{m2}a_{pm2}P_2)$	(c')

There are eight possible ecological equilibria, whose expressions are given in **table B.1**.

Equilibrium	
<i>Null</i>	$P_1^* = P_2^* = M^* = 0$
P_1	$P_1^* = \frac{r_{m1}}{c_{m1}} ; P_2^* = M^* = 0$
P_2	$P_1^* = 0 ; P_2^* = \frac{r_{m2}}{c_{m2}} ; M^* = 0$

M	$P_1^* = 0; P_2^* = 0; M^* = \frac{r_m}{c_m}$
P_1P_2	$P_1^* = \frac{c_{p2}r_{p1} - c_{p21}r_{p2}}{c_{p1}c_{p2} - c_{p12}c_{p21}}; P_2^* = \frac{-c_{p12}r_{p1} + c_{p1}r_{p2}}{c_{p1}c_{p2} - c_{p12}c_{p21}}; M^* = 0$
P_1M	$P_1^* = \frac{c_m r_{p1} + a_{pm1} r_m}{c_{p1} c_m - e_{m1} a_{pm1}^2}; P_2^* = 0; M^* = \frac{e_{m1} a_{pm1} r_{p1} + c_{p1} r_m}{c_{p1} c_m - e_{m1} a_{pm1}^2}$
P_2M	$P_1^* = 0; P_2^* = \frac{c_m r_{p2} + a_{pm2} r_m}{c_{p2} c_m - e_{m2} a_{pm2}^2}; M^* = \frac{e_{m2} a_{pm2} r_{p2} + c_{p2} r_m}{c_{p2} c_m - e_{m2} a_{pm2}^2}$
P_1P_2M	See after

Table B.1: Analytical expression of the ecological equilibria within the plant-pollinator community.

$$P_1^* = \frac{(c_{p2}c_m - e_{m2}a_{pm2}^2)r_{p1} + (e_{m2}a_{pm1}a_{pm2} - c_m c_{p21})r_{p2} + (c_{p2}a_{pm1} - c_{p21}a_{pm2})r_m}{(c_{p1}c_{p2} - c_{p12}c_{p21})c_m - c_{p2}e_{m1}a_{pm1}^2 - c_{p1}e_{m2}a_{pm2}^2 + a_{pm1}a_{pm2}(c_{p21}e_{m1} + c_{p12}e_{m2})}$$

$$P_2^* = \frac{(e_{m1}a_{pm1}a_{pm2} - c_m c_{p12})r_{p1} + (c_{p1}c_m - e_{m1}a_{pm1}^2)r_{p2} + (c_{p1}a_{pm2} - c_{p12}a_{pm1})r_m}{(c_{p1}c_{p2} - c_{p12}c_{p21})c_m - c_{p2}e_{m1}a_{pm1}^2 - c_{p1}e_{m2}a_{pm2}^2 + a_{pm1}a_{pm2}(c_{p21}e_{m1} + c_{p12}e_{m2})}$$

$$M^* = \frac{(c_{p2}e_{m1}a_{pm1} - c_{p12}e_{m2}a_{pm2})r_{p1} + (c_{p1}e_{m2}a_{pm2} - c_{p21}e_{m1}a_{pm1})r_{p2} + (c_{p1}c_{p2} - c_{p12}c_{p21})r_m}{(c_{p1}c_{p2} - c_{p12}c_{p21})c_m - c_{p2}e_{m1}a_{pm1}^2 - c_{p1}e_{m2}a_{pm2}^2 + a_{pm1}a_{pm2}(c_{p21}e_{m1} + c_{p12}e_{m2})}$$

The criteria for the stability of each of these ecological equilibria, assuming its feasibility (i.e. that it corresponds to positive densities), are given in **table B.2**. These criteria correspond to the eigenvalues of the Jacobian matrix, at each equilibrium, presenting negative real parts.

Equilibrium	
<i>Null</i>	$r_{p1} < 0; r_{p2} < 0; r_m < 0$
P_1	$-r_{p1} < 0; r_{p2} - c_{p12} \left(\frac{r_{p1}}{c_{p1}} \right) < 0; r_m + e_{m1} a_{pm1} \left(\frac{r_{p1}}{c_{p1}} \right) < 0$
P_2	$r_{p1} - c_{p21} \left(\frac{r_{p2}}{c_{p2}} \right) < 0; -r_{p2} < 0; r_m + e_{m2} a_{pm2} \left(\frac{r_{p2}}{c_{p2}} \right) < 0$
M	$r_{p1} + a_{pm1} \left(\frac{r_m}{c_m} \right) < 0; r_{p2} < 0 + a_{pm2} \left(\frac{r_m}{c_m} \right); -r_m < 0$
P_1P_2	$c_{p1}c_{p2} - c_{p12}c_{p21} > 0; r_m + e_{m1}a_{pm1}P_1^* + e_{m2}a_{pm2}P_2^* < 0$

P_1M	$c_{p1}c_m - e_{m1}a_{pm1}^2 > 0 ; r_{p2} - c_{p12}P_1^* + a_{pm2}M^* < 0$
P_2M	$c_{p2}c_m - e_{m2}a_{pm2}^2 > 0 ; r_{p1} - c_{p21}P_2^* + a_{pm1}M^* < 0$
P_1P_2M	Ruth-Hurwitz criterion (Murray 2002), see after

Table B.2: Stability of the ecological equilibria within the plant-pollinator community.

$$a_1 \stackrel{\text{def}}{=} c_{p1}P_1^* + c_{p2}P_2^* + c_mM^* > 0$$

$$a_3 \stackrel{\text{def}}{=} P_1^*P_2^*M^* [(c_{p1}c_{p2} - c_{p12}c_{p21})c_m - c_{p2}e_{m1}a_{pm1}^2 - c_{p1}e_{m2}a_{pm2}^2 + a_{pm1}a_{pm2}(c_{p21}e_{m1} + c_{p12}e_{m2})] > 0$$

$$a_2 \stackrel{\text{def}}{=} P_1^*M^*(c_{p1}c_m - e_{m1}a_{pm1}^2) + P_2^*M^*(c_{p2}c_m - e_{m2}a_{pm2}^2) + P_1^*P_2^*(c_{p1}c_{p2} - c_{p12}c_{p21})$$

$$a_1a_2 - a_3 > 0$$

III. Plant-herbivore community

In the absence of pollinators, the dynamics of the plant-herbivore community are given by:

$\frac{dP_1}{dt} = P_1(r_{p1} - c_{p1}P_1 - c_{p21}P_2 - a_{ph1}H)$	(a'')
$\frac{dP_2}{dt} = P_2(r_{p2} - c_{p2}P_2 - c_{p12}P_1 - a_{ph2}H)$	(b'')
$\frac{dH}{dt} = H(r_h - c_hH + e_{h1}a_{ph1}P_1 + e_{h2}a_{ph2}P_2)$	(c'')

There are eight possible ecological equilibria, whose expressions are given in **table B.3**.

Equilibrium	
<i>Null</i>	$P_1^* = P_2^* = H^* = 0$
P_1	$P_1^* = \frac{r_{p1}}{c_{p1}} ; P_2^* = H^* = 0$
P_2	$P_1^* = 0 ; P_2^* = \frac{r_{p2}}{c_{p2}} ; H^* = 0$
H	$P_1^* = 0 ; P_2^* = 0 ; H^* = \frac{r_h}{c_h}$
P_1P_2	$P_1^* = \frac{c_{p2}r_{p1} - c_{p21}r_{p2}}{c_{p1}c_{p2} - c_{p12}c_{p21}} ; P_2^* = \frac{-c_{p12}r_{p1} + c_{p1}r_{p2}}{c_{p1}c_{p2} - c_{p12}c_{p21}} ; H^* = 0$
P_1H	$P_1^* = \frac{c_h r_{p1} - a_{ph1} r_h}{c_{p1} c_h + e_{h1} a_{ph1}^2} ; P_2^* = 0 ; H^* = \frac{e_{h1} a_{ph1} r_{p1} + c_{p1} r_h}{c_{p1} c_h + e_{h1} a_{ph1}^2}$

P_2H	$P_1^* = 0; P_2^* = \frac{c_h r_{p2} - a_{ph2} r_h}{c_{p2} c_h + e_{h2} a_{ph2}^2}; H^* = \frac{e_{h2} a_{ph2} r_{p2} + c_{p2} r_h}{c_{p2} c_h + e_{h2} a_{ph2}^2}$
P_1P_2H	See after

Table B.3: Analytical expression of the ecological equilibria within the plant-herbivore community.

$$P_1^* = \frac{(c_{p2} c_h + e_{h2} a_{ph2}^2) r_{p1} - (e_{h2} a_{ph1} a_{ph2} + c_h c_{p21}) r_{p2} + (c_{p21} a_{ph2} - c_{p2} a_{ph1}) r_h}{(c_{p1} c_{p2} - c_{p12} c_{p21}) c_h + c_{p2} e_{h1} a_{ph1}^2 + c_{p1} e_{h2} a_{ph2}^2 - a_{ph1} a_{ph2} (c_{p21} e_{h1} + c_{p12} e_{h2})}$$

$$P_2^* = \frac{-(e_{h1} a_{ph1} a_{ph2} + c_h c_{p12}) r_{p1} + (c_{p1} c_h + e_{h1} a_{ph1}^2) r_{p2} + (c_{p12} a_{ph1} - c_{p1} a_{ph2}) r_h}{(c_{p1} c_{p2} - c_{p12} c_{p21}) c_h + c_{p2} e_{h1} a_{ph1}^2 + c_{p1} e_{h2} a_{ph2}^2 - a_{ph1} a_{ph2} (c_{p21} e_{h1} + c_{p12} e_{h2})}$$

$$H^* = \frac{(c_{p2} e_{h1} a_{ph1} - c_{p12} e_{h2} a_{ph2}) r_{p1} + (c_{p1} e_{h2} a_{ph2} - c_{p21} e_{h1} a_{ph1}) r_{p2} + (c_{p1} c_{p2} - c_{p12} c_{p21}) r_h}{(c_{p1} c_{p2} - c_{p12} c_{p21}) c_h + c_{p2} e_{h1} a_{ph1}^2 + c_{p1} e_{h2} a_{ph2}^2 - a_{ph1} a_{ph2} (c_{p21} e_{h1} + c_{p12} e_{h2})}$$

The criteria for the stability of each of these ecological equilibria, assuming its feasibility (i.e. that it corresponds to positive densities), are given in **table B.4**. These criteria correspond to the eigenvalues of the Jacobian matrix, at each equilibrium, presenting negative real parts.

Equilibrium	
None	$r_{p1} < 0; r_{p2} < 0; r_h < 0$
P_1	$-r_{p1} < 0; r_{p2} - c_{p12} \left(\frac{r_{p1}}{c_{p1}} \right) < 0; r_h + e_{h1} a_{ph1} \left(\frac{r_{p1}}{c_{p1}} \right) < 0$
P_2	$r_{p1} - c_{p21} \left(\frac{r_{p2}}{c_{p2}} \right) < 0; -r_{p2} < 0; r_h + e_{h2} a_{ph2} \left(\frac{r_{p2}}{c_{p2}} \right) < 0$
H	$r_{p1} - a_{ph1} \left(\frac{r_h}{c_h} \right) < 0; r_{p2} - a_{ph2} \left(\frac{r_h}{c_h} \right) < 0; -r_h < 0$
P_1P_2	$c_{p1} c_{p2} - c_{p12} c_{p21} > 0; r_h + e_{h1} a_{ph1} P_1^* + e_{h2} a_{ph2} P_2^* < 0$
P_1H	$r_{p2} - c_{p12} P_1^* - a_{ph2} H^* < 0$
P_2H	$r_{p1} - c_{p21} P_2^* - a_{ph1} H^* < 0$
P_1P_2H	Ruth-Hurwitz criterion (Murray 2002), see after

Table B.4: Stability of the ecological equilibria within the plant-herbivore community.

$$a_1 \stackrel{\text{def}}{=} c_{p1} P_1^* + c_{p2} P_2^* + c_h H^* > 0$$

$$a_3 \stackrel{\text{def}}{=} P_1^* P_2^* H^* [(c_{p1} c_{p2} - c_{p12} c_{p21}) c_h + c_{p2} e_{h1} a_{ph1}^2 + c_{p1} e_{h2} a_{ph2}^2 - a_{ph1} a_{ph2} (c_{p21} e_{h1} + c_{p12} e_{h2})] > 0$$

$$a_2 \stackrel{\text{def}}{=} P_1^* H^* (c_{p1} c_h + e_{h1} a_{ph1}^2) + P_2^* H^* (c_{p2} c_h + e_{h2} a_{ph2}^2) + P_1^* P_2^* (c_{p1} c_{p2} - c_{p12} c_{p21})$$

$$a_1 a_2 - a_3 > 0$$

IV. Plant-pollinator and plant-herbivore communities, depending on the plant community structure

Fig. S2 presents the ecological dynamics (i.e. ecological equilibria and their stability) for both the plant-pollinator (**Fig. S2 b-c-d**) and the plant-herbivore community (**Fig. S2 e-f-g**) according to the strengths of pollination and herbivory (i.e. (a_{pm1}, a_{pm2}) and (a_{ph1}, a_{ph2})), as well as the structure of the plant community (**Fig. S2 a**).

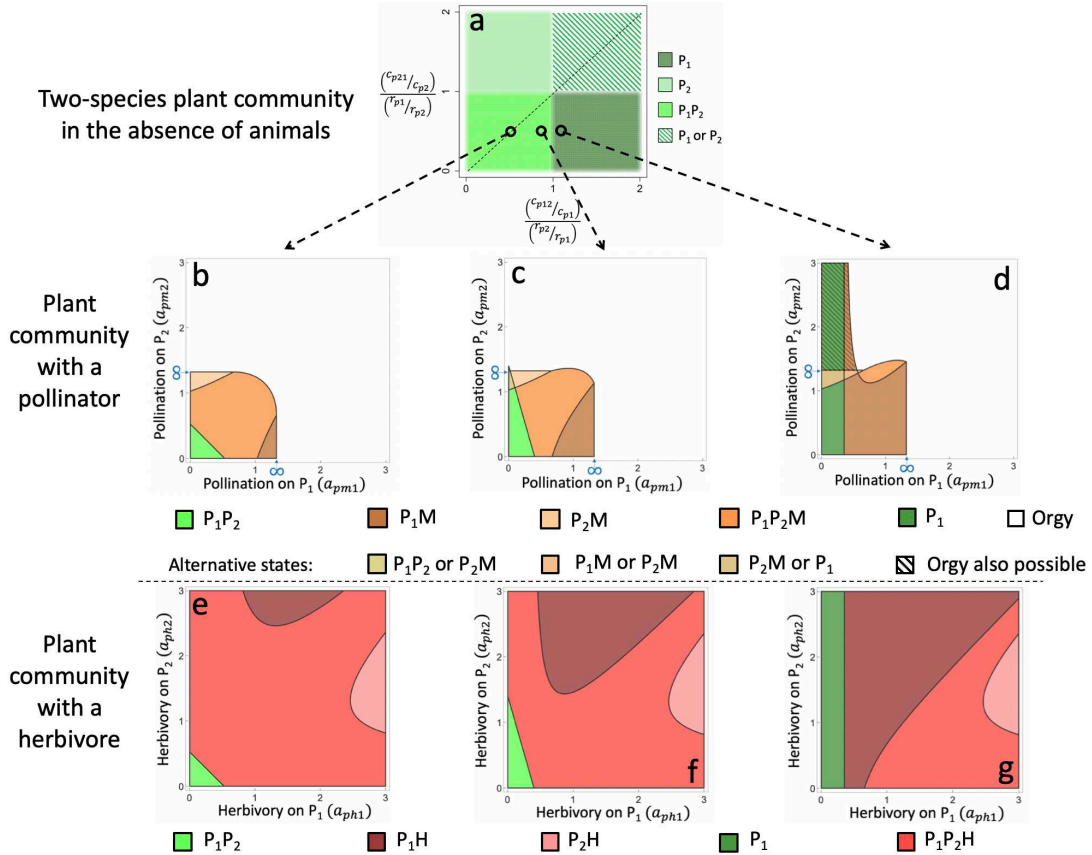


Fig. S2: The plant-animal communities depend on both competition among plant species and plant-animal interaction strengths. a. Plant community structure in the absence of animal species. **b-c-d** Ecological dynamics of the plant-pollinator community depending on the strength of plant-pollinator interactions ($c_{p21} = 0.35$ and $c_{p12} = 0.35$ (b); 0.6 (c); 0.77 (d)). Other parameters as in **table 1**. **e-f-g** Ecological dynamics of the plant-herbivore community depending on the strength of plant-herbivore interactions ($c_{p21} = 0.35$ and $c_{p12} = 0.35$ (e); 0.6 (f); 0.77 (g)). Other parameters as in **table 1**.

In the case of equally abundant plant species in the absence of animals, both the pollinator (**Fig. S2 b**, green) or the herbivore (**Fig. S2 e**, green) cannot survive if their respective interactions with plant species are too weak. An important difference between the two communities is that unbounded population growth is obtained when either one plant-pollinator interaction is too strong (**Fig. S2. b**, orgy in white). In contrast, the plant-herbivore community always displays stable ecological dynamics (**Fig. S2 e**). A second important difference concerns the effect of each interaction on the maintenance of plant coexistence. While strong pollination on P_1 provokes the extinction of P_2 and conversely (beige and brown areas in **Fig. S2 b**), strong herbivory on P_1 (or P_2) provokes the extinction of P_1 (or P_2) itself (light and dark red areas in **Fig. S2 e**). Such a difference is a direct consequence of pollination being beneficial to plants vs. herbivory being detrimental to them.

When both plant species coexist despite one (P_1) being a superior competitor, the ecological pattern is simply distorted in favor of that superior competitor (**Fig. S2 b vs. c**, **Fig. S2 e vs. f**). The distortion is even more pronounced when one plant species (P_1) excludes the other one in the absence of animals (**Fig. S2 d & g**). Note two important features. **(1)** Both the pollinator or the herbivore can potentially restore the coexistence of plant species. Such an outcome requires the pollinator to preferentially interact with the inferior competitor (**Fig. S2 d**), or the herbivore to preferentially consume the superior competitor (**Fig. S2 g**). **(2)** Depending on the relative strength of plant-pollinator interactions, the plant-pollinator community may display alternative stable states (**Fig S2 d**). The occurrence of different states depends on the initial densities within the community. In some cases (hatched areas in **Fig S2 d**), unbounded population growth may also be observed depending on initial densities.

V. Plant-pollinator-herbivore community

The dynamics of the community when all species are present follow the equations:

$\frac{dP_1}{dt} = P_1(r_{p1} - c_{p1}P_1 - c_{p21}P_2 + a_{pm1}M - a_{ph1}H)$	(1')
$\frac{dP_2}{dt} = P_2(r_{p2} - c_{p2}P_2 - c_{p12}P_1 + a_{pm2}M - a_{ph2}H)$	(2')
$\frac{dM}{dt} = M(r_m - c_mM + e_{m1}a_{pm1}P_1 + e_{m2}a_{pm2}P_2)$	(3')
$\frac{dH}{dt} = H(r_h - c_hH + e_{h1}a_{ph1}P_1 + e_{h2}a_{ph2}P_2)$	(4')

There are 16 different equilibria possible as each of the four species can either be present or absent. Their expressions are given in **table B.5**.

Equilibrium	
<i>Null</i>	$P_1^* = P_2^* = M^* = H^* = 0$
P_1	$P_1^* = \frac{r_{m1}}{c_{m1}}; P_2^* = M^* = H^* = 0$
P_2	$P_1^* = 0; P_2^* = \frac{r_{m2}}{c_{m2}}; M^* = H^* = 0$
M	$P_1^* = 0; P_2^* = 0; M^* = \frac{r_m}{c_m}; H^* = 0$
H	$P_1^* = 0; P_2^* = 0; M^* = 0; H^* = \frac{r_h}{c_h}$
P_1P_2	$P_1^* = \frac{c_{p2}r_{p1} - c_{p21}r_{p2}}{c_{p1}c_{p2} - c_{p12}c_{p21}}; P_2^* = \frac{-c_{p12}r_{p1} + c_{p1}r_{p2}}{c_{p1}c_{p2} - c_{p12}c_{p21}}; M^* = H^* = 0$
P_1M	$P_1^* = \frac{c_m r_{p1} + a_{pm1} r_m}{c_{p1} c_m - e_{m1} a_{pm1}^2}; P_2^* = 0; M^* = \frac{e_{m1} a_{pm1} r_{p1} + c_{p1} r_m}{c_{p1} c_m - e_{m1} a_{pm1}^2}; H^* = 0$
P_2M	$P_1^* = 0; P_2^* = \frac{c_m r_{p2} + a_{pm2} r_m}{c_{p2} c_m - e_{m2} a_{pm2}^2}; M^* = \frac{e_{m2} a_{pm2} r_{p2} + c_{p2} r_m}{c_{p2} c_m - e_{m2} a_{pm2}^2}; H^* = 0$
P_1H	$P_1^* = \frac{c_h r_{p1} - a_{ph1} r_h}{c_{p1} c_h + e_{h1} a_{ph1}^2}; P_2^* = M^* = 0; H^* = \frac{e_{h1} a_{ph1} r_{p1} + c_{p1} r_h}{c_{p1} c_h + e_{h1} a_{ph1}^2}$
P_2H	$P_1^* = 0; P_2^* = \frac{c_h r_{p2} - a_{ph2} r_h}{c_{p2} c_h + e_{h2} a_{ph2}^2}; M^* = 0; H^* = \frac{e_{h2} a_{ph2} r_{p2} + c_{p2} r_h}{c_{p2} c_h + e_{h2} a_{ph2}^2}$
P_1P_2M	Same expression as in the “plant-pollinator community” section (I.2)
P_1P_2H	Same expression as in the “plant-pollinator community” section (I.3)
P_1MH	$P_1^* = \frac{c_h c_m r_{p1} + c_h a_{pm1} r_m - c_m a_{ph1} r_h}{c_h c_m c_{p1} - c_h e_{m1} a_{pm1}^2 + c_m e_{h1} a_{ph1}^2}$ $P_2^* = 0$ $M^* = \frac{c_h e_{m1} a_{pm1} r_{p1} + (c_{p1} c_h + e_{h1} a_{ph1}^2) r_m - e_{m1} a_{pm1} a_{ph1} r_h}{c_h c_m c_{p1} - c_h e_{m1} a_{pm1}^2 + c_m e_{h1} a_{ph1}^2}$ $H^* = \frac{c_m e_{h1} a_{ph1} r_{p1} + e_{h1} a_{pm1} a_{ph1} r_m + (c_{p1} c_m - e_{m1} a_{pm1}^2) r_h}{c_h c_m c_{p1} - c_h e_{m1} a_{pm1}^2 + c_m e_{h1} a_{ph1}^2}$
P_2MH	$P_1^* = 0$ $P_2^* = \frac{c_h c_m r_{p2} + c_h a_{pm2} r_m - c_m a_{ph2} r_h}{c_h c_m c_{p2} - c_h e_{m2} a_{pm2}^2 + c_m e_{h2} a_{ph2}^2}$ $M^* = \frac{c_h e_{m2} a_{pm2} r_{p2} + (c_{p2} c_h + e_{h2} a_{ph2}^2) r_m - e_{m2} a_{pm2} a_{ph2} r_h}{c_h c_m c_{p2} - c_h e_{m2} a_{pm2}^2 + c_m e_{h2} a_{ph2}^2}$ $H^* = \frac{c_m e_{h2} a_{ph2} r_{p2} + e_{h2} a_{pm2} a_{ph2} r_m + (c_{p2} c_m - e_{m2} a_{pm2}^2) r_h}{c_h c_m c_{p2} - c_h e_{m2} a_{pm2}^2 + c_m e_{h2} a_{ph2}^2}$

$P_1 P_2 MH$	See after

Table B.5: Analytical expression of the ecological equilibria within the plant-pollinator-herbivore community.

To simplify the expressions, the densities when all species are present- i.e. coexistence equilibrium – are given using the nondimensionalized formulation (**Appendix A**).

$$P_1^* = \frac{r_{p1} \text{Num}(P_1^*)}{c_{p1} \text{Den}(P_1^*)}; P_2^* = \frac{r_{p1} \text{Num}(P_2^*)}{c_{p2} \text{Den}(P_2^*)}$$

With

$$\begin{aligned} \text{Num}(P_1^*) = & (1 + \lambda_{h2} \alpha_{ph2}^2 - \lambda_{m2} \alpha_{pm2}^2) + \rho_2 (\lambda_{m2} \alpha_{pm2} \alpha_{pm1} - \lambda_{h2} \alpha_{ph2} \alpha_{ph1} - \alpha_{21}) \\ & + \rho_m (\alpha_{pm1} - \alpha_{21} \alpha_{pm2} + \lambda_{h2} \alpha_{ph2} (\alpha_{pm1} \alpha_{ph2} - \alpha_{pm2} \alpha_{ph1})) + \rho_h (-\alpha_{ph1} + \alpha_{21} \alpha_{ph2} \\ & + \lambda_{m2} \alpha_{pm2} (\alpha_{pm2} \alpha_{ph1} - \alpha_{pm1} \alpha_{ph2})) \end{aligned}$$

$\text{Num}(P_2^*)$ is obtained by inverting 1 and 2 indexes in the expression of $\text{Num}(P_1^*)$.

$$\begin{aligned} \text{Den}(P_1^*) = & \text{Den}(P_2^*) \\ = & 1 - \alpha_{12} \alpha_{21} + \lambda_{h1} \alpha_{ph1}^2 + \lambda_{h2} \alpha_{ph2}^2 - \lambda_{m1} \alpha_{pm1}^2 - \lambda_{m2} \alpha_{pm2}^2 \\ & + \alpha_{pm1} \alpha_{pm2} (\lambda_{m1} \alpha_{21} + \lambda_{m2} \alpha_{12}) - \alpha_{ph1} \alpha_{ph2} (\lambda_{h1} \alpha_{21} + \lambda_{h2} \alpha_{12}) - (\alpha_{pm1} \alpha_{ph2} \\ & - \alpha_{pm2} \alpha_{ph1}) (\lambda_{m1} \lambda_{h2} \alpha_{pm1} \alpha_{ph2} - \lambda_{m2} \lambda_{h1} \alpha_{pm2} \alpha_{ph1}) \end{aligned}$$

$$M^* = \frac{r_{p1}}{c_m} (\rho_m + \lambda_{m1} \alpha_{pm1} P_1^* + \lambda_{m2} \alpha_{pm2} P_2^*); H^* = \frac{r_{p1}}{c_h} (\rho_h + \lambda_{h1} \alpha_{ph1} P_1^* + \lambda_{h2} \alpha_{ph2} P_2^*)$$

Stability:

Stability was computed using the Ruth-Hurwitz criterion (Murray 2002) in four dimensions.

Appendix C: Analytical study of community eco-evolutionary dynamics in the case of one animal evolving

I. Plant phenotype dissimilarity and trade-off

As illustrated by **Fig. S3**, the shape of the trade-off experienced by animal species – i.e. preferentially interacting with P_1 at the expense of the interaction with P_2 or conversely – is given by the dissimilarity of plant phenotypes $t_{p2} - t_{p1}$. Indeed, the shape of such a trade-off shifts from being convex at small dissimilarities (1.5 in **Fig. S3**, i.e. weak trade-off) to being concave at important dissimilarities (4 in **Fig. S3**, i.e. strong trade-off). Note that we use the terms convex/concave as usually done in the eco-evolutionary literature (e.g. Kisdi 2006; Rueffler et al. 2006), which was initially based on the convexity of the fitness set (Levins 1962) – i.e. the fitness of all potential strategies. Important results are that convex trade-offs are associated with the selection of a generalist strategy as it is more advantageous than specializing on either resource, while a concave trade-off selects for specializing on either one resource depending on initial conditions (de Mazancourt and Dieckmann 2004; Kisdi 2006; Rueffler et al. 2006). Moreover, disruptive selection can arise in the case of a slightly concave trade-off.

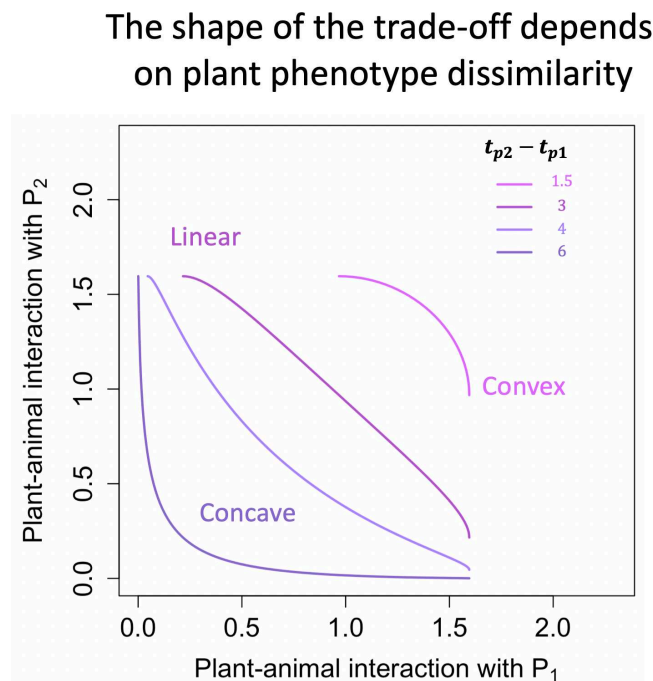


Fig. S3: The shape of the trade-off depends on the dissimilarity of plant phenotypes. Trade-off intensity increases from 1.5 to 6, corresponding respectively to a convex and concave trade-off. A linear trade-off corresponds to the transition between a convex and a concave trade-off.

II. Adaptive dynamics

II.1. Pollinator evolution

We present here the analytical study of pollinator evolution within a plant-pollinator or plant-pollinator-herbivore community. The analytical expressions presented hereafter, indeed, do not directly depend on the presence of herbivores. The dependence is indirect, through the modification of the plant densities at ecological equilibrium (P_1^*, P_2^*) .

The fitness of invasion w , which indicates whether a rare mutant M' with phenotype t'_m can invade the resident population M with phenotype t_m at ecological equilibrium, corresponds to the per capita growth rate of that mutant when rare. The mutant invades if its positive, otherwise it goes extinct.

$$\begin{aligned} w(t'_m, t_m) &\stackrel{\text{def}}{=} \left. \frac{dM'}{Mdt} \right|_{M' \ll M^*} = r_m - c_m M' - c_m M^* + e_{m1} a'_{pm1} P_1^* + e_{m2} a'_{pm2} P_2^* \\ &= r_m - c_m M^* + e_{m1} a'_{pm1} P_1^* + e_{m2} a'_{pm2} P_2^* \end{aligned}$$

$\Leftrightarrow w(t'_m, t_m) = e_{m1}(a_{pm1}' - a_{pm1})P_1^* + e_{m2}(a_{pm2}' - a_{pm2})P_2^*$	(A)
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The last equality ensuing from the ecological equilibrium of the resident pollinator population (i.e. $r_m - c_m M^* + e_{m1} a_{pm1} P_1^* + e_{m2} a_{pm2} P_2^* = 0$). As for the notation, $a'_{pm} \stackrel{\text{def}}{=} a_{pm}(t'_m)$ and $a_{pm} \stackrel{\text{def}}{=} a_{pm}(t_m)$. Assuming mutations of small phenotypic amplitude, the rate of the sequence of trait substitution is proportional to the selection gradient (Dieckmann and Law 1996).

$\begin{aligned} \text{Selection gradient} &\stackrel{\text{def}}{=} \left. \frac{\partial w(t'_m, t_m)}{\partial t'_m} \right _{t'_m = t_m} \\ &= -\frac{e_{m1}(t_m - t_{p1})}{\sigma_{Pol1}^2} a_{pm1} P_1^* + \frac{e_{m2}(t_{p2} - t_m)}{\sigma_{Pol2}^2} a_{pm2} P_2^* \end{aligned}$	(B)
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This expression shows that at $t_m = 0 \stackrel{\text{def}}{=} \frac{t_{p1} + t_{p2}}{2}$, selection favors increasing the matching with the most profitable plant-species, profitability being defined by the quantity $\frac{e_m a_{pm} P^*}{\sigma_{Pol}^2}$.

Evolutionary singularities:

Evolutionary singularities are phenotypes that nullify the selection gradient. If $t_{p1} = t_{p2}$, there is only one singularity $t_m^* = t_{p1} = t_{p2}$. Assuming $t_{p1} \neq t_{p2}$, we show there is at least one evolutionary singularity and all singularities are in $]t_{p1}, t_{p2}[$.

Proof:

If $t_m \leq t_{p1}$, $\left. \frac{\partial w(t'_m, t_m)}{\partial t'_m} \right|_{t'_m=t_m} > 0$. If $t_m \geq t_{p2}$, $\left. \frac{\partial w(t'_m, t_m)}{\partial t'_m} \right|_{t'_m=t_m} < 0$. This implies that all singularities are in $]t_{p1}, t_{p2}[$. Moreover, the Intermediate Value Theorem indicates that the selection gradient necessarily vanishes in $]t_{p1}, t_{p2}[$, so that there is at least one singularity. This ends the proof.

A singularity satisfies the following equation, where $a_{pm}^* \stackrel{\text{def}}{=} a_{pm}(t_m^*)$:

$$0 = -\frac{e_{m1}(t_m^* - t_{p1})}{\sigma_{Pol1}^2} a_{pm1}^* P_1^* + \frac{e_{m2}(t_{p2} - t_m^*)}{\sigma_{Pol2}^2} a_{pm1}^* P_2^*$$

It can be rewritten:

$\frac{t_{p2} - t_m^*}{t_{p2} - t_{p1}} = \frac{\frac{e_{m1} a_{pm1}^* P_1^*}{\sigma_{Pol1}^2}}{\frac{e_{m1} a_{pm1}^* P_1^*}{\sigma_{Pol1}^2} + \frac{e_{m2} a_{pm2}^* P_2^*}{\sigma_{Pol2}^2}}$	(C)
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In the case where plant species have equal abundances in the absence of the pollinator, an evolutionary singularity exists at $t_m^* = \frac{t_{p1} + t_{p2}}{2} \stackrel{\text{def}}{=} 0$.

Proof:

It is assumed that the ecological parameters of P_1 and P_2 are identical (see table 1 in the main document). At $t_m = 0$, $\frac{e_{m1} a_{pm1}^*}{\sigma_{Pol1}^2} = \frac{e_{m2} a_{pm2}^*}{\sigma_{Pol2}^2}$, because $e_{m1} = e_{m2}$, $a_{pm01} = a_{pm02}$ and $\sigma_{Pol1} = \sigma_{Pol2}$. Moreover, the symmetry of the community context implies that $P_1^* = P_2^*$. At the end, both sides of equation (C) are equal to $\frac{1}{2}$ so that $t_m = 0$ indeed nullifies the selection gradient. This ends the proof.

The nature of an evolutionary is defined by two properties: convergence and invasibility. These properties are given by the sign of the second derivatives of the fitness of invasion, according to equations (D) & (E).

Invasibility	$\left. \frac{\partial^2 w(t'_m, t_m)}{\partial t_m'^2} \right _{t'_m=t_m=t_m^*} > 0$	(D)
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Convergence	$\left. \frac{\frac{\partial w(t'_m, t_m)}{\partial t'_m}}{dt_m} \right _{t'_m=t_m} \Big _{t_m=t_m^*} < 0$	(E)
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Here we have:

$$\left. \frac{\partial^2 w(t'_m, t_m)}{\partial t_m'^2} \right|_{t'_m=t_m=t_m^*} = \frac{e_{m1} a_{pm1}^* P_1^*}{\sigma_{Pol1}^2} \left[\frac{(t_m^* - t_{p1})^2}{\sigma_{Pol1}^2} - 1 \right] + \frac{e_{m2} a_{pm2}^* P_2^*}{\sigma_{Pol2}^2} \left[\frac{(t_m^* - t_{p2})^2}{\sigma_{Pol2}^2} - 1 \right]$$

And

$$\begin{aligned} & \left. \frac{\frac{\partial w(t'_m, t_m)}{\partial t'_m}}{dt_m} \right|_{t'_m=t_m} \Big|_{t_m=t_m^*} \\ &= \left. \frac{\partial^2 w(t'_m, t_m)}{\partial t_m'^2} \right|_{t'_m=t_m=t_m^*} \\ & - \left[\frac{e_{m1} a_{pm1}^*}{\sigma_{Pol1}^2} (t_m^* - t_{p1}) \frac{dP_1^*}{dt_m} \right]_{t_m=t_m^*} + \frac{e_{m2} a_{pm2}^*}{\sigma_{Pol2}^2} (t_m^* - t_{p2}) \frac{dP_2^*}{dt_m} \Big|_{t_m=t_m^*} \end{aligned}$$

Note that if plant densities are held constant ($\frac{dP_1^*}{dt_m} = \frac{dP_2^*}{dt_m} = 0$) – i.e. in the absence of eco-evolutionary feedback – the conditions for invasibility and convergence are opposite.

Regarding the singularity $t_m^* = \frac{t_{p1} + t_{p2}}{2} \stackrel{\text{def}}{=} 0$, in the case of identical ecological parameters for plant species (the indexing of plant species is forgotten on purpose as $P_1^* = P_2^* = P^*$ etc.):

$$\left. \frac{\partial^2 w(t'_m, t_m)}{\partial t_m'^2} \right|_{t'_m=t_m=t_m^*=0} = \frac{2e_m a_{pm}^* P^*}{\sigma_{Pol}^2} \left[\frac{t_{p2}^2}{\sigma_{Pol}^2} - 1 \right]$$

So that this singularity is invisable if and only if $t_{p2} > \sigma_{Pol}$. The singularity is thus non-invasible for weak trade-off $t_{p2} - t_{p1} \stackrel{\text{def}}{=} 2t_{p2} < 2\sigma_{Pol}$. Moreover:

$$\begin{aligned}
& \left. \frac{\frac{\partial w(t'_m, t_m)}{\partial t'_m}}{dt_m} \right]_{t'_m=t_m} \Bigg|_{t_m=t_m^*=0} \\
&= \frac{2e_m a_{pm}^* P^*}{\sigma_{Pol}^2} \left[\frac{t_{p2}^2}{\sigma_{Pol}^2} - 1 \right] - \frac{e_m a_{pm}^*}{\sigma_{Pol}^2} \left(t_{p2} \frac{dP_1^*}{dt_m} \Big|_{t_m=t_m^*=0} - t_{p2} \frac{dP_2^*}{dt_m} \Big|_{t_m=t_m^*=0} \right) \\
&= \frac{2e_m a_{pm}^* P^*}{\sigma_{Pol}^2} \left[\frac{t_{p2}^2}{\sigma_{Pol}^2} - 1 \right] + \frac{2e_m a_{pm}^*}{\sigma_{Pol}^2} \left(t_{p2} \frac{dP_2^*}{dt_m} \Big|_{t_m=t_m^*=0} \right)
\end{aligned}$$

The last equality resulting from the fact that $\left. \frac{dP_1^*}{dt_m} \right]_{t_m=t_m^*=0} = - \left. \frac{dP_2^*}{dt_m} \right]_{t_m=t_m^*=0}$ due to the symmetrical configuration of the community when $t_m = t_m^* = 0$. It is possible to rigorously demonstrate such equality by remarking that $\left. \frac{da_{pm1}}{dt_m} \right]_{t_m=0} = - \left. \frac{da_{pm2}}{dt_m} \right]_{t_m=0}$ and deriving the expressions of P_1^* and P_2^* given in **appendix B.II**. We finally obtain:

$$\left. \frac{\frac{\partial w(t'_m, t_m)}{\partial t'_m}}{dt_m} \right]_{t'_m=t_m} \Bigg|_{t_m=t_m^*=0} = \frac{2e_m a_{pm}^*}{\sigma_{Pol}^2} \left[\frac{t_{p2}^2}{\sigma_{Pol}^2} P^* + t_{p2} \frac{dP_2^*}{dt_m} \Big|_{t_m=t_m^*=0} - P^* \right]$$

The expression $\frac{t_{p2}^2}{\sigma_{Pol}^2} P^* + t_{p2} \frac{dP_2^*}{dt_m} \Big|_{t_m=t_m^*=0} - P^*$ is a polynomic in t_{p2} , thus it is a continuous function of the variable t_{p2} . When $t_{p2} = 0$, the function is negative ($= -P^* < 0$), which implies it is negative in a vicinity of 0. This means that there exists a given $\delta > 0$ such as

$$\left. \frac{\frac{\partial w(t'_m, t_m)}{\partial t'_m}}{dt_m} \right]_{t'_m=t_m} \Bigg|_{t_m=t_m^*=0} < 0 \text{ if } t_{p2} < \delta. \text{ In other words, the singularity } t_m^* = 0 \text{ is convergent}$$

when $t_{p2} \approx t_{p1}$, which corresponds to a weak trade-off.

II.2. Herbivore evolution

As in the case of pollinator evolution, the analysis presented here applies to the evolution of the herbivore with or without the presence of the pollinator population. When the latter is present, the expressions of plant abundances (P_1^*, P_2^*) are modified.

Fitness of invasion:

We consider a mutant with phenotype t'_h within a resident herbivore population of phenotype t_h .

$\Leftrightarrow w(t'_h, t_h) = e_{h1}(a_{ph1}' - a_{ph1})P_1^* + e_{h2}(a_{ph2}' - a_{ph2})P_2^*$	(F)
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Notations $a'_{ph} \stackrel{\text{def}}{=} a_{ph}(t'_h)$ and $a_{ph} \stackrel{\text{def}}{=} a_{ph}(t_h)$.

Selection gradient

$\left. \frac{\partial w(t'_h, t_h)}{\partial t'_h} \right]_{t'_h=t_h} = -\frac{e_{h1}(t_h - t_{p1})}{\sigma_{Her1}^2} a_{ph1} P_1^* + \frac{e_{h2}(t_{p2} - t_h)}{\sigma_{Her2}^2} a_{ph2} P_2^* \quad (G)$
--

This expression shows that at $t_h = 0 \stackrel{\text{def}}{=} \frac{t_{p1} + t_{p2}}{2}$, selection favors increasing the matching with the most profitable plant species, profitability being defined by the quantity $\frac{e_m a_{pm} P^*}{\sigma_{pol}^2}$.

If $t_{p1} = t_{p2}$, there is only one singularity $t_h^* = t_{p1} = t_{p2}$ and it is a CSS. If $t_{p1} \neq t_{p2}$, using the Intermediate Value Theorem, we show there is at least one singularity and all singularities are in $]t_{p1}, t_{p2}[$.

Evolutionary singularities:

They satisfy:

$$0 = \frac{e_{h1}(t_h^* - t_{p1})}{\sigma_{Her1}^2} a_{ph1}^* P_1^* - \frac{e_{h2}(t_{p2} - t_h^*)}{\sigma_{Her2}^2} a_{ph2}^* P_2^*$$

It can be rewritten:

$\frac{t_{p2} - t_h^*}{t_{p2} - t_{p1}} = \frac{\frac{e_{h1} a_{ph1}^* P_1^*}{\sigma_{Her1}^2}}{\frac{e_{h1} a_{ph1}^* P_1^*}{\sigma_{Her1}^2} + \frac{e_{h2} a_{ph2}^* P_2^*}{\sigma_{Her2}^2}} \quad (H)$

Like in the case of pollinator evolution, when plant species have equal abundances in the absence of the herbivore, an evolutionary singularity exists at $t_h^* = \frac{t_{p1} + t_{p2}}{2} \stackrel{\text{def}}{=} 0$.

Convergence and invasibility of evolutionary singularities:

Invasibility is equivalent to:

$$\left. \frac{\partial^2 w(t'_h, t_h)}{\partial t_h'^2} \right]_{t'_h=t_h=t_h^*} = \frac{e_{h1} a_{ph1}^* P_1^*}{\sigma_{Her1}^2} \left[\frac{(t_h^* - t_{p1})^2}{\sigma_{Her1}^2} - 1 \right] + \frac{e_{h2} a_{ph2}^* P_2^*}{\sigma_{Her2}^2} \left[\frac{(t_h^* - t_{p2})^2}{\sigma_{Her2}^2} - 1 \right] > 0$$

In particular, the singularity at $t_h^* = 0$, in the case of identical plant species, is non-invasible if the trade-off is weak.

Proof:

$$\left. \frac{\partial^2 w(t'_h, t_h)}{\partial t_h'^2} \right]_{t'_h=t_h=t_h^*=0} = \frac{2e_h a_{ph}^* P^*}{\sigma_{Her}^2} \left[\frac{t_{p2}^2}{\sigma_{Her}^2} - 1 \right]$$

Which is positive if and only if $t_{p2} > \sigma_{Her}$. The singularity is thus non-invasible as long as the trade-off satisfies: $t_{p2} - t_{p1} \stackrel{\text{def}}{=} 2t_{p2} < 2t_{p2}$.

Convergence is equivalent to:

$$\begin{aligned} & \left. \frac{\frac{\partial w(t'_h, t_h)}{\partial t_h'}}{dt_h} \right]_{t'_h=t_h} \\ & \left. \right]_{t_h=t_h^*} \\ & = \left. \frac{\partial^2 w(t'_h, t_h)}{\partial t_h'^2} \right]_{t'_h=t_h=t_h^*} \\ & - \left[\frac{e_{h1} a_{ph1}^*}{\sigma_{Her1}^2} (t_h^* - t_{p1}) \frac{dP_1^*}{dt_h} \right]_{t_h=t_h^*} + \frac{e_{h2} a_{ph2}^*}{\sigma_{Her2}^2} (t_h^* - t_{p2}) \frac{dP_2^*}{dt_h} \right]_{t_h=t_h^*} < 0 \end{aligned}$$

Regarding the singularity at $t_h^* = 0$, in the case of identical plant species (i.e. identical ecological parameters), it is convergent when the trade-off is weak.

Indeed, as $\left. \frac{dP_1^*}{dt_h} \right]_{t_h=t_h^*=0} = - \left. \frac{dP_2^*}{dt_h} \right]_{t_h=t_h^*=0}$ (symmetrical eco-evolutionary setting), we have:

$$\left. \frac{\frac{\partial w(t'_h, t_h)}{\partial t_h'}}{dt_h} \right]_{t'_h=t_h} \left. \right]_{t_h=t_h^*=0} = \frac{2e_h a_{ph}^*}{\sigma_{Her}^2} \left[\frac{t_{p2}^2}{\sigma_{Her}^2} P^* + t_{p2} \frac{dP_2^*}{dt_h} \right]_{t_h=t_h^*=0} - P^*$$

Which is negative at $t_{p2} = 0$, and hence in the vicinity of $t_{p2} = 0$ (continuity argument), i.e. when the trade-off is weak.

Note finally, that if plant densities are held constant ($\frac{dP_1^*}{dt_h} = \frac{dP_2^*}{dt_h} = 0$) – i.e. in the absence of eco-evolutionary feedback – the conditions for invasibility and convergence are opposite.

Also, the equality $\left. \frac{dP_1^*}{dt_h} \right|_{t_h=t_h^*=0} = - \left. \frac{dP_2^*}{dt_h} \right|_{t_h=t_h^*=0}$ can directly be obtained from the expressions of P_1^* and P_2^* given in **appendix B.III**, by remarking that $\left. \frac{da_{ph1}}{dt_h} \right|_{t_h=0} = - \left. \frac{da_{ph2}}{dt_h} \right|_{t_h=0}$.

II.3. Disruptive selection is only possible in the case of herbivore evolution

Considering that the ecological parameters are identical for both plant species, we analytically demonstrate that in the case of pollinator evolution within a plant-pollinator community, the singular generalist strategy (i.e. $t_m^* = \frac{t_{p1}+t_{p2}}{2} \stackrel{\text{def}}{=} 0$) cannot be a branching point. In contrast, a branching point is possible when the evolving animal is a herbivore (i.e. at $t_h^* = \frac{t_{p1}+t_{p2}}{2} \stackrel{\text{def}}{=} 0$).

First, let us recapitulate the conditions for invasibility and convergence of the generalist singular strategy in the case of pollinator and herbivore (**table C.1**), derived in the previous sections:

	Non-invasibility	Convergence
Pollinator	$\left. \frac{\partial^2 w(t'_m, t_m)}{\partial t_m'^2} \right _{t'_m=t_m=t_m^*=0} < 0$	$\left. \frac{\partial^2 w(t'_m, t_m)}{\partial t_m'^2} \right _{t'_m=t_m=t_m^*=0} + \frac{e_m a_{pm}^*}{\sigma_{Pol}^2} t_{p2} \left[\left. \frac{dP_2^*}{dt_m} \right _{t_m=t_m^*=0} - \left. \frac{dP_1^*}{dt_m} \right _{t_m=t_m^*=0} \right] < 0$
Herbivore	$\left. \frac{\partial^2 w(t'_h, t_h)}{\partial t_h'^2} \right _{t'_h=t_h=t_h^*=0} < 0$	$\left. \frac{\partial^2 w(t'_h, t_h)}{\partial t_h'^2} \right _{t'_h=t_h=t_h^*=0} + \frac{e_h a_{ph}^*}{\sigma_{Her}^2} t_{p2} \left[\left. \frac{dP_2^*}{dt_h} \right _{t_h=t_h^*=0} - \left. \frac{dP_1^*}{dt_h} \right _{t_h=t_h^*=0} \right] < 0$

Table C.1: Conditions for non-invasibility and convergence of the evolutionary singularity at $\frac{t_{p1}+t_{p2}}{2} \stackrel{\text{def}}{=} 0$

We have already shown (**appendix C.II.1 & 2**) that the evolutionary singularity is a CSS in both cases when the trade-off is weak, and that it becomes invisable as the trade-off intensifies.

The decisive argument of the undergoing proof is that $\left[\frac{dP_2^*}{dt_m} \right]_{t_m=t_m^*=0} - \frac{dP_1^*}{dt_m} \Big|_{t_m=t_m^*=0} > 0$ while $\left[\frac{dP_2^*}{dt_h} \right]_{t_h=t_h^*=0} - \frac{dP_1^*}{dt_h} \Big|_{t_h=t_h^*=0} < 0$. As a result, as the trade-off intensifies, convergence is lost before non-invasibility in the case of pollinators, while it is lost after non-invasibility in the case of herbivores.

Let us now calculate the expression $\left[\frac{dP_2^*}{dt_m} \right]_{t_m=t_m^*=0} - \frac{dP_1^*}{dt_m} \Big|_{t_m=t_m^*=0}$.

Noting explicitly the dependence on the pollinator trait t_m , the ecological equilibrium is written:

$$0 = r_p - c_p P_1^*(t_m) - c_{pi} P_2^*(t_m) + a_{pm1}(t_m) M^*(t_m)$$

$$0 = r_p - c_p P_2^*(t_m) - c_{pi} P_1^*(t_m) + a_{pm2}(t_m) M^*(t_m)$$

Where $c_{pi} = c_{p12} = c_{p21}$. Combining these two equalities to eliminate $M^*(t_m)$, and using $\frac{da_{pm1}}{dt_m} \Big|_{t_m=0} = -\frac{da_{pm2}}{dt_m} \Big|_{t_m=0}$, we obtain:

$\left[\frac{dP_2^*}{dt_m} \right]_{t_m=t_m^*=0} - \frac{dP_1^*}{dt_m} \Big _{t_m=t_m^*=0} = \frac{2t_{p2}(c_p + c_{pi})}{\sigma_{Pol}^2(c_p - c_{pi})} \left[P_M^* - \frac{r_p}{c_p + c_{pi}} \right]$	(I)
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Where $P_M^* = P_1^*_{t_m=0} = P_2^*_{t_m=0}$.

Similarly, using $\frac{da_{ph1}}{dt_h} \Big|_{t_h=0} = -\frac{da_{ph2}}{dt_h} \Big|_{t_h=0}$, and with the notation $P_H^* = P_1^*_{t_h=0} = P_2^*_{t_h=0}$, we obtain:

$\left[\frac{dP_2^*}{dt_h} \right]_{t_h=t_h^*=0} - \frac{dP_1^*}{dt_h} \Big _{t_h=t_h^*=0} = \frac{2t_{p2}(c_p + c_{pi})}{\sigma_{Her}^2(c_p - c_{pi})} \left[P_H^* - \frac{r_p}{c_p + c_{pi}} \right]$	(J)
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Finally, remarking that $\frac{r_p}{c_p + c_{pi}}$ is the density of plant species in the absence of animals, it follows from the positive effect of pollination on plant densities that $\left[P_M^* - \frac{r_p}{c_p + c_{pi}} \right] \geq 0$. If it was not the case, then both $\frac{dP_1}{dt}$ and $\frac{dP_2}{dt}$ would be strictly positive (equation 1-2, main document), which

contradict the assumption of ecological equilibrium. In contrast, $\left[P_H^* - \frac{r_p}{c_p + c_{pi}} \right] \leq 0$, because herbivory reduces plant densities. If it was not the case, both $\frac{dP_1}{dt}$ and $\frac{dP_2}{dt}$ would be strictly negative (equation 1-2, main document).

The last result implies that $\left[\frac{dP_2^*}{dt_m} \Big|_{t_m=t_m^*=0} - \frac{dP_1^*}{dt_m} \Big|_{t_m=t_m^*=0} \right] > 0$ while $\left[\frac{dP_2^*}{dt_h} \Big|_{t_h=t_h^*=0} - \frac{dP_1^*}{dt_h} \Big|_{t_h=t_h^*=0} \right] < 0$, which ends the proof.

An example of the herbivore evolutionary dynamics following a branching event is presented in **Fig. S4**. The branching leads to the coexistence of two herbivore morphs (dimorphic population), each one preferentially consuming one plant species, i.e. a cohort of two specialist herbivores.

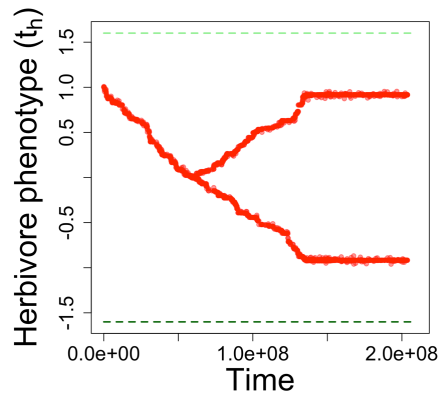


Fig. S4: Evolutionary dynamics of the herbivore phenotype subject to disruptive selection (i.e. branching point). The green dotted lines indicate plant phenotypes ($t_{p2} = -t_{p1} = 1.6$). Parameters: ($c_{p12} = c_{p21} = 0.4$, $a_{ph0} = 3.5$). Other parameters as in **table 1**.

III. Completing the results presented in Fig. 1: Figure S5.

The contrasting evolutionary dynamics arising from pollinator vs. herbivore evolution are still observed when one plant species is a slightly better competitor (**Fig. S5 b vs. c**). In particular, disruptive selection is only observed in the case of herbivore evolution. In addition, the evolution of the pollinator phenotype cannot prevent the competitive exclusion of the inferior competitor plant species (**Fig. S5d**), when this plant is already excluded in the absence of animal species. In the case where plants coexist in the absence of animals despite one plant species being a superior competitor, plant coexistence is maintained in the presence of the evolving herbivore (**Fig. S5e**).

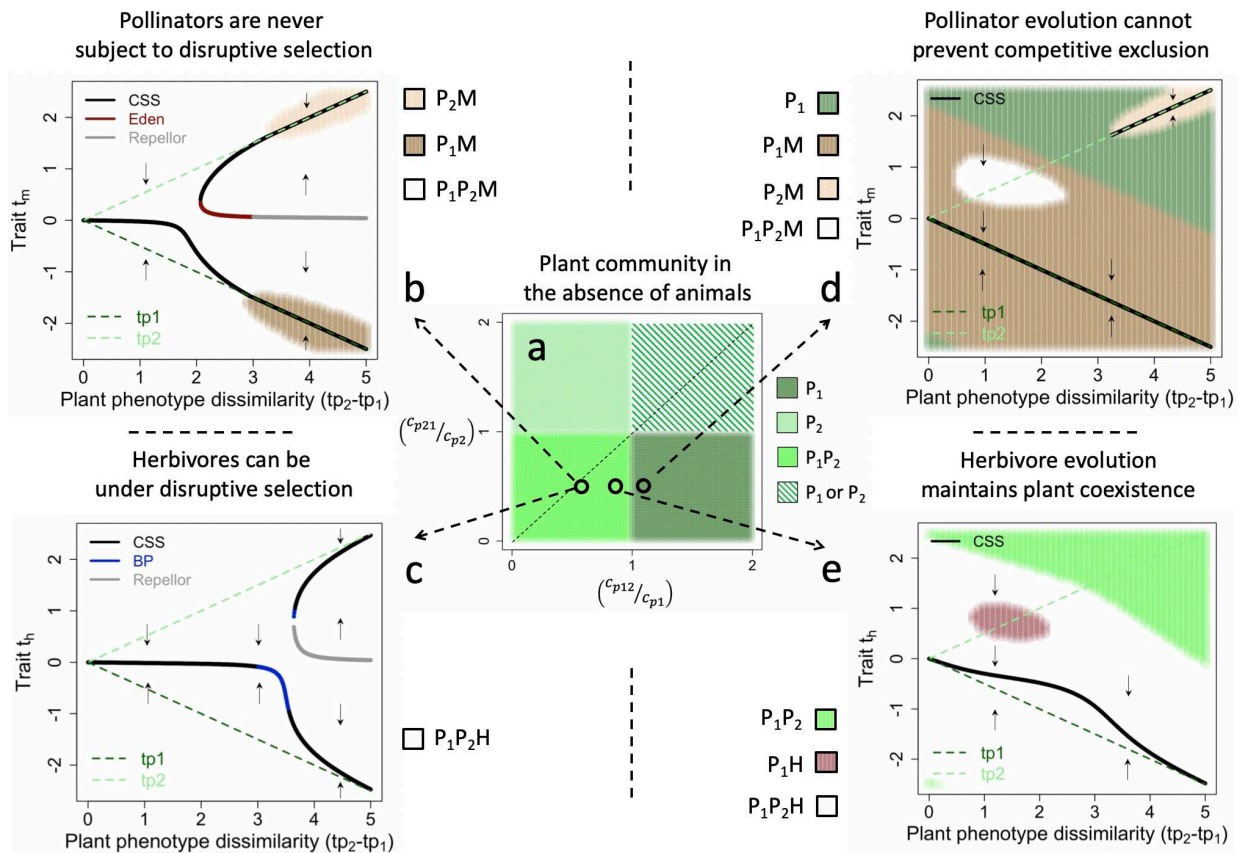


Fig. S5: Completing Fig. 1: Contrasting pollinator vs. herbivore eco-evolutionary dynamics within a 2-plant species community. **a.** Plant community in the absence of animal species (see Fig. S1 for details). **b.** Pollinator evolution within a plant community of almost similarly abundant plant species in the absence of animals. Parameters: ($c_{p12} = 0.37, c_{p21} = 0.35, a_{pm0} = 4$) **c.** Herbivore evolution within a plant community of almost similarly abundant plant species in the absence of animals. Parameters: ($c_{p12} = 0.37, c_{p21} = 0.35, a_{ph0} = 4$) **d.** Pollinator evolution within a plant community in which P_2 is competitively excluded in the absence of animals. Parameters: ($c_{p12} = 0.735, c_{p21} = 0.35, a_{pm0} = 4$) **e.** Herbivore evolution within a plant community dominated by P_1 in the absence of animals. Parameters: ($c_{p12} = 0.77, c_{p21} = 0.35, a_{ph0} = 4.5$) Other parameters as in **table 1**.

Appendix D: Studying animal coevolution

As presented in the main document we studied the effect of animal coevolution on the maintenance of coexistence using numerical simulations of community eco-evolutionary dynamics. Here, we present first the different simulation outcomes and how they were treated, before presenting the results (robustness analysis) in the case of a stronger trade-off than that presented in the main document. The results appear robust to such a modification.

I. Outcomes of simulations

For a given pair (a_{pm0}, a_{ph0}) , a simulation starts by randomly drawing initial animal phenotypes $(t_{mInitial}, t_{hInitial})$. When launching the simulation, the initial ecological conditions do not always enable the stable coexistence of plants, pollinators and herbivores, leading to the simulation ending at the first timestep. Such simulations were excluded from our analysis as we aim at exploring the effect of animal coevolution, for which ecological viability is a prerequisite. When more than two-thirds of the simulations for a given pair (a_{pm0}, a_{ph0}) , we consider that such pair is not compatible with ecological viability and thus out of the scope of our analysis. For simulations that do not instantaneously crash, the simulation ends if one species goes extinct, unbounded population growth is observed (i.e. unstable ecological dynamics) or the ending time is reached (10^9 for $t_{p2} - t_{p1} = 1.5$ and $2 \cdot 10^9$ for $t_{p2} - t_{p1} = 3$).

II. Results in the case of a strong trade-off $t_{p2} - t_{p1} = 3$

In the case of $t_{p2} - t_{p1} = 3$, note that some simulations ended because of the accumulation of animal morphs with similar phenotypes (the maximal number of animal morphs S_{max} is given by a simulation parameter to avoid too large calculation times). Those simulations represent less than 5% of the total set of simulations. The long-term eco-evolutionary stable state being reached in these simulations (as indicated by the dynamics observed by relaunching some of these simulations while allowing a larger S_{max}), so we decided to include them in our analysis. Note that these 5% simulations are currently rerunning with a larger S_{max} to make our investigation perfectly rigorous when submitting the present paper for publication.

II.1. How does the eco-evolutionary outcome depend on the relative strength of pollination vs. herbivory?

The results obtained at this stronger trade-off are qualitatively similar (see statistical model, *equation (stats)*) to those obtained at the weaker trade-off $t_{p2} - t_{p1} = 1.5$. Indeed, stable coexistence is essentially maintained when herbivory is as strong, or slightly stronger than pollination (**Fig. S6**). Note however that (1) the disruption of coexistence as a result of the extinction of one species is more frequently observed, and (2) when pollination is very strong, even similarly strong herbivory is not sufficient to maintain coexistence along co-evolutionary trajectories (top-left of **Fig. S6**).

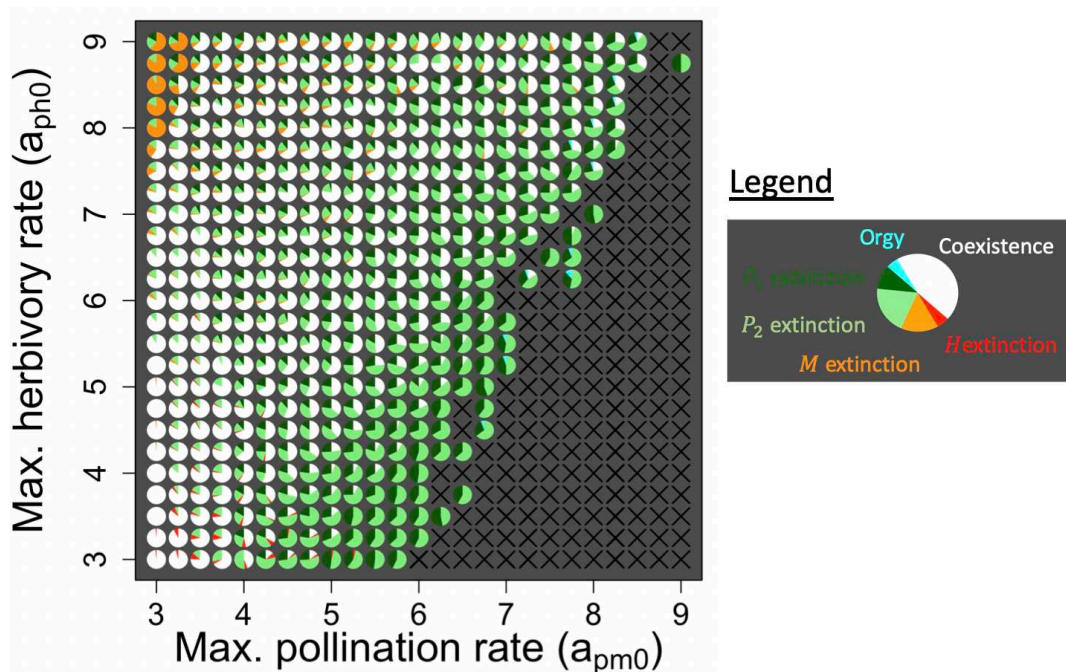


Fig. S6: Relative importance of the different simulation outcomes depending on the relative strength of pollination vs. herbivory (a_{pm0} , a_{ph0}). The different possible outcomes are indicated in the legend. These outcomes are obtained after animals coevolve during $2 \cdot 10^9$ timesteps. It is also possible that initially (i.e. first timestep), stable plant-pollinator-herbivore coexistence is not obtained. When it was the case, the simulation was excluded so that the proportions presented in this figure do not account for the simulations that crashed instantaneously. The pairs (a_{pm0}, a_{ph0}) characterized by more than two-thirds of initial crashes (over 50 simulations) are indicated by a black cross, and are ignored in our analysis. Interspecific plant competition: ($c_{p12} = 0.5, c_{p21} = 0.35$). Trade-off intensity ($t_{p2} = -t_{p1} = 1.5$). Other parameters as in **table 1**.

Statistical model fitted:

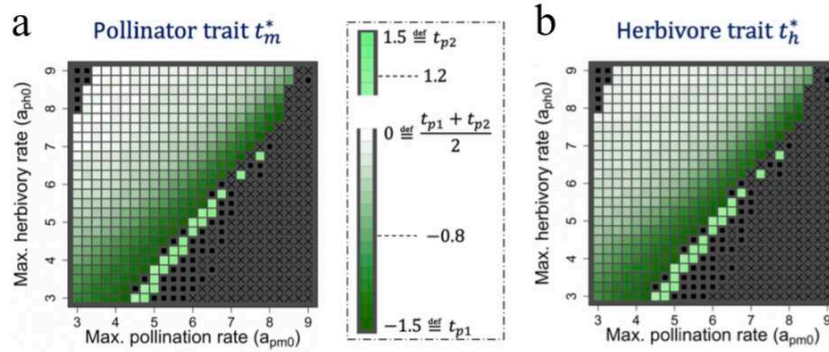
$\text{logit}(p_{coex}) \stackrel{\text{def}}{=} \log\left(\frac{p_{coex}}{1 - p_{coex}}\right)$ $= 18.4 \quad \underbrace{-2.4}_{\text{Small NicheOverlap}} \quad - 3.9a_{pm0} - 1.84a_{ph0} + 0.41a_{pm0}a_{ph0}$	(Stats)
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The fitted model explains 43% of the total variance in the probability of coexistence maintenance.

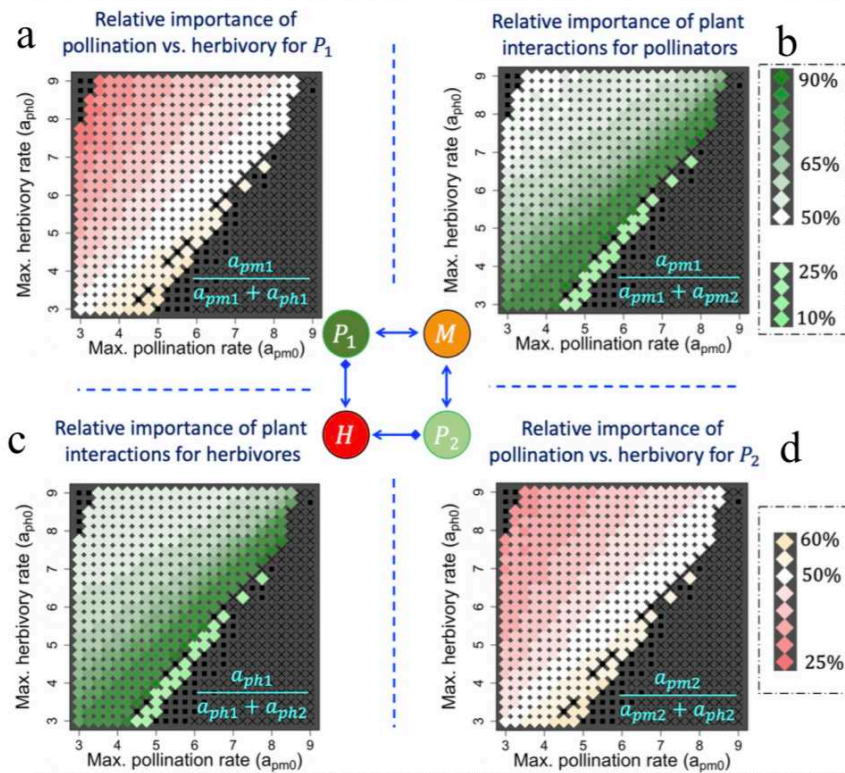
II.2. Understanding the maintenance of coexistence

In order to unravel the mechanisms underlying the maintenance of coexistence, we study the plant-animal trait-matching arising from coevolutionary dynamics when coexistence is maintained (**Fig. S7A**), and its consequences on the structure of the community (**Fig. S7B**), as well as on the distribution of densities within such a maintained community (**Fig. S7C**). The results are qualitatively similar to those obtained at a smaller trade-off (**Fig. S7 vs. Fig. 5**), with one notable difference. When the maximal rate of pollination is intermediate, coexistence can be maintained over a wider region than at weaker trade-offs due to its maintenance when herbivory is slightly weaker than pollination. Note however that these situations are rather infrequent, representing less than 10% of simulations outcomes while most simulations end with the extinction of one plant species (**Fig. S6**). Nevertheless, the final eco-evolutionary setting supporting the maintenance of coexistence qualitatively differs from that supporting such maintenance in the vast majority of cases. Indeed, both animal phenotypes closely match the phenotype (t_{p2}) of the inferior competitor plant (**Fig. S7A**, light green), and consequently specialize (**Fig S7B b & d**, light green) on that second plant species (P_2). The community is then characterized by pollinators being slightly more abundant than herbivores (**Fig. S7C b**), while the inferior competitor plant is much more abundant than the superior competitor, the latter plant species being close to extinction (**Fig. S7C a**). A possible explanation for such a pattern is that the important plant phenotype dissimilarity is responsible for the existence of a fitness valley at generalist animal strategies. As a result, animals specialize in the inferior competitor if both their phenotypes are initially close to its plant phenotype. When it is not the case, coevolutionary dynamics lead them to specialize in the superior competitor, which provokes the competitive exclusion of the inferior competitor plant species.

A. Animal coevolution



B. Community structure



C. Density distribution

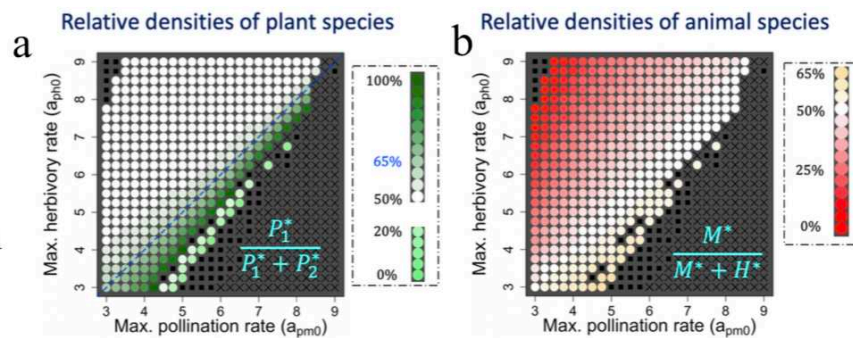


Fig. S7: Community arising from animal coevolution when coexistence is maintained, depending on the relative strength of pollination vs. herbivory. A. Plant-animal trait matching. a. Final pollinator phenotype (t_m^*) **b.** Final herbivore phenotype (t_h^*) **B. Community structure. a.** Relative importance of pollination vs. herbivory for P_1 . **b.** Relative importance of P_1 -pollinator interaction vs. P_2 -pollinator interaction for the pollinator species. **c.** Relative importance of pollination vs. herbivory for P_2 . **d.** Relative importance of P_1 -herbivore

interaction vs. P_2 -herbivore interaction for the herbivore species. **C. Distribution of densities.** **a.** Relative density of plant species. The blue line represents the relative plant densities in the absence of animal species, i.e. $P_1^* = 0.65(P_1^* + P_2^*)$ **b.** Relative densities of animal species. ($c_{p12} = 0.5, c_{p21} = 0.35$), ($t_{p2} = -t_{p1} = 1.5$). . Other parameters as in **table 1**.

References

- de Mazancourt, C., and U. Dieckmann. 2004. Trade-Off Geometries and Frequency-Dependent Selection. *The American Naturalist* 164:765–778.
- Dieckmann, U., and R. Law. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of Mathematical Biology* 34:579–612.
- Kisdi, É. 2006. Trade-off geometries and the adaptive dynamics of two co-evolving species. *Evolutionary Ecology Research* 8:959–973.
- Levins, R. 1962. Theory of Fitness in a Heterogeneous Environment. I. The Fitness Set and Adaptive. *The American Naturalist* 96:361–373.
- Murray, J. D. 2002. Appendix 2: Routh-Hurwitz conditions, Jury conditions, Descartes' rule of signs and exact solutions of a cubic. Pages 702–705 in *Mathematical Biology* (Second.). Springer-Verlag Berlin Heidelberg.
- Rueffler, C., T. J. M. Van Dooren, and J. A. J. Metz. 2006. The evolution of resource specialization through frequency-dependant and frequency-independant mechanisms. *The American Naturalist* 167:81.

V.
General
Discussion

In studying the eco-evolutionary dynamics of plant-pollinator-herbivore communities, the approach we have undertaken led us to successively consider scenarios of increasing eco-evolutionary complexity. First, we investigated the ecological dynamics of a community – i.e. a plant-pollinator-herbivore module - consisting of a plant species simultaneously interacting with a pollinator and a herbivore species. Then, we studied how such an interplay between pollination and herbivory – i.e. ecological trade-off – affects the evolutionary dynamics of a plant trait involved in both interactions. Finally, we examined the (co)-evolution of pollinator and herbivore species within a two plant-species floral landscape, the latter potentially emerging as a result of disruptive selection on plant phenotypes arising from the interplay of pollination and herbivory. The natural next step would be to explore the potential for the evolutionary emergence of plant-pollinator-herbivore networks within our framework. Before presenting the implications of our results towards such a decisive perspective (section V), let us synthesize some key ideas emerging from the cross-cutting discussion of the results of our different chapters.

(1) Pollinators and herbivores often have similar preferences for plant phenotypes

A large body of empirical literature reports shared animal preference for plant phenotypes. Such a pattern has notably been documented in the case of flower color (Irwin *et al.* 2003; Frey 2004), floral display (Ehrlén *et al.* 2002; Gómez 2003; Cariveau *et al.* 2004), flowering phenology (Brody 2008), chemical volatiles (Andrews *et al.* 2007; Theis *et al.* 2014), nectar quantity (Adler & Bronstein 2004) or reproductive system (Asikainen & Mutikainen 2005).

First, the results of our first chapter show that balanced pollination vs. herbivory strengths promote the stability of the plant-pollinator-herbivore community. Favoring such a balanced interaction pattern, shared animal preferences are thus associated with stable communities and consequently widespread. The underlying rationale is that stability implies a much longer community “lifespan”. When sampling natural communities, plant-pollinator-herbivore communities displaying shared animal preferences are thus much more frequently encountered than the communities that do not display such a pattern.

This line of thought presents the advantage of putting forth a rather novel argument – community stability - to explain shared pollinator-herbivore preferences, which might be

relevant for some communities. I, however, doubt that it might be a convincing explanation for the ubiquity of such a preference pattern for the two following reasons.

(1) Is it true that balanced pollination vs. herbivory strengths promotes stability in natural plant-pollinator-herbivore communities? On the one hand, our results critically depend on our assumptions of linear functional responses for both plant-animal interactions, i.e. animal intake rates that linearly increase with plant density. Mougi & Kondoh (2014), for instance, find opposite results – i.e. unbalanced pollination vs. herbivory strengths promote stable coexistence - by still assuming a linear functional response for herbivory, but a saturating one for pollination. Note that a saturating functional response seems conceptually more realistic as floral visits involve a handling-time (Herrera 1989), but the key question is whether plant densities in natural communities are effectively reaching the levels at which saturation becomes measurable. In some communities, it might be possible that other constraints (e.g. herbivory, parasitism, competition) impede such abundant density levels. On the other hand, natural plant-pollinator-herbivore communities seldom consist of an isolated set of three interacting species, but rather correspond to networks of diverse interacting plants, pollinators and herbivores species. Does the stability of such a complex network require that all plant-pollinator-herbivore submodules display a balance between the strength of pollination and herbivory? In my opinion, the extension of our results to such a network scale would rather suggest that a balance between a summation of the strengths of pollination vs. a summation of the strengths of herbivory is required. We notably have shown that stable plant-pollinator-herbivore coexistence could be achieved despite the plant-pollinator subcommunity displaying unstable ecological dynamics (**Fig 3 in chapter I**, infinity symbol). Likewise, a plant-pollinator-herbivore network could be stable despite one or several submodules displaying unstable ecological dynamics - owing to unbalanced plant-animal interactions – when considered in isolation.

(2) Do shared preferences imply balanced pollination vs. herbivory strengths? Pollinator species may differ in the “quality” – e.g. quantity of pollen removed/deposited per visit - of the pollination service they provide for a given plant species (Herrera 1987; Ivey *et al.* 2003) For instance, the efficiency of pollinators usually decreases with their degree of generalism as a result of pollen loss due to interspecific pollen transfer (Morales & Traveset 2008). Likewise, the negative effect of herbivory on plant fitness may strongly differ between herbivore species (e.g. Albon *et al.* 2007; Liu *et al.* 2015). Consider now a plant species that interacts with both a low-quality pollinator species and a highly voracious herbivore species. In such a system, the strengths of pollination vs. herbivory are certainly highly unbalanced, even in the case of similar animal preferences. In our framework, the “efficiency” of animal species is captured by the

maximal plant-animal interaction rates (a_{pm0} vs. a_{ph0}), as well as by the interaction niche widths (σ_{Pol} vs. σ_{Her}). Our results (e.g. **Fig. 4 in chapter II**, **Fig. 4 in chapter III**) clearly demonstrate that community eco-evolutionary dynamics qualitatively depend on these parameters.

The second explanation for shared animal preferences comes from the results of our third chapter. We show that the coevolutionary dynamics of animal species very often lead to similar animal phenotypes – i.e. similar preference for plant phenotypes – maintained by stabilizing selection (i.e. a CSS singularity). Such dynamics are the consequence of herbivores being selected to increase their niche overlap with pollinators, so that their indirect benefit from pollination-induced plant growth is maximal. As pollinators are, in contrast, selected toward reducing their niche overlap with herbivores, it remains unclear why herbivores always “win” the ensuing evolutionary race (e.g. fluctuating selection in **Fig. 3, chapter III**). It might notably be a consequence of the dimensionality (one) of our framework trait space, which makes pollinators bound to be “joined” by herbivores as phenotypes are constrained within the interval $[t_{p1}, t_{p2}]$. We thus plan on testing the robustness of these results to the variation of trait space dimensionality before publishing this third chapter. Assuming such robustness, a necessary condition for our results, derived in the case of fixed plant phenotypes, to extend to natural communities is that animal species evolve much faster than plant species, at least regarding plant-animal interaction traits. Such an assumption may strongly depend on the plant-pollinator-herbivore community considered, as there are no obvious reasons to believe that plant species are evolving slower than their animal interacting species. For instance, the rate of mutation in plant species seems comparable to that of invertebrates, both slightly inferior to that of mammals (Lynch 2010). The genome size, however, which positively correlates to the mutation rate (Lynch 2010), spans four orders of magnitude in angiosperm plant species (Michael 2014). This suggests that differences in mutation rates might exist in specific plant-animal communities. Differences in generation times (e.g. Thomas *et al.* 2010) or standing genetic variation (e.g. Bitter *et al.* 2019) may also play a part. It seems reasonable to think, for instance, that gene flow within mobile animal populations is generally higher than within sessile plant species, thus favoring increased standing genetic variation in animals.

To avoid any misinterpretation, note that similar rates of evolution do not, a priori, preclude the possibility of similar animal preferences emerging from coevolutionary dynamics. It just impedes the direct extension of our particular results. In fact, the key traits structuring

plant-animal interactions are subject to diverse selective pressures. Some of these are, of course, a result of plant-animal interactions. Coevolutionary dynamics thus certainly plays a part in the emergence of shared animal preferences. But some selective pressures arise as a result of other factors, such as competition for light which might select for increased plant size (Craine & Dybzinski 2013), a trait that has been shown to affect plant-animal interactions (e.g. Gómez 2003). The open question is therefore whether the coevolution between plants, pollinators and herbivores is sufficient – i.e. endogenous properties – to explain the ubiquity of such a preference pattern, or if additional aspects are necessary. Our study of animal coevolution suggests that the former might be true, but studying the three species coevolution remains necessary to confirm these results. Despite the several limitations discussed, shared preferences may also promote community stability, at least in some cases. Shared animal preferences for plant phenotypes could therefore be an example of evolution fostering community stability (Loeuille 2010).

(2) Diversification: the role of mutualism vs. antagonism, but also of their interplay

Diversification – i.e. the emergence of polymorphism as a result of disruptive selection – has been a key focus of our investigation.

In the third chapter, we investigate the potential for the diversification of pollinators vs. herbivores within a two-species floral landscape (i.e. two resources with distinct traits available). We show that the diversification of the herbivore phenotype is possible for intermediate plant phenotype dissimilarity (i.e. intermediate trade-off, e.g. **Fig. 1c in chapter III**), while that of pollinators (not consumers in our framework) is never possible (e.g. **Fig. 1b in chapter III**). The theoretical emergence of two specialist consumers as a result of disruptive selection arising from the availability of two distinct resources is actually well-established (Kisdi & Geritz 1999; Kisdi 2002; Abrams 2006; Rueffler *et al.* 2006b), as well as empirically documented (e.g. Darwin's finches in the Galapagos archipelago, Schluter & Grant 1984; Grant & Grant 2003). As emphasized by Rueffler *et al.* (2006), the key driver of such dynamics is that a monomorphic consumer population specialized in a given resource causes the latter to be relatively rare compared to the resource it is not specialized in (**Fig 5 a vs. b vs. c**), i.e. the fact that the considered interaction is an antagonism. When the trade-off becomes concave (**Fig. S3 in appendix C.I, chapter III**) – i.e. plant phenotype dissimilarity is important enough so that specialist consumers have a bigger total consumption than a generalist consumer – frequency-

independent selection favors specialism. Frequency-dependent selection, which favors consuming the less consumed resource, can however counteract the former selective pressures. In such a case, selection toward a fitness minimum (i.e. invasibility) becomes possible, i.e. toward a branching point. In contrast, a monomorphic mutualist population (our pollinators for instance) specialized in a given resource causes the latter to be relatively abundant compared to the resource it is not specialized in (**Fig 5 d vs. e vs. f**). As a result, frequency-independent selection away from fitness minima is reinforced by the ensuing frequency-dependent selection. In other words, the qualitative difference between antagonism and mutualism emerges from the opposite sign of their respective eco-evolutionary feedback, negative for antagonism (**Fig. 5A**) and positive for mutualism (**Fig. 5B**). Such a qualitative difference – i.e. diversification is restricted by mutualism and favored by antagonism – has been found in several theoretical studies with distinct theoretical frameworks (Kopp & Gavrilets 2006; Yoder & Nuismer 2010; Maliet *et al.* 2020).

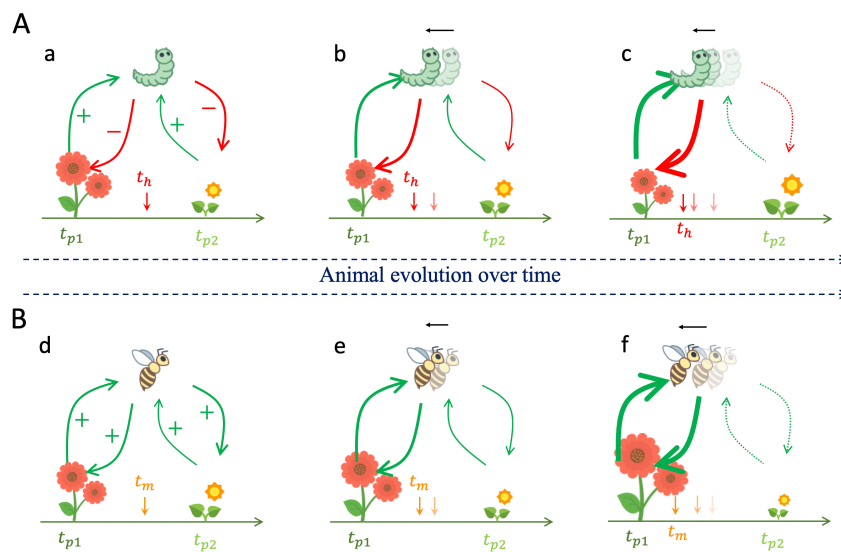


Fig. 5: The opposite eco-evolutionary feedback arising from pollination vs. herbivore evolution. Plant sizes reflect their relative abundances. The thickness of the arrows figuring plant-animal interactions increases with their relative strength. **A. Herbivore evolution over time.** As herbivores start to specialize on the most abundant plant species, the latter relative abundance decreases, so that further specialization is dampened. The eco-evolutionary feedback is negative. **B. Pollinator evolution over time.** As pollinators start to specialize on the most abundant plant species, the latter relative abundance increases, so that further specialization is reinforced. The eco-evolutionary feedback is positive.

In contrast, we show that the diversification of the plant phenotype requires pollination and herbivory to be of similar magnitudes (**Fig. 3 in chapter II**). In this case, both the mutualistic and the antagonistic interactions are necessary as disruptive selection arises from

their interplay. Nevertheless, herbivory appears as the main driver of diversification as indicated by (1) the more frequent occurrence of disruptive selection as the maximal strength of herbivory increases (i.e. $a_{ph0} \nearrow, \sigma_{Her} \searrow$, **Fig. 4 in chapter II**). In essence, disruptive selection corresponds to extreme phenotypes being favored over intermediate ones - i.e. the existence of a fitness minimum (Rueffler *et al.* 2006a) - which is a consequence of the presence of herbivores, not pollinators. In that regard, the review of Rueffler *et al.* (2006a) on the relationship between disruptive selection and diversification is quite insightful. The authors distinguish between two types of disruptive selection (i.e. fitness minima): one that leads to diversification and one that does not, the difference resulting from the direction favored by selection – toward or away - when not within the region of disruptive selection. In the language of adaptive dynamics, such a view considers that disruptive selection corresponds to invisible singular strategies. Diversification occurs when the singularity is convergent – i.e. a branching point – while it does not when it is divergent – i.e. a repeller – (see Box 1 in Rueffler *et al.* 2006a). While such a unifying outlook is probably debatable from an empirical point of view, it is certainly valuable from a conceptual one. It notably supports the idea that the antagonism (i.e. herbivory) drives the diversification of the plant phenotype in our framework. Above all, it puts forth the essential feature of disruptive selection, i.e. selection of extreme phenotypes. By doing so, it points towards, in my opinion, the unique ecological interaction underlying most diversification processes, i.e. niche-overlap competition (MacArthur & Levins 1967). To avoid any confusion, note that I am talking of well-mixed populations, and not of situations characterized by limited gene flow that might cause diversification as a result of differences in local selective pressures or drift.

The diversification dynamics obtained in our framework can now be analyzed under the unifying perspective of niche-overlap competition – i.e. interacting partners having a negative fitness effect on each other, which intensifies with the similarity of their phenotypes. In the case of herbivores within a two-floral landscape (**chapter III**), conspecifics compete by depleting the same plant resources, i.e. exploitative competition (**Box 1, Introduction**). Because they consume and deplete resources in the exact same manner, such an indirect interaction is stronger between individuals that have the same phenotype (t_h). Under the right conditions (intermediate trade-off $t_{p2} - t_{p1}$), this interaction becomes sufficient for selection to favor extreme phenotypes, thus alleviating exploitative competition. In the case of plants interacting with both pollinators and herbivores (**chapter II**), conspecific compete with each other by increasing the

density of their common herbivore enemy, i.e. apparent competition (Holt 1977, **Fig. 1b in Introduction**). Such an indirect interaction is stronger between conspecifics with similar phenotypes (t_p). Under the right conditions (strong trade-off $t_h - t_m$, similar strengths of pollination vs. herbivory $a_{pm}M^* \approx a_{ph}H^*$), this interaction becomes sufficient for selection to favor extreme phenotypes, thus alleviating apparent competition. In particular, a balance between the strengths of pollination and herbivory is needed because strong apparent competition requires the strength of herbivory (a_{ph}) to be strong, but also the density of herbivores to be high, and thus a strong pollination (a_{pm}) which indirectly benefits herbivores (**Fig. 1 in Chapter I**). In contrast, pollinator diversification is never observed because, in our framework, no process is providing support for niche-overlap competition to emerge. As we model mutualism, indeed, the sole possible indirect interaction between conspecific pollinators is facilitation. Individual pollinators benefit each other by increasing the density of their common plant partner, an indirect effect that is stronger between individuals with the same phenotype (t_m). As a result, our pollinator population remains monomorphic alongside evolutionary dynamics.

Yet, a large body of literature, reviewed by Chomicki *et al.* (2019), provide support for mutualism being an important driver of diversification within natural communities. In particular, several studies emphasize the role of plant-pollinator coevolution in explaining the higher diversification rates within angiosperms (Hodges & Arnold 1995; Sargent 2004; Hernández-Hernández & Wiens 2020). How to explain the contrast with our results?

Mutualisms involve costs (Bronstein 2001). On the one hand, nectar production is costly for plant species (Pyke 1991), and its quality – nutritive for instance - may be quite variable (Nepi *et al.* 2001). It implies that nectar supply is limited so that pollinator species may compete for accessing the (best) nectar reward (and floral resources in general). On the other hand, pollinators invest time (searching, handling) and energy in order to pollinate. It implies that (1) pollination supply is limited, and (2) pollinators are likely to preferentially visit the most “profitable” – i.e. most benefit for the lowest cost, owing to adaptive foraging (e.g. Valdovinos *et al.* 2016) – plant species. Moreover, there is also a “quality” component to pollination as evidenced by the variation in pollination efficiency with varying pollinator species (e.g. Ivey *et al.* 2003; Lefebvre *et al.* 2019). As a result, plant populations are competing to get preferentially visited by (the best) pollinator species (Mitchell *et al.* 2009). Incorporating the costs associated with the plant-pollinator interaction shows that plants might be competing for pollination, while

pollinators might be competing for floral resources. In both cases, competition strength depends on niche overlap: the more similar are the sets of plants visited by two pollinators, or the sets of pollinators visiting two plant species, the stronger the competition between the two pollinators, or the two-plant species. As we did not consider the costs of pollination, our framework precludes pollination niche-overlap competition (but see **VI. Perspectives**), likely explaining why the diversification of pollinators is never observed.

An aspect of the “quality” component of pollination is of particular relevance given our subject. The quality of pollination decreases as a result of interspecific pollen transfer, which happens when a generalist pollinator is visiting more than one plant species. Such a mechanism potentially – and several empirical evidence actually exists (Campbell & Motten 1985; Bell *et al.* 2005) - underlies strong pollination niche-overlap competition between plant species (Morales & Traveset 2008; Mitchell *et al.* 2009). This mechanism might be responsible for the divergence of floral traits in several cases, as suggested by various studies reviewed in Morales & Traveset (2008). It might notably foster increased plant-pollinator specialization, as well as pollinator shifts toward niche partitioning, and thus favor diversification as a result of reproductive isolation (Kay & Sargent 2009). Partner shift is actually thought to be a key driver by which mutualism, not only pollination, positively impact diversification rates (Chomicki *et al.* 2019). For instance, Gervasi & Schiestl (2017) experimentally demonstrate that several plant traits – size, emitted chemicals and mating system – can diverge, within a few generations, as a result of evolving in the context of different pollinator species.

Let us conclude this discussion on diversification by mentioning the recent results of Zeng & Wiens (2021). The authors conducted a meta-analysis to investigate if, and how, different types of ecological interaction affect within-clade diversification rates. They find that interactions with a positive fitness effect (e.g. mutualism) increase diversification rates, while interactions that have a negative effect on fitness (e.g. competition, predation for prey) reduce diversification rates. As pointed out by the authors, theoretical results (e.g. Yoder & Nuismer 2010; Maliet *et al.* 2020; our results) provide the exact opposite pattern. A rather convincing explanation (Zeng & Wiens 2021) is that contrasting conclusions arise from the contrasting scales at which theoretical (microevolutionary timescale, phenotype diversification) vs. empirical questions (macroevolutionary (i.e. phylogenies), speciation) on diversification are usually addressed. Both mutualisms and antagonisms can promote or dampen the potential for diversification depending on the time or organizational scale considered. In particular, the processes by which mutualisms foster diversification - increasing population densities, range sizes or ecological opportunities (extension of realized niche) (Chomicki *et al.* 2019) – may

have a relatively more significant impact on the macroevolutionary timescale. In contrast, niche-overlap competition may matter most at the microevolutionary timescale, which we investigate in the present work. As we have seen, such competition can arise from mutualisms, but it remains an intrinsic feature of antagonistic interactions, which essentially entail costs. In addition, mutualism often underlies a reduction in gene flow (Chomicki *et al.* 2019), if not reproductive isolation, while it remains rare for antagonistic interactions.

(3) Multispecies coexistence: the role of mutualism vs. antagonism depends on the eco-evolutionary context

The maintenance of multispecies coexistence has also been at the core of our investigation. Through our different chapters, we have shown that pollination or herbivory affect such maintenance, sometimes positively and sometimes negatively. We argue that such seemingly inconsistent findings are actually consistent, and that the effect of a given plant-animal interaction depends on the level of eco-evolutionary complexity considered. Two elements of such complexity appear critical: the diversity of (competing) species per functional guild – i.e. plant guild, pollinator guild and herbivore guild – and accounting for the effect of evolution on ecological dynamics.

Consider the effect of plant-animal interactions on multispecies coexistence when the plant guild consists of one (**chapter I**) or two species (**chapter III**), in the absence of evolution. In the first case (**Fig. 1 in chapter I**), pollination favors coexistence by increasing the densities of all the species within the community, while herbivory decreases the densities of plants and pollinators, thus threatening the maintenance of coexistence. In the second case (**Fig. S2 in appendix B.IV, chapter III**), pollination and herbivory can either foster or impede the maintenance of coexistence, depending on their level of specialization. Pollinators can indeed enable plant coexistence when they specialize more in the inferior competitor species, even if the latter is competitively excluded in the absence of animals (**Fig. S2d**, $a_{pm1} < a_{pm2}$). The same outcome can result from the presence of herbivores, but if they specialize in the inferior competitor (**Fig. S2g**, $a_{ph1} > a_{ph2}$). In contrast, pollinators can trigger competitive exclusion among plant species if they specialize in the superior competitor (**Fig. S2c**, $a_{pm1} > a_{pm2}$). Likewise, herbivores specializing in the inferior competitor can provoke its competitive exclusion (**Fig. S2f**, $a_{ph1} < a_{ph2}$).

Let us now consider how, in this second case, animal evolution modifies the pattern derived from the sole consideration of ecological dynamics. The investigation conducted in **chapter III** shows that the animal degree of specialization is constrained by evolutionary dynamics. More precisely, both animal species are selected to preferentially interact with the most abundant species (equations 8-9 in chapter III), i.e. the superior competitor in our framework. As a result (**Fig. 1, Fig. 2 in chapter III**), plant coexistence is always threatened by the presence of (evolving) pollinators, while it is always favored by the presence of (evolving) herbivores. This is still true when animals are coevolving (**Fig. 4 in chapter III**). To further understand such a contrasting influence of pollinator vs. herbivore evolution, it is insightful to distinguish between the two types of mechanisms that (conceptually) support the maintenance of multispecies coexistence (Chesson 2000, see **Fig. 6**): equalizing (**Fig. 6a**), which reduce average fitness differences, and stabilizing (**Fig. 6b**), which reinforce negative intraspecific effects over interspecific ones. The opposite influence of herbivores vs. pollinators is mediated by both types of mechanisms. First, it is straightforward that herbivore evolution has an equalizing effect on the fitness of the two competing plant species, while plant fitness difference is exacerbated by pollinator evolution. But evolutionary-induced herbivore specialization has also a stabilizing effect as it makes the apparent competition between conspecific plant individuals stronger than that between non-conspecific individuals. In contrast, pollinator specialization makes the apparent facilitation between conspecific plant individuals stronger than that between non-conspecific individuals. It is thus destabilizing as it alleviates more negative intraspecific effects than negative interspecific ones. In summary, the effects of pollinators (negative) vs. herbivores (positive) on both equalizing and stabilizing mechanisms are of opposite sign, owing to the opposite sign in ecological feedback loops. But these effects are also of different magnitudes. For a similar asymmetry in plant densities, evolution indeed leads to a much stronger specialization in pollinators than herbivores, owing to the opposite sign in eco-evolutionary feedback (**Fig. 5 A vs. B**). As a result, the negative effect of pollinators is stronger than the positive effect of herbivores. Note that this applies when comparing pollinator vs. herbivore evolution. It is no longer true in the case of animal coevolution, as animals converge toward the same phenotype (i.e. same specialization, **Fig. 3 & 5 in chapter III**).

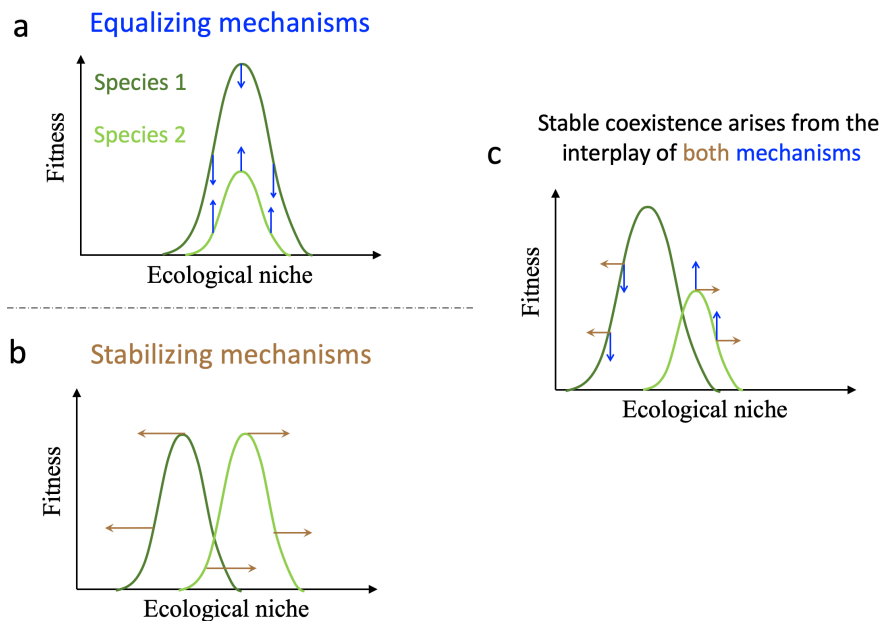


Fig. 6: Stable coexistence depends on the interplay of equalizing and stabilizing mechanisms (Chesson 2000). **a. Equalizing mechanisms** are those that reduce average fitness differences. **b. Stabilizing mechanisms** are those that make negative intraspecific density-dependence stronger than interspecific negative density-dependence. Reduction of niche overlap is often (but not always) of such mechanisms. **c. The interplay of equalizing and stabilizing mechanisms** enables stable coexistence. More precisely, for a given level of fitness differences, a given level of niche partitioning (regarding negative density-dependent processes) is necessary to “stabilize” coexistence. Otherwise, the species with higher fitness (species 1 here) competitively excludes (asymptotically) the other species.

Because stabilizing mechanisms rest on negative density-dependence processes, it has early been considered that multispecies coexistence is mostly driven by competitive and antagonistic interactions (May 1981; Chesson 2000; Ricklefs 2010), rather than mutualisms. Exploitative competition may notably be responsible for the emergence of resource partitioning, which has been shown to support the maintenance of diversity in several empirical systems (e.g. Wilson & Lindow 1994; Gilbert *et al.* 2008; Di Bitetti *et al.* 2010). Such resource partitioning among predator species also favors the coexistence of prey species. More generally, specialist natural enemies, by holding down the density of each species independently, should favor coexistence by directing negative density-dependence - i.e. apparent competition - within species rather than among species (Chesson 2000). Compelling evidence indicates, for instance, that such a mechanism – the Janzen-Conwell hypothesis (Janzen 1970; Connell 1971) - might be responsible for maintaining tree diversity within tropical forests (Wills *et al.* 1997; Comita *et al.* 2014).

But negative feedback on densities can also emerge from mutualistic interactions. Bever (2002) reports, for instance, such dynamics in the case of a plant-mycorrhizal fungi interaction

characterized by asymmetrical benefits between the two mutualistic partners. The author shows that in the presence of several species of fungi, the one - *Scutellospora calospora* - that grows more in association with the focal plant species - *Plantago lanceolata* - is not the one that best promotes *Plantago*'s growth. As a result, an increase in the density of *Plantago* leads to an increase in the relative abundance of *S. calospora*, which makes the plant species more frequently associated with *S. calospora*, and consequently reduces its density. Challenging the early view that the role of competition and antagonism is prevailing, Chomicki *et al.* (2019) show that there are a variety of processes by which mutualisms can positively contribute – via both stabilizing or equalizing mechanisms - to the maintenance of coexistence. If mutualisms have started to be acknowledged as potential drivers of multispecies coexistence relatively recently, I feel that it is partly because the processes by which they positively contribute to coexistence are subtler, and require going beyond the defining (+, +) relationship to account for the mechanistic specificities of a given mutualistic interaction.

The latter remark also points towards what constitutes, in my opinion, a major qualitative difference between mutualism and antagonism (Boucher *et al.* 1982; Abrams 1987): from a mechanistic point of view, the diversity of interactions encompassed by the term mutualism (i.e. (+, +) interaction, **Box 1**) is much wider than that encompassed by the term antagonism (i.e. (+, -) interaction, **Box 1**), most antagonistic interactions falling into predation, herbivory or parasitism. Yet, in the current context of global changes, the role of mutualisms in supporting the maintenance of coexistence could be increasingly important and prevalent, precisely as a result of what unifies the tremendous variety of mutualistic interactions, i.e. the reciprocal fitness positive effect for interacting species. Indeed, global changes are responsible for important declines in species abundances (e.g. Potts *et al.* 2010; Barnosky *et al.* 2011; Sánchez-Bayo & Wyckhuys 2019). As a result, negative-density dependences may be alleviated so that species are less limited by competition, but increasingly limited by their ability to avoid low-density effects such as demographical stochasticity, or Allee effects. Note that this is, of course, a simplified view. Competition may also increase as a result of a relatively greater reduction in resources, or the introduction of an invasive competitor (Tylianakis *et al.* 2008). Likewise, negative density dependence may be reinforced due to some mutualisms shifting into antagonisms (Toby Kiers *et al.* 2010). In some situations, the positive effects of mutualisms on population densities may, nevertheless, enable some species to escape low-density extinction vortex (i.e. positive feedback leading to a reinforcing

extinction risk as densities are declining, Gilpin & Soulé 1986), increasing the likelihood that they might adapt to their new environment (evolutionary rescue, Carlson *et al.* 2014).

All in all, both mutualisms and antagonisms are important drivers of multispecies coexistence. Their effects on the maintenance of such coexistence may greatly vary depending on the community context in which they occur. Within such a community, in addition, the interaction pattern emerges as a result of species coevolution. Accounting for evolution also allows extending the thinking from diversity maintenance to diversification itself. Once more, depending on the community context considered, the potential for diversification may be enhanced or dampened by both mutualisms and antagonisms. Our results even show that disruptive selection may arise from their interplay. First and foremost, our results therefore advocate in favor of accounting for both evolution and the multispecies community context in which species are embedded to gain novel insights into the processes supporting biodiversity in natural ecosystems (**see VII. Conclusion**).

VI.

Perspectives

Towards the evolutionary emergence of plant-pollinator-
herbivore networks

Food web models enabling the evolutionary emergence of complex trophic networks sharing many features with empirical webs significantly improved our understanding of the mechanisms supporting biodiversity in nature (e.g. Caldarelli *et al.* 1998; Loeuille & Loreau 2005; Allhoff *et al.* 2015). While the emergence of complex networks including both trophic and mutualistic interactions has also been achieved by some authors, the resulting communities were highly unstable as mutualist species tended to fill all the available niches (e.g. Yoshida 2003). In our tripartite framework, mutualist vs. antagonist niches are markedly separated so that such dynamics are not possible. Our framework may thus provide a promising avenue toward the evolutionary emergence of mutualistic-antagonistic networks in general, plant-pollinator-herbivore networks in particular.

(1) Evolutionary emergence of plant-pollinator-herbivore networks in our framework

First of all, let us recapitulate the different diversification processes we obtain within our framework of plant-pollinator-herbivore communities (**Fig. 7**). In **chapter II**, we show that the plant phenotype may be subject to disruptive selection arising from the interplay of pollination and herbivory. The consecutive dimorphism can maintain in some cases (e.g. **Fig. 7a**), but in most cases (e.g. **Fig. 7b**), it is lost as a result of one morph – the one strongly interacting with both animal species – competitively excluding the other morph. When considering the evolution of animal species in the presence of two plants with distinct phenotypes in **chapter III**, we show that the diversification of the herbivore phenotype is possible (e.g. **Fig. 7c**). It leads to the stable coexistence of two morphs, each specialized in the consumption of one plant species. Actually, even in the case of animal coevolution (e.g. **Fig. 7d**), herbivore diversification is possible. Note that this result was not presented in **chapter III** as it was obtained only recently, and is part of the ongoing work needed to complete the paper before submission. In contrast, the diversification of pollinators is never observed within our framework.

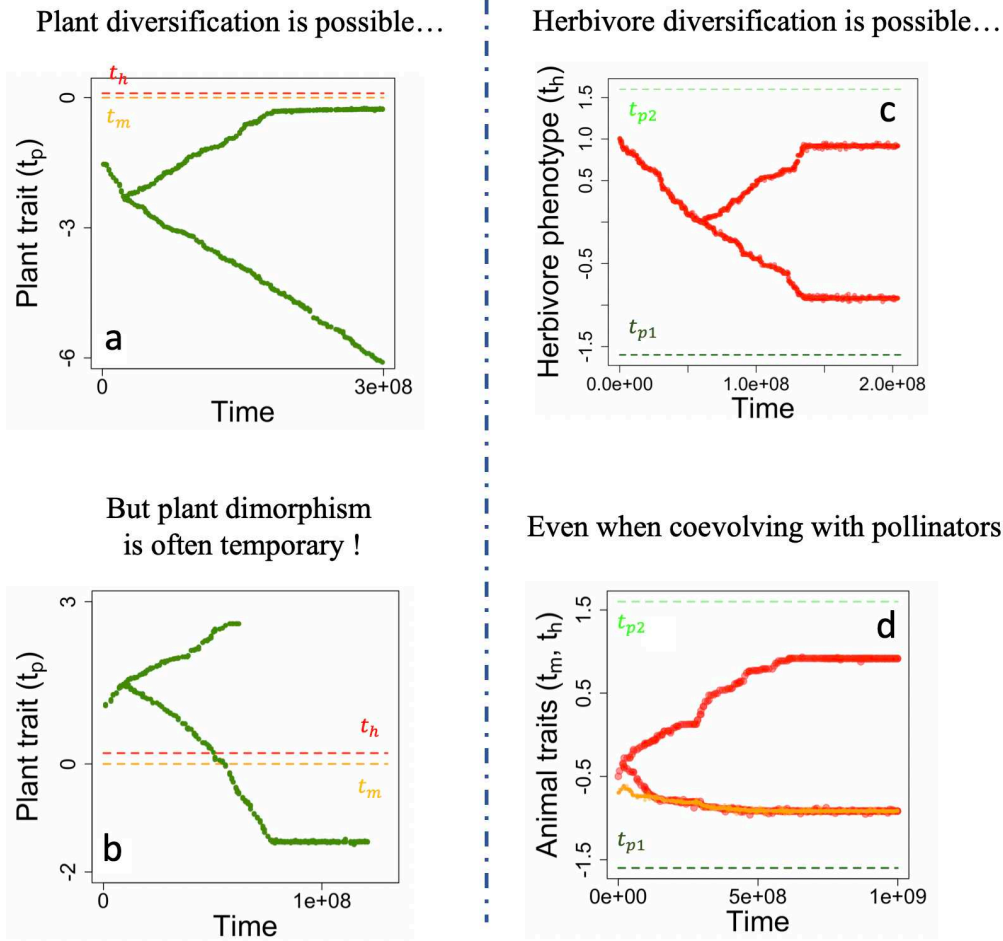


Fig. 7: Summary of the diversification processes observed within our framework. a. Plant diversification resulting from the interplay of pollination and herbivory. Parameters: General ($r_p = 10, r_m = -1, r_h = -4, c_p = 0.6, c_m = 0.5, c_h = 0.4, e_m = 0.2, e_h = 0.3$); Plant-animal interactions ($t_m = 0, t_h = 0.1, a_{pm0} = 5, a_{ph0} = 9, \sigma_{pol} = 1.7, \sigma_{pol} = 2$). **b. Plant dimorphism is lost** as a result of competition between the two plant morphs. Parameters: as in a, except ($t_h = 0.2, a_{pm0} = 6, a_{ph0} = 7.5, \sigma_{pol} = 3, \sigma_{pol} = 2.8$). **c. Herbivore diversification** leads to the emergence of two morphs, each specializing in one plant species. Parameters: General ($r_{p1} = r_{p2} = 10, r_h = -1, c_{p1} = c_{p2} = 0.7, c_m = c_h = 0.5, e_m = e_h = 0.2$); Plant traits ($t_{p2} = -t_{p1} = 1.6$); Interspecific ($c_{p12} = c_{p21} = 0.4, a_{ph0} = 3.5$). **d. Herbivore diversification in the case of animal coevolution** within a two-species floral landscape. The herbivore phenotype corresponds to the red curve, while the pollinator phenotype corresponds to the orange curve. Parameters: as in c, except ($c_{p12} = c_{p21} = 0.35, a_{ph0} = 6.5, a_{pm0} = 5$) and with ($r_m = -1, c_m = 0.5, e_m = 0.2$).

As previously discussed, a probable explanation for not observing pollinator diversification is that our framework does not include any process that could support niche-overlap competition between conspecific pollinators (i.e. $c_m(t_{m1}, t_{m2})$, **equation P.1**).

$c_m(t_{m1}, t_{m2}) = c_{m0} \left[(1 - \alpha) + \alpha e^{\frac{-(t_{m1} - t_{m2})^2}{2\sigma_c^2}} \right]$	(P. 1)
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Where:

- c_{m0} is the maximal rate of intraspecific competition (our c_m so far).
- σ_c controls how fast intraspecific competition decreases as pollinator phenotype dissimilarity increases (i.e. intraspecific competition niche width).
- α indicates how important is the niche-overlap dependence of intraspecific competition.

We have demonstrated in **chapter III (appendix C.II.3)** that disruptive selection – i.e. a branching point: convergent and invisable – is not possible for pollinators because, at the generalist evolutionary singularity (e.g. **Fig. 1b in chapter III**), invisibility implies non-convergence. Noting $w(t'_m, t_m)$ the fitness of invasion of a pollinator mutant with phenotype t'_m within a resident pollinator population with phenotype t_m (reminder in **Box 3, Introduction**), the argument is, in essence:

$$\left\{ \begin{array}{l} (1) \quad \text{Non - invasibility} \Leftrightarrow \left. \frac{\partial^2 w(t'_m, t_m)}{\partial t_m'^2} \right]_{t'_m=t_m=t_m^*=0} < 0 \\ (2) \quad \text{Convergence} \Leftrightarrow \left. \frac{\partial^2 w(t'_m, t_m)}{\partial t_m'^2} \right]_{t'_m=t_m=t_m^*=0} + f(t_m^*) < 0 \\ (3) \quad f(t_m^*) \geq 0 \end{array} \right.$$

Here, we show (**Box 4**) that introducing niche-overlap competition does not modify the existence and position of evolutionary singularities, neither their convergence. It only modifies their invasibility, making it easier to achieve. It is thus reasonable to think that such a modification of our framework might allow the diversification of the pollinator phenotype.

Biologically, such niche-overlap competition could correspond to the competition between conspecific pollinators for floral resources such as nectar. We also pointed out, in the discussion, that our framework does not account for the competition of plant individuals for pollinators. Incorporating niche-overlap competition in plants – i.e. $c_p(t_{p1}, t_{p2})$ – thus appears biologically relevant.

Box 4: Effect of niche-overlap competition on evolutionary singularities

Here, we prove that introducing niche-overlap competition makes facilitates the invasibility of evolutionary singularities. Their existence, position or convergence is, in contrast, not modified.

Pollinator population dynamics in our initial (old) and novel (new) - i.e. with niche-overlap competition – frameworks are:

$\frac{dM}{Mdt} = r_m - c_{m0}M + e_{m1}a_{pm1}P_1 + e_{m2}a_{pm2}P_2$	(old)
$\frac{dM}{Mdt} = r_m - c_m(t_m, t_m)M + e_{m1}a_{pm1}P_1 + e_{m2}a_{pm2}P_2$	(new)

$$\text{With } c_m(t_{m1}, t_{m2}) = c_{m0} \left[(1 - \alpha) + \alpha e^{-\frac{(t_{m1}-t_{m2})^2}{2\sigma_c^2}} \right]$$

In this new framework, the fitness of invasion - $w_{new}(t'_m, t_m)$ - of a rare mutant M' (t'_m) with a resident population M at ecological equilibrium (P_1^*, P_2^*, M^*, H^*) is written:

$$\begin{aligned} w_{new}(t'_m, t_m) &\stackrel{\text{def}}{=} \left. \frac{dM'}{M'dt} \right|_{M' \ll M^*} \\ &= r_m - \frac{c_m(t'_m, t'_m)M'}{\ll c_m(t'_m, t'_m)M^*} - c_m(t'_m, t_m)M^* + e_{m1}a'_{pm1}P_1^* + e_{m2}a'_{pm2}P_2^* \\ &= r_m - c_m(t'_m, t_m)M^* + e_{m1}a'_{pm1}P_1^* + e_{m2}a'_{pm2}P_2^* \\ &= r_m - c_{m0}M^* + e_{m1}a'_{pm1}P_1^* + e_{m2}a'_{pm2}P_2^* + [c_{m0} - c_m(t'_m, t_m)]M^* \end{aligned}$$

$\Leftrightarrow w_{new}(t'_m, t_m) = w_{old}(t'_m, t_m) + [c_{m0} - c_m(t'_m, t_m)]M^*$	(B4.1)
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Where

- $a'_{pm1} = a_{pm1}(t'_m)$ and $a'_{pm2} = a_{pm2}(t'_m)$
- $w_{old}(t'_m, t_m) \stackrel{\text{def}}{=} r_m - c_{m0}M^* + e_{m1}a'_{pm1}P_1^* + e_{m2}a'_{pm2}P_2^*$ is the invasion fitness in our initial framework (see **Appendix C.II.1** in **chapter III**).

Let us now calculate the new gradient of selection $\left. \frac{\partial w_{new}(t'_m, t_m)}{\partial t'_m} \right|_{t'_m=t_m}$. We have $\frac{\partial c_m(t'_m, t_m)}{\partial t'_m} =$

$-\alpha c_{m0} \frac{(t'_m - t_m)}{\sigma_c^2} e^{-\frac{(t'_m - t_m)^2}{2\sigma_c^2}}$, which implies:

$$\left. \frac{\partial w_{new}(t'_m, t_m)}{\partial t'_m} \right|_{t'_m=t_m} = \left. \frac{\partial w_{old}(t'_m, t_m)}{\partial t'_m} \right|_{t'_m=t_m} + \alpha c_{m0} \underbrace{\frac{(t_m - t_m)}{\sigma_{cc}^2}}_{=0} e^{-\frac{(t_m - t_m)^2}{2\sigma_c^2}}$$

$\Leftrightarrow \left. \frac{\partial w_{new}(t'_m, t_m)}{\partial t'_m} \right _{t'_m=t_m} = \left. \frac{\partial w_{old}(t'_m, t_m)}{\partial t'_m} \right _{t'_m=t_m}$	(B4.2)
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Equality (B4.2) shows that the fitness of invasion is not modified by the introduction of niche-overlap competition. Evolutionary singularities t_m^* are, by definition, phenotypes that nullify the gradient of selection. Their existence and position are thus not modified by niche-overlap competition. As indicated by equation (B4.3), convergence directly depends on invasion fitness. It is therefore not affected by the introduction of niche-overlap competition.

$$\text{Non-convergence} \Leftrightarrow \left. \frac{\frac{\partial w_{new}(t'_m, t_m)}{\partial t'_m}}{dt_m} \right|_{t'_m=t_m} \Bigg|_{t_m=t_m^*} > 0 \quad (B4.3)$$

Finally, the criterion for invasibility (equation B4.4) is modified by niche-overlap competition.

$$\text{Invasibility} \Leftrightarrow \left. \frac{\partial^2 w_{new}(t'_m, t_m)}{\partial t_m'^2} \right|_{t'_m=t_m=t_m^*} > 0 \quad (B4.4)$$

Indeed, $\frac{\partial^2 c_m(t'_m, t_m)}{\partial t_m'^2} = \frac{-\alpha c_{m0}}{\sigma_{cc}^2} e^{-\frac{(t'_m-t_m)^2}{2\sigma_c^2}} \left[1 - \frac{(t'_m-t_m)^2}{\sigma_{cc}^2} \right]$ so that, from the equality (B4.1), we have:

$$\begin{aligned} \left. \frac{\partial^2 w_{new}(t'_m, t_m)}{\partial t_m'^2} \right|_{t'_m=t_m=t_m^*} &= \left. \frac{\partial^2 w_{old}(t'_m, t_m)}{\partial t_m'^2} \right|_{t'_m=t_m=t_m^*} - \frac{\partial^2 c_m(t'_m, t_m)}{\partial t_m'^2} M^* \\ &= \left. \frac{\partial^2 w_{old}(t'_m, t_m)}{\partial t_m'^2} \right|_{t'_m=t_m=t_m^*} + \frac{\alpha c_{m0}}{\sigma_{cc}^2} \underbrace{e^{-\frac{(t_m^*-t_m^*)^2}{2\sigma_c^2}}}_{=1} \left[1 - \underbrace{\frac{(t_m^*-t_m^*)^2}{\sigma_{cc}^2}}_{=0} \right] M^* \end{aligned}$$

$$\Leftrightarrow \left. \frac{\partial^2 w_{new}(t'_m, t_m)}{\partial t_m'^2} \right|_{t'_m=t_m=t_m^*} = \left. \frac{\partial^2 w_{old}(t'_m, t_m)}{\partial t_m'^2} \right|_{t'_m=t_m=t_m^*} + \frac{\alpha c_{m0}}{\sigma_{cc}^2} M^* \quad (B4.5)$$

Equality (B4.5) demonstrates that niche-overlap competition facilitates the invasibility of evolutionary singularities.

As expected, at least in the absence of herbivore species, pollinator diversification in response to the availability of two plant resources becomes possible (**Fig. 8a**, $\alpha = 0.4$). In the case of plants, our simulations show that only a slight dependence of competition on niche-overlap ($\alpha = 0.1$, i.e. 10%) enables not only to maintain the dimorphisms that were previously lost (e.g. **Fig. 7b**), but even novel diversifications to occur (**Fig. 8b**).

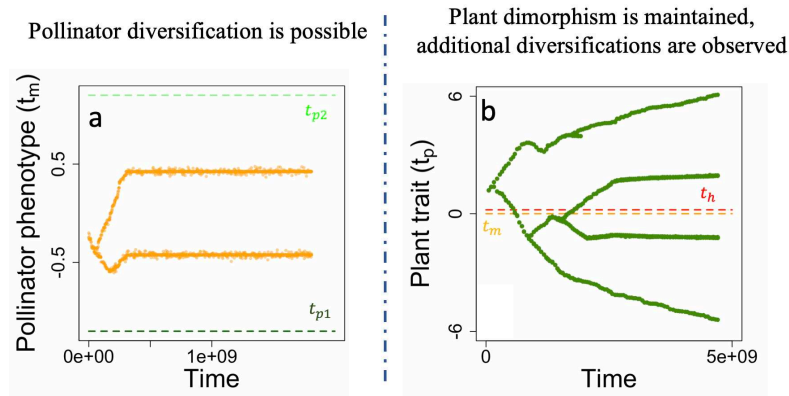


Fig. 8: Niche-overlap competition promotes diversification within our framework. a. Pollinator diversification becomes possible. Parameters: General ($r_{p1} = r_{p2} = 10, r_m = -1, c_{p1} = c_{p2} = 0.7, e_m = 0.2$); Niche-overlap competition ($c_{m0} = 0.8, \alpha = 0.4, \sigma_c = 1.2$); Plant traits ($t_{p2} = -t_{p1} = 1.2$); Interspecific ($c_{p12} = c_{p21} = 0.35, a_{pm0} = 4$). **b. Plant dimorphism is maintained, and additional diversifications are possible.** This is actually the same branching as in **Fig. 7b** (not maintained), with niche-overlap competition this time ($c_{p0} = 0.6, \alpha = 0.1, \sigma_c = 3$).

Note finally that these preliminary results do not indicate that the evolutionary emergence of plant-pollinator-herbivore will be obtained. In particular, the diversification of the plant species has to occur first as in the presence of one plant resource, animals are necessarily subject to directional selection toward the plant phenotype. The latter suggests that the strong trade-off (i.e. $t_h - t_m \approx 0$, **chapter II**) required for disruptive selection to arise might be obtained. But as this trade-off is continuously modified along coevolutionary trajectories, it remains unclear whether plant diversification can occur while all species are coevolving simultaneously. It might notably be interesting to investigate the effect of differential evolutionary rates – i.e. mutation rates, mutational amplitude – on coevolutionary dynamics.

(2) Empirical data on plant-pollinator-herbivore networks

Assuming that we can make plant-pollinator-herbivore networks emerge within our framework, the next step would be to compare the properties of our evolutionary emerged communities to such empirical communities. With the precious help of Pr. Elisa Thébault (thanks Elisa!), we have been able to identify five published studies analyzing novel empirical plant-pollinator-herbivore tripartite networks (**table P.1**).

Reference	Location	Sampling period	Type of ecosystem	Additional remarks
Melián <i>et al.</i> (2009)	Doñana Biological Reserve, Spain	1981-1984	Mediterranean scrub	Data compiled from 20 different studies
Sauve <i>et al.</i> (2016)	Norwood farm, United Kingdom	2007-2008	Agroecosystem	
Welti & Joern (2018)	Konza Prairie Biological Station, Kansas, USA	2014	Tallgrass prairie	
Hackett <i>et al.</i> (2019)	Hengistbury Head, United Kingdom & Tautuku Peninsula, New Zealand	2013 & 2014-2015	Ocean-adjacent peninsulas consisting of a mosaic of habitats	Several habitats including grassland, woodland, salt marsh and sand dune
Morrison <i>et al.</i> (2020)	Sixteen sites in Santa Cruz and Monterey, California, USA	2016-2017	Two types of habitat: natural (chaparral vegetation) and agricultural (crop mixture vs. monoculture)	

Table P.1: Results of the bibliographical research aiming at identifying data of empirical plant-pollinator-herbivore networks.

Our bibliographical research highlights that the available empirical data on plant-pollinator-herbivore networks is rather limited. Most studies – except Melián *et al.* (2009) – were published after 2016, likely as a result of several influential studies advocating for an integrative framework encompassing the diversity of ecological interactions (Fontaine *et al.*

2011; Kéfi *et al.* 2012). For the study of Melián *et al.* (2009), the authors had to compile data from approximately 20 studies that focused on either the plant-herbivore or the plant-pollinator network. They took advantage of the long scientific history of the Doñana Biological Reserve in southern Spain. Likewise, it is possible that in other locations – biological stations in particular - other studies focusing on either herbivory or pollination have produced empirical networks that could be reasonably merged to obtain complete tripartite networks. In particular, as open data practices are developing, such datasets might actually already be available in open databases such as the Global Biotic Interactions database, the Interaction Web Database or the Global Web Database, to name only a few. Because exploring so many databases by hand is unfeasible, an idea would be to perform a first (automatic) exploration to quantify the “potential” for merging networks. More precisely, the idea would be to develop a computer code to identify all the plant-pollinator and plant-herbivore networks that share at least one common plant species, and that were sampled relatively close in space and time. It might then be interesting to investigate, in a second step, the networks identified by the algorithm in more detail.

VII.

Conclusion

The need to account for evolution within a multispecies
community context

Our investigation of the eco-evolutionary dynamics within plant-pollinator-herbivore communities emphasizes the need to account for the diversity of species and ecological interactions, while allowing for evolution, in order to thoroughly understand the mechanisms underlying the maintenance of species coexistence.

Consider the use of pesticides, for instance, which is nowadays a common agricultural practice (Matson *et al.* 1997). While they are targeted at the species – i.e. “pests”, such as herbivores – that are damaging cultivated plants, it is clear that they also induce extra-mortality in non-targeted species (Loeuille *et al.* 2013), including pollinators (Potts *et al.* 2010). The strong selective pressures arising from the use of pesticides, in addition, foster the emergence of resistant mutants. The evolutionary emergence of pesticide resistance is a widespread phenomenon responsible for huge economic costs (Palumbi 2001). It is notably ubiquitous in insect pests (Whalon *et al.* 2008), which are often herbivores, owing to their short generation times and high population densities. The latter characteristics indeed favor their evolutionary rescue (Gomulkiewicz & Holt 1995; Carlson *et al.* 2014). Pollinators, in contrast, often have longer life cycles and lower densities so that they are likely more vulnerable. Georgelin *et al.* (2015) show, for instance, that such a difference in evolutionary potential can lead to the evolutionary murder of pollinators by herbivores, although both species are coevolving toward increased resistance in response to insecticide inputs. The example of pesticides, among many others (Loeuille *et al.* 2013), clearly demonstrate how a more integrative approach – in terms of ecology and evolution – may improve agricultural management practices.

The impact of climate change on biodiversity is another example that advocates for such an integrative approach. A large number of predictions regarding this impact are based on envelope models (Colwell & Rangel 2009), which build a multivariate statistical representation of species niches by linking data of species occurrences with climatic variables. Future species distributions are then predicted according to the climatic scenario considered (e.g. Pearson *et al.* 2002). Such an approach implicitly assumes that species niches are fixed. But important reshufflings of species interactions are expected in the context of global change (Tylianakis *et al.* 2008). Likewise, evolution is likely to modify the species fundamental niches in many cases (e.g. body size reduction in aquatic ecosystems, Daufresne *et al.* 2009). Consider the brown argus butterfly - *Aricia agestis* – in Great Britain for instance. As most lepidopteran species, this butterfly switches from consuming plant tissues (herbivorous larvae) to consuming floral nectar (pollinator adult) along ontogeny, which provides a novel mechanism by which

mutualisms and antagonisms may be intimately intertwined in nature. Historically a specialist of *Helianthemum nummularium* as a larval host plant, Pateman *et al.* (2012) show that *Aricia agestis* has been able to widen its foraging strategy, and is now also largely using *Geranium mole*. Such an evolutionary niche widening – Buckley *et al.* (2012) show it has a genetic signature – enabled the butterfly to significantly expand its range poleward in response to climate warming. The example of *Aricia agestis* highlights how the interplay between evolution and ecological interactions may alter – in this case positively, but potentially also negatively – our predictions regarding the impact of global changes on biodiversity.

Studies undertaking an integrative approach which accounts for both ecological and evolutionary dynamics within complex community contexts (e.g. Yacine *et al.* (2021) provided as an appendix) would allow to better assess under which conditions a given process can be safely ignored, or on the contrary, is essential to consider. Given the tremendous pace at which our environment is currently changing, developing such an understanding is of paramount importance nowadays more than ever (Stockwell *et al.* 2003; Lavergne *et al.* 2010).

References (sections V, VI, VII)

- Abrams, P.A. (1987). On classifying interactions between populations. *Oecologia*, 73, 272–281.
- Abrams, P.A. (2006). Adaptive Change in the Resource-Exploitation Traits of a Generalist Consumer: the Evolution and Coexistence of Generalists and Specialists. *Evolution (N. Y.)*, 60, 427.
- Adler, L.S. & Bronstein, J.L. (2004). Attracting antagonists: Does floral nectar increase leaf herbivory? *Ecology*, 85, 1519–1526.
- Albon, S.D., Brewer, M.J., O'Brien, S., Nolan, A.J. & Cope, D. (2007). Quantifying the grazing impacts associated with different herbivores on rangelands. *J. Appl. Ecol.*, 44, 1176–1187.
- Allhoff, K.T., Ritterskamp, D., Rall, B.C., Drossel, B. & Guill, C. (2015). Evolutionary food web model based on body masses gives realistic networks with permanent species turnover. *Sci. Rep.*, 5, 10955.
- Andrews, E.S., Theis, N. & Adler, L.S. (2007). Pollinator and herbivore attraction to Cucurbita floral volatiles. *J. Chem. Ecol.*, 33, 1682–1691.
- Asikainen, E. & Mutikainen, P. (2005). Preferences of pollinators and herbivores in gynodioecious *Geranium sylvaticum*. *Ann. Bot.*, 95, 879–886.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., *et al.* (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51–57.
- Bell, J.M., Karron, J.D. & Mitchell, R.J. (2005). Interspecific competition for pollination lowers seed production and outcrossing in *Mimulus ringens*. *Ecology*, 86, 762–771.
- Bever, J.D. (2002). Negative feedback within a mutualism: Host-specific growth of mycorrhizal fungi reduces plant benefit. *Proc. R. Soc. B Biol. Sci.*, 269, 2595–2601.
- Di Bitetti, M.S., De Angelo, C.D., Di Blanco, Y.E. & Paviolo, A. (2010). Niche partitioning and species coexistence in a Neotropical felid assemblage. *Acta Oecologica*, 36, 403–412.
- Bitter, M.C., Kapsenberg, L., Gattuso, J.P. & Pfister, C.A. (2019). Standing genetic variation fuels rapid adaptation to ocean acidification. *Nat. Commun.*, 10, 5821.
- Boucher, D.H., James, S. & Keeler, K.H. (1982). *The ecology of mutualism. Annu. Rev. Ecol. Syst. Vol. 13.*
- Brody, A.K. (2008). Effects of Pollinators, Herbivores, and Seed Predators on Flowering Phenology. *Ecology*, 78, 1624–1631.
- Bronstein, J.L. (2001). The Costs of Mutualism. *Am. Zool.*, 41, 825–839.
- Buckley, J., Butlin, R.K. & Bridle, J.R. (2012). Evidence for evolutionary change associated with the recent range expansion of the British butterfly, *Aricia agestis*, in response to climate change. *Mol. Ecol.*, 21, 267–280.
- Caldarelli, G., Higgs, P.G. & McKane, A.J. (1998). Modelling coevolution in multispecies communities. *J. Theor. Biol.*, 193, 345–358.
- Campbell, D.R. & Motten, A.F. (1985). The Mechanism of Competition for Pollination between Two Forest Herbs. *Ecology*, 66, 554–563.
- Cariveau, D., Irwin, R.E., Brody, A.K., Garcia-Mayeya, L.S. & Von Der Ohe, A. (2004). Direct and indirect effects of pollinators and seed predators to selection on plant and floral traits. *Oikos*, 104, 15–26.
- Carlson, S.M., Cunningham, C.J. & Westley, P.A.H. (2014). Evolutionary rescue in a changing world. *Trends Ecol. Evol.*, 29, 521–530.
- Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.

- Chomicki, G., Weber, M., Antonelli, A., Bascompte, J. & Kiers, E. T. (2019). The Impact of Mutualisms on Species Richness. *Trends Ecol. Evol.*, 34, 698–711.
- Colwell, R.K. & Rangel, T.F. (2009). Hutchinson’s duality: The once and future niche. *Proc. Natl. Acad. Sci.*, 106, 19651–19658.
- Comita, L.S., Queenborough, S.A., Murphy, S.J., Eck, J.L., Xu, K., Krishnadas, M., *et al.* (2014). Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *J. Ecol.*, 102, 845–856.
- Connell, J.H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dyn. Popul.*, 298, 312.
- Craine, J.M. & Dybzinski, R. (2013). Mechanisms of plant competition for nutrients, water and light. *Funct. Ecol.*, 27, 833–840.
- Daufresne, M., Lengfellner, K. & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proc. Natl. Acad. Sci. U. S. A.*, 106, 12788–12793.
- Ehrlén, J., Käck, S. & Ågren, J. (2002). Pollen limitation, seed predation and scape length in *Primula farinosa*. *Oikos*, 97, 45–51.
- Fontaine, C., Guimarães Jr, P.R., Kéfi, S., Loeuille, N., Memmott, J., van der Putten, W.H., *et al.* (2011). The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.*, 14, 1170–1181.
- Frey, F.M. (2004). Opposing natural selection from herbivores and pathogens may maintain floral-color variation in *Claytonia virginica* (Portulacaceae). *Evolution (N. Y.)*, 58, 2426–2437.
- Georgelin, E., Kylafis, G. & Loeuille, N. (2015). Eco-Evolutionary Dynamics of Plant-Insect Communities Facing Disturbances. Implications for Community Maintenance and Agricultural Management. *Adv. Ecol. Res.*, 52, 91–114.
- Gervasi, D.D.L. & Schiestl, F.P. (2017). Real-time divergent evolution in plants driven by pollinators. *Nat. Commun.*, 8, 1–8.
- Gilbert, B., Srivastava, D.S. & Kirby, K.R. (2008). Niche partitioning at multiple scales facilitates coexistence among mosquito larvae. *Oikos*, 117, 944–950.
- Gilpin, M.E. & Soulé, M.E. (1986). Minimum viable populations: processes of extinction. In: *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, MA.
- Gómez, J.M. (2003). Herbivory reduces the strength of pollinator-mediated selection in the Mediterranean herb *Erysimum mediohispanicum*: Consequences for plant specialization. *Am. Nat.*, 162, 242–256.
- Gomulkiewicz, R. & Holt, R.D. (1995). When does Evolution by Natural Selection Prevent Extinction? *Evolution (N. Y.)*, 49, 201–207.
- Grant, B.R. & Grant, P.R. (2003). What Darwin’s Finches Can Teach Us about the Evolutionary Origin and Regulation of Biodiversity. *Bioscience*, 53, 965–975.
- Hackett, T.D., Sauve, A.M.C., Davies, N., Montoya, D., Tylianakis, J.M. & Memmott, J. (2019). Reshaping our understanding of species’ roles in landscape-scale networks. *Ecol. Lett.*, 22, 1367–1377.
- Hernández-Hernández, T. & Wiens, J.J. (2020). Why are there so many flowering plants? A multiscale analysis of plant diversification. *Am. Nat.*, 195, 948–963.
- Herrera, C.M. (1987). Components of Pollinator “Quality”: Comparative Analysis of a Diverse Insect Assemblage. *Oikos*, 50, 79.
- Herrera, C.M. (1989). Pollinator abundance, morphology, and flower visitation rate: analysis of the “quantity”

- component in a plant-pollinator system. *Oecologia*, 80, 241–248.
- Hodges, S.A. & Arnold, M.L. (1995). Spurring plant diversification: Are floral nectar spurs a key innovation? *Proc. R. Soc. B Biol. Sci.*, 262, 343–348.
- Holt, R.D. (1977). Predation, apparent competition, and the structure of prey communities. *Theor. Popul. Biol.*, 12, 197–229.
- Irwin, R.E., Strauss, S.Y., Storz, S., Emerson, A. & Guibert, G. (2003). The Role of Herbivores in the Maintenance of a Flower Color Polymorphism in Wild Radish. *Ecology*, 84, 1733–1743.
- Ivey, C.T., Martinez, P. & Wyatt, R. (2003). Variation in pollinator effectiveness in swamp milkweed, *Asclepias incarnata* (Apocynaceae). *Am. J. Bot.*, 90, 214–225.
- Janzen, D.H. (1970). Herbivores and the Number of Tree Species in Tropical Forests. *Am. Nat.*, 104, 501–528.
- Kay, K.M. & Sargent, R.D. (2009). The role of animal pollination in plant speciation: Integrating ecology, geography, and genetics. *Annu. Rev. Ecol. Evol. Syst.*, 40, 637–656.
- Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., *et al.* (2012). More than a meal... integrating non-feeding interactions into food webs. *Ecol. Lett.*, 15, 291–300.
- Kisdi, É. (2002). Dispersal: Risk spreading versus local adaptation. *Am. Nat.*, 159, 579–596.
- Kisdi, É. & Geritz, S.A.H. (1999). Adaptive dynamics in allele space: Evolution of genetic polymorphism by small mutations in a heterogeneous environment. *Evolution (N. Y.)*, 53, 993–1008.
- Kopp, M. & Gavrillets, S. (2006). Multilocus genetics and the coevolution of quantitative traits. *Evolution (N. Y.)*, 60, 1321–1336.
- Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. (2010). Biodiversity and Climate Change: Integrating Evolutionary and Ecological Responses of Species and Communities. *Annu. Rev. Ecol. Evol. Syst.*, 41, 321–350.
- Lefebvre, V., Daugeron, C., Villemant, C. & Fontaine, C. (2019). Empidine dance flies pollinate the woodland geranium as effectively as bees. *Biol. Lett.*, 15.
- Liu, J., Feng, C., Wang, D., Wang, L., Wilsey, B.J. & Zhong, Z. (2015). Impacts of grazing by different large herbivores in grassland depend on plant species diversity. *J. Appl. Ecol.*, 52, 1053–1062.
- Loeuille, N. (2010). Influence of evolution on the stability of ecological communities. *Ecol. Lett.*, 13, 1536–1545.
- Loeuille, N., Barot, S., Georgelin, E., Kylafis, G. & Lavigne, C. (2013). Eco-evolutionary dynamics of agricultural networks: Implications for sustainable management. *Adv. Ecol. Res.*, 49, 339–435.
- Loeuille, N. & Loreau, M. (2005). Evolutionary emergence of size-structured food webs. *Proc. Natl. Acad. Sci.*, 102, 5761–5766.
- Lynch, M. (2010). Evolution of the mutation rate. *Trends Genet.*, 26, 345–352.
- MacArthur, R. & Levins, R. (1967). The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *Am. Nat.*, 101, 377–385.
- Maliet, O., Loeuille, N. & Morlon, H. (2020). An individual-based model for the eco-evolutionary emergence of bipartite interaction networks. *Ecol. Lett.*, 23, 1623–1634.
- Matson, P.A., Parton, W.J., Power, A.G. & Swift, M.J. (1997). Agricultural intensification and ecosystem properties. *Science*, 277, 504–509.
- May, R.M. (1981). Models for two interacting populations. In: *Theoretical ecology: principles and applications (2nd edition)* (ed. May, R.). Blackwell: Oxford, UK, pp. 78–104.

- Melián, C.J., Bascompte, J., Jordano, P. & Křivan, V. (2009). Diversity in a complex ecological network with two interaction types. *Oikos*, 118, 122–130.
- Michael, T.P. (2014). Plant genome size variation: Bloating and purging DNA. *Briefings Funct. Genomics Proteomics*, 13, 308–317.
- 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.
- Morales, C.L. & Traveset, A. (2008). Interspecific pollen transfer: Magnitude, prevalence and consequences for plant fitness. *CRC Crit. Rev. Plant Sci.*, 27, 221–238.
- Morrison, B.M.L., Brosi, B.J. & Dirzo, R. (2020). Agricultural intensification drives changes in hybrid network robustness by modifying network structure. *Ecol. Lett.*, 23, 359–369.
- Mougi, A. & Kondoh, M. (2014). Instability of a hybrid module of antagonistic and mutualistic interactions. *Popul. Ecol.*, 56, 257–263.
- Nepi, M., Pacini, E. & Vesprini, J.L. (2001). Nectar biodiversity: a short review. *Acta Hort.*, 561, 123–126.
- Palumbi, S.R. (2001). Humans as the world's greatest evolutionary force. *Science*, 293, 15–24.
- Pateman, R.M., Hill, J.K., Roy, D.B., Fox, R. & Thomas, C.D. (2012). Temperature-Dependent Alterations in Host Use Drive Rapid Range Expansion in a Butterfly. *Science*, 336, 1028–1030.
- Pearson, R.G., Dawson, T.P., Berry, P.M. & Harrison, P.A. (2002). SPECIES: A spatial evaluation of climate impact on the envelope of species. *Ecol. Modell.*, 154, 289–300.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends Ecol. Evol.*, 25, 345–353.
- Pyke, G.H. (1991). What does it cost a plant to produce floral nectar? *Nature*, 350, 58–59.
- Ricklefs, R.E. (2010). Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *PNAS*, 107, 1265–1272.
- Rueffler, C., Van Dooren, T.J.M., Leimar, O. & Abrams, P.A. (2006a). Disruptive selection and then what? *Trends Ecol. Evol.*, 21, 238–245.
- Rueffler, C., Van Dooren, T.J.M. & Metz, J.A.J. (2006b). The evolution of resource specialization through frequency-dependant and frequency-independant mechanisms. *Am. Nat.*, 167, 81.
- Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.*, 232, 8–27.
- Sargent, R.D. (2004). Floral symmetry affects speciation rates in angiosperms. *Proc. R. Soc. B Biol. Sci.*, 271, 603–608.
- Sauve, A.M.C., Thébault, E., Pocock, M.J.O. & Fontaine, C. (2016). How plants connect pollination and herbivory networks and their contribution to community stability. *Ecology*, 97, 908–917.
- Schluter, D. & Grant, P.R. (1984). Determinants of morphological patterns in communities of Darwin's finches. *Am. Nat.*, 123, 175–196.
- Stockwell, C.A., Hendry, A.P. & Kinnison, M.T. (2003). Contemporary evolution meets conservation biology. *Trends Ecol. Evol.*, 18, 94–101.
- Theis, N., Barber, N.A., Gillespie, S.D., Hazzard, R. V. & Adler, L.S. (2014). Attracting mutualists and antagonists: Plant trait variation explains the distribution of specialist floral herbivores and pollinators on

- crops and wild gourds. *Am. J. Bot.*, 101, 1314–1322.
- Thomas, J.A., Welch, J.J., Lanfear, R. & Bromham, L. (2010). A generation time effect on the rate of molecular evolution in invertebrates. *Mol. Biol. Evol.*, 27, 1173–1180.
- Toby Kiers, E., Palmer, T.M., Ives, A.R., Bruno, J.F. & Bronstein, J.L. (2010). Mutualisms in a changing world: An evolutionary perspective. *Ecol. Lett.*, 13, 1459–1474.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.*
- Valdovinos, F.S., Brosi, B.J., Briggs, H.M., Moisset de Espanés, P., Ramos-Jiliberto, R. & Martinez, N.D. (2016). Niche partitioning due to adaptive foraging reverses effects of nestedness and connectance on pollination network stability. *Ecol. Lett.*, 19, 1277–1286.
- Welti, E.A.R. & Joern, A. (2018). Fire and grazing modulate the structure and resistance of plant–floral visitor networks in a tallgrass prairie. *Oecologia*, 186, 517–528.
- Whalon, M.E., Mota-Sanchez, D. & Hollingworth, R.M. (2008). *Global pesticide resistance in arthropods*.
- Wills, C., Condit, R., Foster, R.B. & Hubbell, S.P. (1997). Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proc. Natl. Acad. Sci. U. S. A.*, 94, 1252–1257.
- Wilson, M. & Lindow, S.E. (1994). Coexistence among epiphytic bacterial populations mediated through nutritional resource partitioning. *Appl. Environ. Microbiol.*, 60, 4468–4477.
- Yacine, Y., Allhoff, K.T., Weinbach, A. & Loeuille, N. (2021). Collapse and rescue of evolutionary food webs under global warming. *J. Anim. Ecol.*, 90, 710–722.
- Yoder, J.B. & Nuismer, S.L. (2010). When Does Coevolution Promote Diversification? *Am. Nat.*, 176, 802–817.
- Yoshida, K. (2003). Evolutionary dynamics of species diversity in an interaction web system. *Ecol. Modell.*, 163, 131–143.
- Zeng, Y. & Wiens, J.J. (2021). Species interactions have predictable impacts on diversification. *Ecol. Lett.*, 24, 239–248.

Appendix

Collapse and rescue of evolutionary food webs under global warming

The following paper has been published in *Journal of Animal Ecology* at the beginning of this year. While the work started during my Master internship with Nicolas, it was finalized during my PhD, explaining why it is provided as an appendix here. This work notably illustrates how community evolution models may be used to investigate the eco-evolutionary resilience of trophic networks confronted with global change.



Collapse and rescue of evolutionary food webs under global warming

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Abstract

1. Global warming is severely impacting ecosystems and threatening ecosystem services as well as human well-being. While some species face extinction risk, several studies suggest the possibility that fast evolution may allow species to adapt and survive in spite of environmental changes.
2. We assess how such evolutionary rescue extends to multitrophic communities and whether evolution systematically preserves biodiversity under global warming.
3. More precisely, we expose simulated trophic networks of co-evolving consumers to warming under different evolutionary scenarios, which allows us to assess the effect of evolution on diversity maintenance. We also investigate how the evolution of body mass and feeding preference affects coexistence within a simplified consumer–resource module.
4. Our simulations predict that the long-term diversity loss triggered by warming is considerably higher in scenarios where evolution is slowed down or switched off completely, indicating that eco-evolutionary feedback indeed helps to preserve biodiversity. However, even with fast evolution, food webs still experience vast disruptions in their structure and functioning. Reversing warming may thus not be sufficient to restore previous structures.
5. Our findings highlight how the interaction between evolutionary rescue and changes in trophic structures constrains ecosystem responses to warming with important implications for conservation and management policies.

KEYWORDS

adaptive dynamics, biodiversity conservation, body mass evolution, climate change, consumer–resource model, eco-evolutionary tipping point, evolutionary rescue, trophic networks

1 | INTRODUCTION

The consequences of global change on biodiversity are now well-documented. They include the extinction of species (Barnosky et al., 2011), changes in species demography, ranges and phenologies (Parmesan & Yohe, 2003) and alterations of ecological interactions (Tylianakis et al., 2008). Significant ecological network reorganizations and changes in ecosystems functioning are therefore expected.

In such a stressful context, it is unclear whether the evolution (or co-evolution) of species will have a net positive or negative effect on network maintenance and stability.

Existing models investigating ecosystem responses to global warming often ignore evolutionary processes and the interaction of species. This is particularly true for 'niche' or 'envelope' models (Colwell & Rangel, 2009) that link data of species occurrence with climatic variables to build a multivariate statistical representation of the species

niche. Future distributions of species are then predicted according to different climate change scenarios (e.g. Pearson et al., 2002) implicitly assuming that niches are fixed. Evolution, however, affects species' fundamental niches while the reshuffling of species interactions can lead to changes in realized niches (Tylianakis et al., 2008). While envelope models are important first steps, they are thus limited in their ability to understand the effects of global warming, and to provide relevant conservation policies (Lavergne et al., 2010).

Ignoring evolution is based on the controversial assumption that ecological and evolutionary processes act on separate time-scales. Recent studies, however, indicate that evolution may act within a few generations (Koch et al., 2014; Olsen et al., 2004), especially in a context of anthropogenic pressures and disturbances (Hendry et al., 2008). For example, many empirical studies (e.g. Daufresne et al., 2009) document warming-induced reductions in body size (reviewed in Sheridan & Bickford, 2011). While a clear identification of evolution versus other processes of phenotypic variations is often lacking, these empirical variations suggest that global warming exerts strong selective pressures on body size. This is crucial because body size is a key biological trait influencing many ecological constraints (Brown et al., 2004), including trophic and competitive interactions. Therefore, variations of body size are likely to affect the whole food web (e.g. O'Gorman et al., 2017). Next to body size, changes in foraging strategies have also been documented in the context of global change, potentially resulting in a rewiring of the corresponding community network. Several studies, for instance, documented contemporary evolution in the diet of native herbivores to include invasive plant species (e.g. Carroll et al., 2005). Another example is the butterfly *Aricia agestis* (United Kingdom), which widened its larval host range as a result of increased temperatures (Pateman et al., 2012). The associated genetic signature (Buckley et al., 2012) strongly suggests this is a case of evolutionary adaptation, that has enabled the species to expand its range poleward.

In some situations, evolution enables species to survive environmental deterioration. Gomulkiewicz and Holt (1995) theorized this concept as 'evolutionary rescue': adaptive evolutionary change restores positive growth in declining populations and prevents extinction. The empirical evidence for evolutionary rescue, as well as the different factors involved, are discussed in detail in the review by Carlson et al. (2014). Effects of evolution are, however, not always positive for biodiversity. Environmental change can alter evolutionary dynamics so that a non-viable phenotype is selected given the new ecological conditions ('evolutionary trapping', Ferriere & Legendre, 2012; empirical e.g. Singer & Parmesan, 2018). Negative effects of evolution on diversity also arise when the evolution of one species drives its interacting partners towards extinction ('evolutionary murder', e.g. Dieckmann et al., 1995). Assessing both positive and negative effects of evolution is crucial to implement relevant conservation decisions (Stockwell et al., 2003).

The last example readily highlights how accounting for the community context is equally important, since the interplay between evolution and species interactions can lead to unexpected behaviours, as illustrated by the two following examples. Within a spatially explicit model of competitive communities, Norberg et al. (2012)

demonstrated that evolution under climate change can create extinction debts long after climate stabilization, but only when competition is accounted for. Osmond et al. (2017) showed that, surprisingly, the maximum environmental change rate an evolving prey population can support increases in the presence of predators. In some cases, the presence of a predator accelerates prey evolution, facilitating its persistence (e.g. selective predation on maladapted prey).

Within a network context, the conditions for and the mechanisms underlying evolutionary rescue can therefore be much more complex compared to monospecific systems. A focal species could be rescued by the evolution of another interacting species ('indirect evolutionary rescue', Yamamichi & Miner, 2015). On the other hand, if evolutionary rescue happens for various species within the network, a focal species could still go extinct if its enemies' (resp. positive interactors) recovery is too fast (resp. too slow) compared to its own (Loeuille, 2019). A key question is therefore whether evolutionary rescue, derived from a monospecific approach, can extend to ecological networks. Single or few species models represent important stepping stones to address this question, because they focus on essential key mechanisms. However, they provide limited insights into the complex indirect interactions occurring in diverse networks (Ellner & Becks, 2011). Although currently rare (but see Norberg et al., 2012), models that consider evolutionary processes within multispecies communities are thus essential.

Here, we ask whether evolutionary rescue at the network scale can promote food web persistence under warming. We address this question using an evolutionary food web model that is based on body masses and feeding preferences. Starting from a single consumer population feeding on a basal resource, the evolution of these two consumer traits leads to the emergence of complex multitrophic communities. Related models have been shown to share many features with empirical food webs (Allhoff et al., 2015; Loeuille & Loreau, 2005). Once the initial build-up is complete, we expose such simulated networks to warming events. We vary both the warming intensity and the mutation rate in order to investigate the interplay between warming, evolution and network diversity maintenance. While this simulation approach provides valuable insights into eco-evolutionary responses to warming at the community scale, it is admittedly difficult to unravel the underlying mechanisms governing these responses. We therefore complement our work by analytically investigating the processes by which evolution facilitates or constrains diversity maintenance within a simplified framework consisting of only one consumer and its resource.

The overarching goal of the present study is to expand existing knowledge from simplified mono-specific systems to complex multispecies networks. We show that with or without evolution, warming is responsible for considerable diversity losses. In line with both theoretical (Binzer et al., 2012; Weinbach et al., 2017) and experimental work (Petchey et al., 1999), we find these losses to be more frequent among upper trophic levels. Evolution has a positive effect on diversity maintenance. It notably enables diversity to progressively and partially recover after a transient collapse. Our results are globally in line with the expectations derived from evolutionary rescue theory (Gomulkiewicz & Holt, 1995).

2 | MATERIALS AND METHODS

2.1 | Model

2.1.1 | Ecological dynamics

The trophic network consists of a set of primary producers providing energy to the whole community [hereafter basal resource of (aggregated) biomass density B_0] and consumer morphs i . Its dynamics follow:

$$\frac{dB_0}{dt} = r \left(1 - \frac{B_0}{K}\right) B_0 - \sum_i a_{i0} B_0 B_i, \quad (1)$$

$$\frac{dB_i}{dt} = \sum_{j=\text{resource/prey}} e a_{ij} B_j B_i - \sum_{j=\text{predator}} a_{ji} B_j B_i - \sum_{j=\text{competitor}} c_{ij} B_j B_i - d_i B_i. \quad (2)$$

The basal resource follows a logistic growth in the absence of higher trophic levels, with intrinsic growth rate r and carrying capacity K (Equation 1). Variations of biomass density B_i of a morph i (Equation 2) are composed of four terms: predation gain, predation loss, losses

due to interference competition, as well as intrinsic losses due to respiration and basic mortality (hereafter respiration). A complete list of parameters and variables is provided in Table 1.

2.1.2 | Temperature dependence

Biochemical reactions and thus metabolic rates are known to grow exponentially with temperature. We therefore incorporate temperature dependency as an Arrhenius function in the resource growth rate r and the respiration rate d_i of consumer i following Brown et al. (2004):

$$r(T) = r_0 \exp\left(\frac{-E(T_0 - T)}{kTT_0}\right), \quad (3)$$

$$d_i(T) = d_{i0} \exp\left(\frac{-E(T_0 - T)}{kTT_0}\right). \quad (4)$$

TABLE 1 Variables and parameters. Dependence on temperature is explicitly indicated. The values given here represent the standard parameter set used in our simulations, unless stated otherwise

Variables and parameters		Biological meaning	Default value	Unit
Variables	B_i	Biomass density of morph i		kg/m ²
	m_i	Body mass of morph i		kg
	f_i	Feeding preference of morph i (i.e. preferred prey size)		kg
Temperature parameters	T	Temperature	[275, 320] (2–47°C)	K
	T_0	Reference temperature	293 (20°C)	K
	E	Activation energy	0.65	eV
	k	Boltzmann Constant	8.617×10^{-5}	eV/K
Ecological parameters	r_0	Growth rate at temperature T_0	1	s ⁻¹
	$r(T)$	Intrinsic growth rate of basal resource		s ⁻¹
	K_0	Carrying capacity at temperature T_0	10	kg/m ²
	$K(T)$	Carrying capacity of basal resource		kg/m ²
	d_0	Respiration rate at temperature T_0	0.3	kg ^{0.25} /s
	$d_i(T)$	Respiration rate of morph i		s ⁻¹
	e	Conversion efficiency	0.85	L
	c_0	Intra-morph competition rate	0.15	m ² /s
	c_{ij}	Competition rate between morph i and morph j		kg ⁻¹ m ² s ⁻¹
	a_{ij}	Attack rate of morph i on morph j		kg ⁻¹ m ² s ⁻¹
	s	Feeding range (width of consumption niche)	0.25	kg
	ϵ	Extinction threshold	210^{-6}	kg/m ²
Evolutionary parameters	μ	Mutation rate	(10^{-1} , 10^{-2} , 10^{-3})	s ⁻¹
	σ	Mutational amplitude	0.25	kg

We furthermore assume that the carrying capacity of the basal resource decreases exponentially with temperature as in Fussmann et al. (2014).

$$K(T) = K_0 \exp\left(\frac{E(T_0 - T)}{kTT_0}\right). \quad (5)$$

Here, k is the Boltzmann constant, E the activation energy and T_0 the reference temperature (Table 1). We assume these relationships to hold over the temperature range we consider here (275–300 K, 2–47°C) (but see Section 4).

2.1.3 | Presentation of evolving traits

Each consumer morph i has two adaptive traits: body mass m_i and feeding preference f_i . Body mass is known to largely constrain trophic interactions (see for instance Woodward et al., 2005). The basal resource has a body mass m_0 that we assume fixed. The feeding preference f_i corresponds to the prey body mass allowing a maximal attack rate. Figure 1 illustrates how traits constrain trophic interactions.

Respiration and attack rates scale with body mass (Brown et al., 2004; Peters, 1983). In our model, attack rates depend on the relative differences between predators' feeding preferences and prey's body masses. Supporting our formulation, several empirical studies indicate that predation intensity is determined by predator-prey body mass ratios (Naisbit et al., 2011; Vucic-Pestic et al., 2010). Around a predator's feeding preference, attack rates are thus distributed right-skewed on an absolute scale, meaning higher predation on smaller prey (Aljetlawi et al., 2004; Brose et al., 2008). We furthermore assume competition to increase for similar feeding preferences, due to niche overlap (MacArthur & Levins, 1967). The feeding niche width is denoted by s (Figure 1) and c_0 is a scaling constant for the interference competition.

$$d_i = m_i^{-0.25} d_0, \quad (6)$$

$$a_{ij} = \frac{m_i^{-0.25}}{\sqrt{2\pi}s} \exp\left(\frac{-(\log(f_i) - \log(m_j))^2}{2s^2}\right), \quad (7)$$

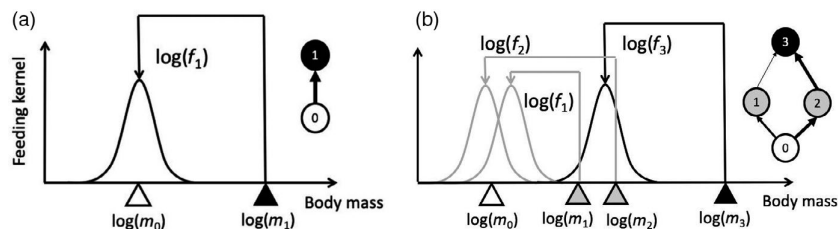


FIGURE 1 (Adapted from Allhoff et al., 2015). (a) Consumer–resource module. The consumer (▲) has a body mass m_1 and feeds on the basal resource (Δ) with maximum attack rate (black curve) because its feeding preference f_1 corresponds to the resource body mass m_0 . Resulting trophic interaction on the right. (b) Complex multitrophic network emerging by co-evolution. The snapshot here shows three morphs: morph 3 (▲) feeds on morphs 1 and 2 (Δ) with respectively low and high attack rates, morphs 1 and 2 feed on the basal resource (Δ) with respectively low and high attack rates. Resulting trophic module on the right. This is a snapshot view; the real networks are dynamic and typically have many more morphs

$$c_{ij} = \frac{c_0}{\sqrt{2\pi}s} \exp\left(\frac{-(\log(f_i) - \log(f_j))^2}{4s^2}\right). \quad (8)$$

2.2 | Methods

2.2.1 | Simulations

Simulations start from a single ancestor morph ($m_1 = 100$ feeding on the basal resource ($m_0 = 1$). The succession of mutation events (one mutation every $\frac{1}{\mu}$ time steps) leads to the emergence of a multitrophic network with typically 30 to 40 morphs and 4 to 5 trophic levels (Allhoff et al., 2015; Loeuille & Loreau, 2005). Proportionally to population abundances, a parent morph is chosen randomly at each mutation event. Mutant traits are then drawn from log-normal distributions centred around the parent's traits. Occasional big mutational steps are allowed (details in Appendix S2.B). The mutant is initially very rare as its initial biomass density corresponds to the extinction threshold ϵ taken from the parent population.

To assess the role of evolution for the maintenance of diversity, we consider two evolutionary scenarios: with evolution ('scenario E') and without evolution ('scenario NE'). Scenario NE consists of the following sequence of events: (a) the network is built-up with a mutation rate μ ; (b) evolution stops ($\mu = 0$) when a quasi-equilibrium is reached; (c) warming occurs; (d) simulation stops when a new quasi-equilibrium is reached. Scenario E follows the same sequence except (b). We consider quasi-equilibrium situations to be reached when the relative trait diversity variability over time is below a critical value (see Appendix S2.B). We are thus not focusing on the transient state following perturbation but on the long-term response to warming, when a steady state is reached.

We ran a total of 420 simulations. For each of the two scenarios (with evolution E and without evolution NE), we ran simulations with all factorial combinations of $\mu = 10^{-1}, 10^{-2}, 10^{-3}$ and $\Delta T = 0, 2, 4, 6, 8, 10, 20$ K or °C (initial temperature is always 275K (2°C)). We ran 10 replicates for each combination of parameters. We focus on the role of μ and ΔT , because a well-supported expectation from evolutionary rescue theory is that evolution is less likely to save the species when the disturbance is high, or when the genetic

variability (here brought by mutation) is low (Carlson et al., 2014; Gomulkiewicz & Holt, 1995). We want to test whether these assumptions remain valid in a multispecies context.

2.2.2 | Evolutionary rescue at the multitrophic network scale

Ferriere and Legendre (2012) propose a broad definition of evolutionary rescue that we adapt to our network context: 'evolutionary rescue occurs when a population subject to environmental change "performs better" under the operation of evolutionary processes than without these processes'. We measure the network performance as the diversity maintained after warming relative to the diversity that was present before (hereafter 'persistence', see Appendix S2.B). Diversity is measured either as trait or species diversity. Trait diversity corresponds to the total number of morphs present at a given time. While this is certainly a valuable measure from a functional and structural point of view, a large focus exists in conservation biology on the preservation of species diversity. Because our model ignores genetic details and focuses on phenotypes, the definition of species is notoriously tricky. For lack of better criteria, we define species as clusters in the phenotypic space (Appendix S2.A). We used statistical models implemented in R-software to compare persistence across scenarios. For each mutation rate, we fitted two ANCOVAs to link trait or species diversity persistence with evolutionary scenarios (evolution E vs. no evolution NE) and warming intensities (details in Appendix S2.C). The results of the statistical analysis are summarized in Table S2.

2.2.3 | Identifying mechanisms in a simplified model

The consumer–resource (CR) module is derived from Equations (1) and (2), assuming one consumer feeding on the resource and potentially its conspecifics (cannibalism).

$$\frac{dB_0}{dt} = r \left(1 - \frac{B_0}{K} \right) B_0 - a_{10} B_1 B_0, \quad (9)$$

$$\frac{dB_1}{dt} = e a_{10} B_0 B_1 - (a_{11} (1 - e) + c_{11}) B_1^2 - d_1 B_1. \quad (10)$$

We use adaptive dynamics (Dieckmann & Law, 1996; Metz et al., 1992) to investigate how warming affects the eco-evolutionary dynamics. Two major assumptions are made: firstly, evolution occurs on longer time-scales than ecology and, secondly, mutations are of small amplitude. Time-scale separation allows the environment felt by the mutant to be clearly defined by the resident population at ecological equilibrium (B_0^* , B_1^*) (analytical expression in Appendix S1.A.1). When the analytical work indicates the system is supposed to go extinct, we assess the potential for evolutionary rescue as in Ferriere and Legendre (2012). More precisely, we undertake simulations to test whether fast evolution may prevent extinction.

For instance, considering trait m_1 (body mass), the invasion fitness $w(m_1^{\text{mut}}, m_1^{\text{res}})$ of a mutant corresponds to its relative growth rate in the resident population when rare. Positive values of w indicate that the mutant frequency increases, eventually replacing the resident. Evolutionary dynamics are captured by the sequence of trait substitutions, and can be approximated by the canonical equation of adaptive dynamics (Dieckmann & Law, 1996). This equation (Appendix S1.B.1) indicates that the trait evolves through time proportionally to the selection gradient, a quantity that captures how the relative fitness $w(m_1^{\text{mut}}, m_1^{\text{res}})$ varies with the mutant trait m_1^{mut} (Appendix S1.B.1). The values of the resident trait m_1^{res} where the selection gradient vanishes are evolutionary singularities. They are classified into continuously stable strategies (CSS, Eshel, 1983), branching points (BP, Geritz et al., 1997) and repellers according to two properties: convergence and invasibility.

Convergence indicates that the trait evolves towards the singularity in its vicinity (convergent: CSS, BP; non-convergent: repeller). Invasibility specifies whether the singularity may be invaded by nearby mutants (non-invasible: CSS; invasible: BP, repeller). Branching points are particularly important in terms of diversity: they yield the emergence of a stable dimorphism in the population due to disruptive selection (e.g. the coexistence of two consumer populations with different body masses). Knowing the evolutionary singularities and their properties (Appendix S1.B.3.d) enables the full determination of the evolutionary dynamics of the consumer population within the CR module.

All in all, this simplified framework allows the eco-evolutionary dynamics of the consumer population confronted with warming to be more easily tractable. Such a thorough understanding allows to highlight key mechanisms that may also act at the co-evolving multitrophic scale. However, we keep in mind that the patterns observed within the CR module framework might not upscale straightforwardly to multitrophic networks due to non-trivial indirect interactions occurring in multispecies communities. In the main text, we study the evolution of the traits m_1 and f_1 separately, but we also tackle the co-evolution of the two traits in the Supporting Information (Figure S2, Appendix S1.B.4).

3 | RESULTS

3.1 | Warming induces diversity losses within trophic networks

Warming is responsible for considerable biodiversity losses within multitrophic networks. This is true with (Figure 2d) or without evolution (Figure 2a). Although diversity recovers fast when evolution is allowed, note that diversity collapses to half of its initial value (Figure 2d). Long after the transient state, diversity stabilizes at smaller values than before warming for a vast majority of simulations, with and without evolution (Figure 2g,h). A warming of 8°C for instance leads to a significant loss of trait diversity (around 32% without evolution, 13% with evolution). For a mutation rate

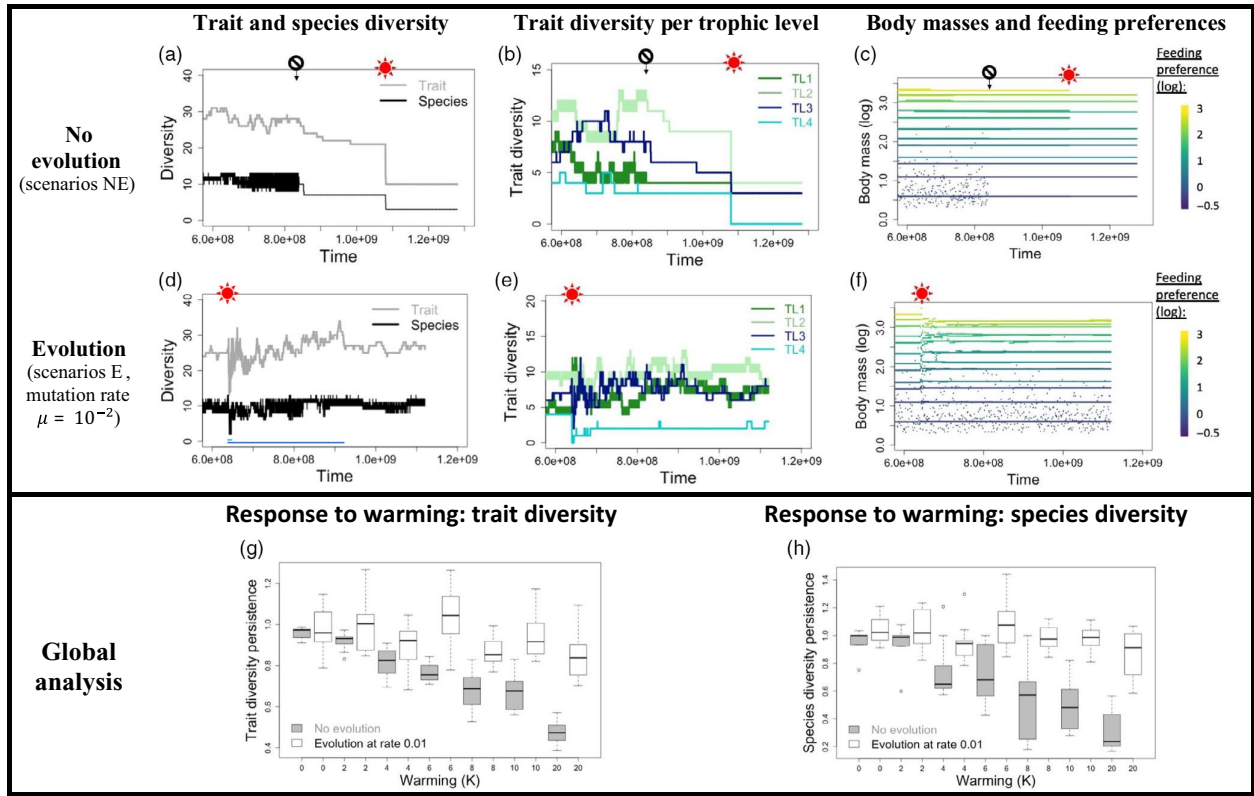


FIGURE 2 Diversity response to warming. (a–c) Diversity and evolutionary dynamics of a simulation where evolution has been stopped (prohibition symbol indicates stopping time) before warming from 275 to 295 K (sun symbol); (d–f) Same outputs with ongoing evolution at warming. (g–h) Boxplots of trait and species diversity persistence according to different warming intensities for scenarios with or without evolution. Each box corresponds to 10 independent replicas. See Table 1 for parameter values

$\mu = 10^{-2}$, the statistical model fitted explains around two thirds of the observed variance, with warming explaining almost one third of it (Table S2.A). The model confirms the expected tendency revealed by Figure 2g,h: stronger warming leads to higher diversity loss. The estimated coefficients governing the linear dependence of persistence on warming intensity are significantly negative without evolution ($\text{Warming}_{\text{Effect}} = -0.024, p_{\text{value}} < 2.10 \cdot 10^{-16}$) or with evolution ($\text{Warming}_{\text{Effect}} + \text{Interaction}_{\text{Effect}} = -0.007, p_{\text{value}} < 10^{-3}$).

Diversity is lost because some consumer populations go extinct following the warming event. As temperature increases, less energy is available at the bottom of the trophic network (decline in basal resource's carrying capacity $K(T)$, Equation 5), while the metabolic requirements increase (increase in respiration loss rate $d_i(T)$, Equation 4). Despite an increase in plants productivity (basal resource's growth rate $r(T)$, Equation 3), the ratio of ingestion to metabolic losses overall decreases with warming. In the CR framework, this decrease is driven by the ratio $\frac{r}{K}$:

$$\frac{\text{Ingestion}}{\text{Metabolism}} \stackrel{\text{def}}{=} \frac{ea_{10}B_0^*(T)}{d_1(T)} = \frac{\left[a_{10} + \frac{r}{d_1} (a_{11}(1-e) + c_0) \right] ea_{10}}{\frac{r}{K} (a_{11}(1-e) + c_0) + ea_{10}^2}. \quad (11)$$

This ingestion ratio reaches the critical value of one at a critical temperature $T_c(f_1)$, above which a consumer with feeding preference f_1

cannot survive (Appendix S1.A). Ingestion is maximal when the consumer's feeding preference matches exactly the basal resource phenotype. No consumer population can therefore survive above the limit temperature $T_{\text{lim}} \stackrel{\text{def}}{=} T_c(f_1 = m_0)$ (Equation 12, Appendix S1.A).

$$T_c(f_1) \leq T_{\text{lim}} \stackrel{\text{def}}{=} \frac{2E}{\frac{2E}{T_0} + k \left(\ln \left(\frac{\sqrt{2\pi}sd_0}{ek_0} \right) \right)}. \quad (12)$$

The limit temperature T_{lim} being independent of the consumer's traits, even fast evolution would not allow any consumer population to survive higher temperatures. Figure 3 for instance shows how evolved body mass depends on temperature. Above T_{lim} (≈ 316.4 K here, grey area), no consumer phenotype is viable. Consumer survival depends on the intensity of warming: a warming from T_1 to T_2 would allow survival while a warming from T_1 to T_3 would lead to extinction. Note also that temperature does not impact evolved body mass in the CR module (analytical proof in Appendix S1.B.2).

Warming can also reduce long-term diversity by changing the selection regime from disruptive to stabilizing. Within the CR framework, such a pattern is observed in the case of feeding preference evolution, for intermediate consumer to resource body mass ratios (Figure 4, details in Appendix S1.B.3.c). As temperature increases,

the convergent singularity changes from an invisible BP to a non-invisible CSS (Figure 4a). Diversification at branching yields the emergence of a stable dimorphism of contrasting feeding preferences ($\approx(m_0, m_1)$, Figure 4c). The initial two-level food chain (t_a , Figure 4d),

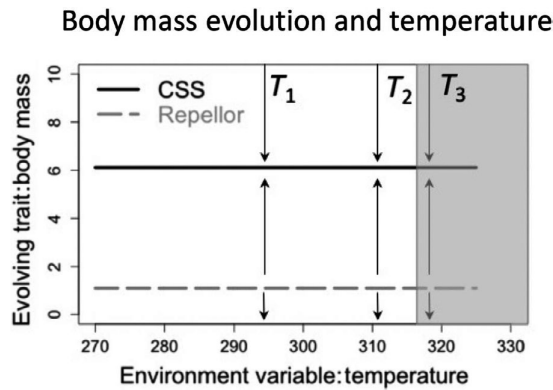


FIGURE 3 Body mass evolution and temperature (E^3 diagram). Grey area cannot support the consumer. Arrows indicate the direction of evolutionary trajectories. Temperatures T_1 , T_2 , and T_3 show different warming scenarios. Parameters: $f_1 = m_0$. Other parameters as in Table 1

consisting of a consumer population feeding equally on the basal resource and conspecifics (cannibalism), evolves into a three-level food chain (t_b , Figure 4d). The intermediate level (Figure 4d, 1) now primarily relies on basal resource consumption, making the upper trophic level (Figure 4d, 2) viable despite being highly cannibalistic. As illustrated in Figure 4b, a warming from T_1 to T_2 at branching (t_a) completely changes the evolutionary dynamics. At T_2 , the loss of the upper trophic level leads to a two-level food chain with a consumer population primarily feeding on the basal resource. Trait diversity is lost and will not recover as selection is stabilizing at T_2 (CSS, Figure 4a). Long-term warming-induced diversity losses can derive from a loss of diversification processes driven by warming.

In our simulated networks, upper trophic levels, corresponding to consumers with high body masses and/or feeding on large prey (Figure 2c,f), are most vulnerable to warming (Figure 2b,e). This may be explained by three factors. Firstly, the analysis of the CR module reveals that a higher body mass is responsible for a sharper decrease in the ingestion ratio with warming (Figure S1, Appendix S1.A.4). Secondly, in a multitrophic context, upper trophic levels suffer from accumulated warming-induced energy losses happening at lower trophic levels. Thirdly, a final reason for the vulnerability of upper trophic levels is their low population sizes. This reduces their

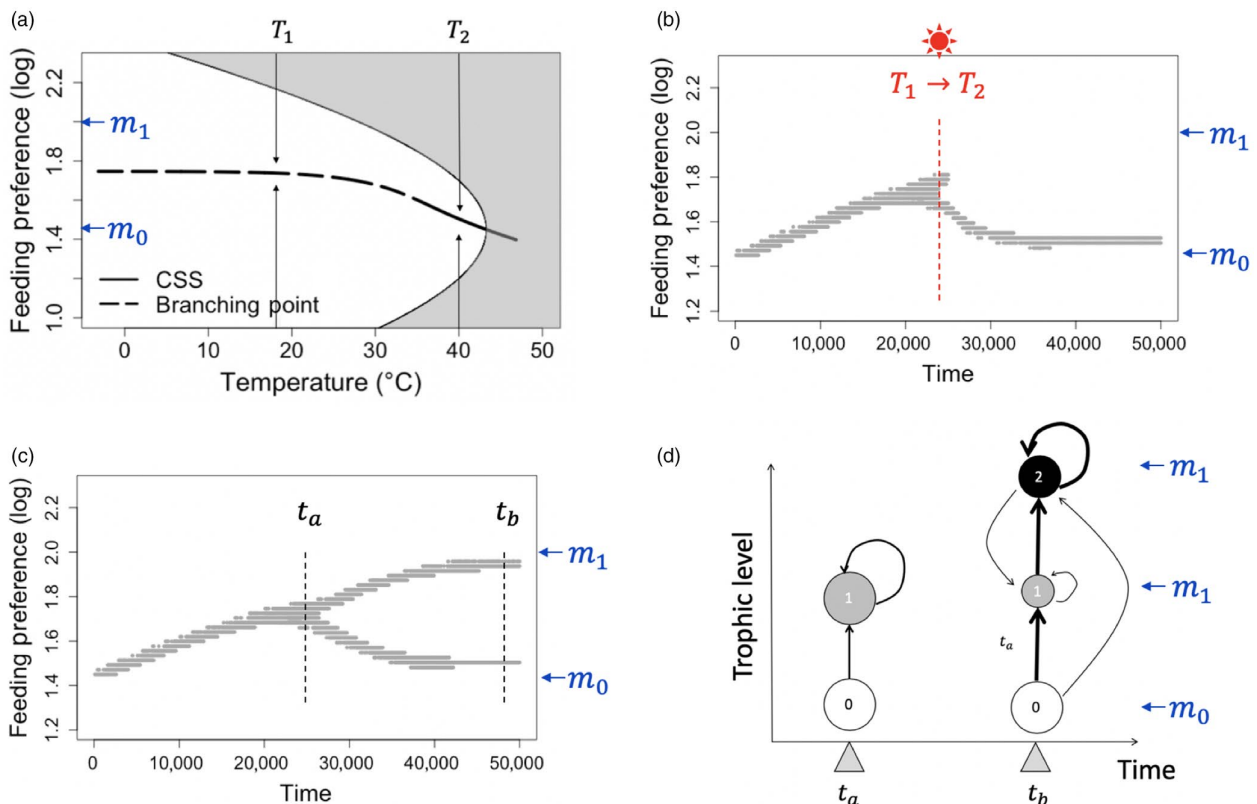


FIGURE 4 Warming switches the selection regime from disruptive to stabilizing (CR module, evolution of feeding preference f_1). $m_1 = 100$, $m_0 = 28.2$ (a) Dependence of singularities on temperature. (b/c) Evolutionary dynamics (mutation rate $\mu = 10^{-2}$, mutation steps $\pm 5\%$) at temperature T_1 (c, Branching Point) or for a warming from T_1 to T_2 occurring at branching (b, sun symbol). (d) Schematic view of the trophic network before (t_a) and long after branching (t_b). Arrow thickness shows the intensity of trophic interactions. Circle size is proportional to the morph density. Other parameters are as in Table 1

evolvability, thus their ability to adapt to new environmental conditions. Warmed trophic networks are consequently flatter. Warming-induced losses of diversifying processes that yield the emergence of upper trophic levels, such as the branching point in Figure 4, could also contribute to the pattern observed.

3.2 | Evolution can mitigate warming-induced diversity losses

Warming triggers diversity losses with or without evolution (Figure 2a,d). However, recovery is possible when morphs can evolve (Figure 2d), while it is not when evolution has been switched off (Figure 2a). Such a recovery necessitates a considerable amount of time. In Figure 2d, it took 200,000 mutation events/generations (light blue line) to reach pre-warming diversity levels and far more for diversity to be stable over time (2.8×10^6 mutation events/generations, dark blue line). The diversity eventually maintained in the trophic network is significantly higher in scenarios with evolution (ANCOVAs, Table S2). The results are quantitatively illustrated on trait diversity for a mutation rate $\mu = 10^{-2}$ but remain consistent across the three mutation rates tested. Evolution has a positive effect on diversity persistence. This effect is both direct ($\text{Evolution}_{\text{Effect}} = 0.06$ 28.4%) and indirect, increasing in importance with warming ($\text{Interaction}_{\text{Effect}} = 0.017$, $p_{\text{value}} < 10^{-8}$, $\text{Var}_{\text{explained}} = 9.5\%$). This interactive effect is strong enough to totally offset the negative linear dependence of diversity persistence on warming in scenarios with evolution for the two other mutation rates tested (10^{-1} , 10^{-3}). In these cases, trait diversity recovers totally after a long transient state. Due to the interaction term, the stronger the warming, the higher the diversity maintained thanks to ongoing evolution across the trophic network (Figure 2g,h). It reaches a maximum of almost 40% at 20°C, with 48% of trait persistence in scenarios without evolution versus 85% in scenarios with evolution. Among evolutionary scenarios, we also tested the theoretically known association between faster evolution and better rescue by comparing diversity maintenance across mutation rates (ANCOVA). Counterintuitively, no significant difference was found (but see Section 4).

The analysis of the CR module highlights two processes that potentially explain how evolution contributes to preserve the diversity in multitrophic networks: evolutionary rescue and an indirect mechanism we label 'diversity-mediated buffering effect'. These processes, which are illustrated in the case of feeding preference f_1 evolution, are explained in detail further below.

It can be shown that the consumer's evolved feeding preference f_1^* is necessarily between its own body mass (m_1) and the body mass of the resource (m_0) (Appendix S1.B.3). The study of feeding preference in this interval is thus sufficient. We define the consumer trait $\alpha \stackrel{\text{def}}{=} \frac{\log(m_1/f_1)}{\log(m_1/m_0)}$ describing the proportion of resource consumption on the total consumer regime. Strictly equivalent to feeding preference evolution, it is more convenient to study the evolution of α that varies between two extreme scenarios: the consumer is essentially cannibalistic ($\alpha = 0$) or primarily

relies on the basal resource ingestion ($\alpha = 1$). The analysis of the CR module reveals that four qualitative outcomes, corresponding to four ecological scenarios, are possible (Appendix S1.B.3.c, Table S1). These scenarios are illustrated in Figure 5. They differ in two key features: (a) the consumer to resource body mass ratio ($L \stackrel{\text{def}}{=} \frac{\log(m_1/m_0)}{s}$) is either small (scenario A), intermediate (scenario B) or large; (b) for large ratios, whether the consumer body mass (m_1) is small (scenario C) or big (scenario D). Note that dynamics presented earlier (Figure 4a) correspond to scenario B (Figure 5c).

Evolutionary rescue can never happen for temperatures above T_{lim} (Equation 12), but is always possible if the final temperature remains below T_{lim} (Figure 5). Consumers that adapt fast enough to the new conditions will avoid extinction, as figured by the white arrows in Figure 5a, c, f, h. For instance, at small CR body mass ratios (scenario A, Figure 5a), a warming from T_1 to T_3 leads the system to enter the non-viability area (black dot in grey area). The food chain can, however, persist if evolution is fast enough (white arrow), as larger values of α are selected, outside the non-viability area. Such values imply higher intakes from the basal resource relative to cannibalism that enable the maintenance of a sufficient ingestion rate despite the deteriorated environmental conditions. The selection of higher intake from the basal resource relative to cannibalism seems consistent across scenarios (Figure 5). Simulations confirm the possibility of evolutionary rescue (Figure 5b). The consumer population collapses, but if α evolves fast enough, the population recovers. Note that if warming is slow from T_1 to T_2 first and then from T_2 to T_3 (Figure 5a), the trait would remain close to the CSS curve, and the population would never be threatened. Progressive warming decreases extinction risk, in agreement with theoretical (Gomulkiewicz & Holt, 1995) and empirical work (Bell & Gonzalez, 2009).

When evolution allows the diversification of the consumer niches, warming is potentially less threatening as the different occupied niches are unlikely to be simultaneously destroyed. We propose to label this mechanism 'diversity-mediated buffering effect'. This can be observed in scenarios where branching leads to a stable dimorphism among consumers (scenarios B and C) so that a three-level food chain emerges (Figure 4). We simulated the eco-evolutionary dynamics following a warming from T_1 to T_2 affecting either the two-level food chain (Figure 4d, just before branching at time t_0) or the three-level food chain (Figure 4d, long after branching at time t_0). While warming at t_0 largely threatens the population, the impact of warming is vastly reduced when temperature changes at t_0 (Figure 5d vs. 5e). Note that while the top trophic level biomass still suffers from the disturbance, the intermediate consumer phenotype actually benefits from warming (Figure 5e). Total consumer biomass increases. Interestingly, the selected intermediate consumer's trait α pre-warming is close to the one selected under warmed conditions (Figure 5e vs. 5d).

Our simulated multitrophic networks emerge via successive branching events starting from a single consumer population initially. As a result, the consumer morphs occupy a wide diversity of niches (Figure 2c,f) that ranges across four trophic levels (Figure 2b,c). In other words, this 'diversity-mediated buffering effect' is at play at

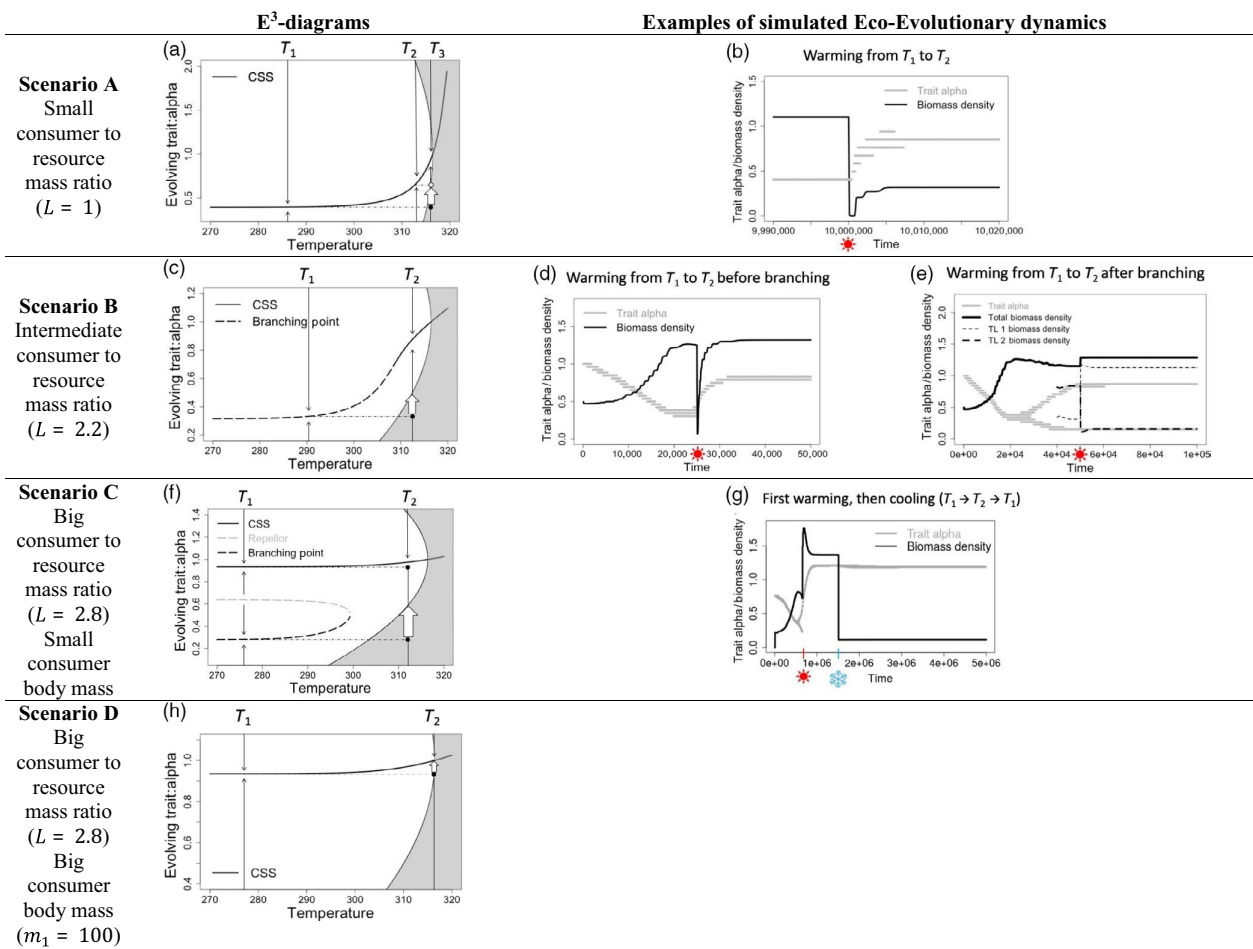


FIGURE 5 (a, c, f, h) E³ diagrams corresponding to scenarios A, B, C and D (Table S1). Grey areas are non-viability regions; the curves indicate the evolutionary singularities. Thin black arrows indicate the direction of evolution and the big white arrows indicate potential evolutionary rescues. (b, d, e) Model simulations with evolutionary rescue occurring (sun indicates warming time). Evolutionary rules: $\mu = 10^{-2}$, and small mutational steps: $5\% f_1$. (g) Model simulation with evolutionary hysteresis occurring (sun: warming; snowflake: cooling). Evolutionary rules: $\mu = 10^{-2}$, and small mutational steps: $1\% f_1$. Parameter values are in Table 1

the multitrophic network scale because multitrophic networks are the result of the consumer niche diversification.

3.3 | Evolution can also exacerbate the consequences of warming on diversity

While evolution often facilitates diversity maintenance in our simulated trophic networks, note that it cannot totally mitigate the negative effect of warming on diversity. Actually, in some cases we found that evolution can even exacerbate the negative consequences of warming-induced diversity losses. For instance, the analysis of the CR model suggests that warming can lead to eco-evolutionary tipping points that would severely depress persistence. Given scenario C, warming from T_1 to T_2 modifies the number

of singularities (Figure 5f). At T_1 , three singularities exist (CSS, Repellor and BP) while at T_2 only the CSS remains. Consequently, starting from a resident consumer's trait near branching, warming would be responsible for a reduction of diversity, as the system switches from selective pressures that allow stable polymorphism (BP) to a monomorphic situation (CSS). While similar to scenario B (Figure 4), a major difference exists. Given the convergent properties of the CSS, decreasing temperature will not recover the initial diversity, as phenotypes remain at the selected CSS. This is a case of evolutionary hysteresis. Simulations confirm such dynamics (Figure 5g). Starting near branching, we warm the system from T_1 to T_2 and observe the loss of the polymorphism. When the system is cooled back to T_1 , the system remains monomorphic. Here, the initial diversity lost to warming cannot be recovered by reducing temperature because of the eco-evolutionary constraints on

consumer's evolution. This result raises the possibility that diversity losses may be long-lasting and difficult to reverse, as a result of abrupt changes in selective regimes.

4 | DISCUSSION

Our investigation into the effect of warming within multitrophic networks shows that warming is responsible for important diversity losses across food webs. While evolution helps to maintain biodiversity, it is certainly not sufficient to totally mitigate diversity losses. Evolution acts in at least two complementary ways: (a) By producing diversified ecological niches, as a result of disruptive selection, it leads to trophic networks that are more resistant to warming; (b) After warming, evolutionary rescue processes across the network lead to gradual and partial recovery. Evolution can, however, also exacerbate the negative consequences of warming, for instance by making them last longer (hysteresis), due to the crossing of eco-evolutionary tipping points. The consistency and coherence of the picture obtained by combining two complementary frameworks, with different scales and complexities, gives confidence on the robustness of our work. Our key results, as discussed in more detail below, have potential implications for the preservation of biodiversity in the context of current warming.

Warming induces important diversity losses within trophic networks. As experimentally observed (Rall et al., 2010), the ratio of ingestion to metabolic losses decreases because less energy is available at the bottom of the food web (primary producers) in a context of increasing metabolic expenditures. As a result, several consumer morphs go extinct. These extinctions are more likely to happen high in the food web. This result seems firmly grounded as several studies using a large diversity of approaches found a similar pattern (Binzer et al., 2012; Petchey et al., 1999; Pounds et al., 1999). Potential explanations combine a sharper decrease in the ingestion ratio for morphs that are closer to their viable minimum; the bottom-up accumulation of deleterious consequences and the low evolvability associated with smaller population sizes and longer generation times. Warming also reduces diversity by altering evolutionary processes. Our CR framework shows that it can modify the selection regime from disruptive to stabilizing (scenarios B and C). Altering diversity patterns through such modifications of selection regimes has deeper implications. Such effects are likely to last longer and be more difficult to reverse because of the additional constraints they entail (e.g. hysteresis). Our results support the idea that conservation ecology should focus more on preserving the processes facilitating and maintaining diversity rather than diversity patterns per se (Smith et al., 1993).

Evolution partly mitigates warming-induced diversity losses within multitrophic networks, as shown by our statistical analysis (Table S2). Two complementary mechanisms are likely at play. First, evolution reduces diversity losses through a 'diversity-mediated buffering effect'. This relies upon two observations: evolution (disruptive selection) leads to the diversification of the consumer niche

(successive branching events) that allows the emergence of multitrophic networks; the greater the diversity of occupied niches at warming, the more robust is the food web because of the increased likelihood of some strategies being resistant (Figure 5d,e). This mechanism is akin to the 'insurance hypothesis' proposed to explain the resilience of diverse systems (Yachi & Loreau, 1999). Second, evolution allows diversity to progressively recover through evolutionary rescue processes. In our CR framework, evolutionary rescue is indeed often possible when evolutionary changes in foraging strategies allow higher energy acquisition or when evolution of body sizes reduces energy requirements. Such changes in either body size or foraging strategy in response to warming have been documented in nature. The meta-analysis of Daufresne et al. (2009) for instance shows a significant decrease in the size of ectothermic aquatic organisms in response to climate change. In the United Kingdom, Pateman et al. (2012) showed that the butterfly *Aricia agestis*, originally a specialist of *Helianthemum nummularium* as a larval host plant, has been able to widen its foraging strategy, allowing its expansion in the face of climate change. It now also largely uses *Geranium mole* which is more abundant in warmer climates.

In our simulated multitrophic networks, evolutionary rescue likely happens for low and intermediate trophic levels (Figure 2f), which evolve faster due to larger population sizes. It is facilitated by occasional mutations with large phenotypic effects. Top trophic levels recover eventually from intermediate trophic level populations that evolve higher body masses and feeding preferences until occupying the niche freed by the extinction of top trophic levels. The recovery of the network's diversity is, however, partial as lower biomass is available from primary production. Surprisingly, we found that higher mutation rates, associated with faster evolution, are not systematically associated with higher diversity persistence. A possible explanation is that, in addition to the intensity of selection, network recovery depends on the variability on which selection can act. Eventually, more frequent mutations do not yield more variability, but redundant phenotypes. This idea is in line with experimental results by Fugère et al. (2020) which clearly highlight that past a certain genetic variability, no improvement is observed in the rescue process. The work of Fugère et al. (2020) additionally illustrates how experimental evolution in microcosms or mesocosms offer promising opportunities for the critical empirical investigations into evolutionary rescue, especially at the multitrophic scale.

Evolution can, however, exacerbate the negative consequences of warming. Evolutionary hysteresis for instance makes them difficult to reverse, lasting longer. It implies strong and possibly irreversible shifts between alternative states corresponding to tipping points (Suding & Hobbs, 2009). In line with previous studies (Dakos et al., 2019), our work emphasizes the importance of considering both evolution and ecological dynamics to understand tipping points, especially in the context of global changes where selective pressures are likely strong. Observed in a simple food chain (CR, Figure 5g), eco-evolutionary tipping points might also exist within complex multitrophic networks but such

an investigation goes beyond the scope of the present paper. We simply note here that the transient state's considerable duration following warming (e.g. Figure 2d) potentially offers opportunities for hysteresis arising from the co-evolution of traits and interactions we did not consider here. What is more, the overall vulnerability of the small populations during the transient state raises additional challenges. Demographic stochasticity or drift could dampen or impede progressive recovery. Important ecosystem services are likely to be degraded for a great period on a human time-scale. However, we note that a recent study of the Cretaceous–Palaeogene mass extinction suggests that functional recovery may happen much faster than diversity recovery (Alvarez et al., 2019).

Our parametrization relies, as much as possible, on available empirical data. Yet, our models are of course a crude simplification focused on a question, making many simplifying assumptions. For instance, we assume the carrying capacity of the basal resource to decrease exponentially with temperature based on the empirical data analysed by Fussmann et al. (2014). This relationship is, however, debated and likely context dependent, varying with the explicit limiting nutrient dynamics (Uszko et al., 2017). Moreover, while there is evidence for an increase in attack rates with temperature (Rall et al., 2010), available data suggest this effect is rather weak (Binzer et al., 2012; Rall et al., 2012). A hump-shaped relationship also seems more realistic when considering wide temperature ranges (Englund et al., 2011). Because it is not the focus of the present work (but see Weinbach et al. (2017) for an analysis of this question on the present model), the lack of a large scientific consensus led us to choose constant attack rates. Likewise, conversion efficiencies show large variations in nature and may depend on trophic positions (Lindeman, 1942). Herbivores (TL1) feeding on primary producers (TL0) typically have lower conversion efficiencies (Yodzis & Innes, 1992). We investigated the robustness of our results by varying this parameter in the CR module (Appendix S1.B.3). At lower efficiencies, we no longer observe evolutionary hysteresis, but typically have evolutionary rescue happening. Hysteresis is thus associated with high conversion efficiencies characteristic of higher trophic level (carnivores, Yodzis & Innes, 1992), which can be interpreted as additional evidence that higher trophic levels are more vulnerable to warming (Binzer et al., 2012). Overall, while lower conversion efficiencies certainly imply lower energy flows resulting in more vulnerable networks, there is no obvious reason to think the positive effects of evolution on diversity maintenance would change.

The concept of evolutionary rescue, originally formulated within a monospecific framework (Gomulkiewicz & Holt, 1995), seems to extend to the community scale as our work suggests that multitrophic networks confronted with warming perform better when evolution is at play (Ferriere & Legendre, 2012). Among these processes, the evolutionary rescue of low and intermediate trophic levels, that facilitates the recovery of higher trophic levels, is key. The diversification of ecological niches ensuing from disruptive selection is equally important as our work unravels a

diversity-mediated buffering effect. As a result, all measures favouring evolvability, such as spatial or temporal variability or the presence of micro-habitat, are likely to make the community more resistant to warming. Likewise, all measures targeting the key factors for evolutionary rescue, as presented in the review by Carlson et al. (2014), should favour trophic networks' persistence and resilience.

Yet, evolutionary processes are not sufficient to preserve biodiversity in the context of global change. Indeed, our work highlights important diversity losses for considerable amounts of time before a partial recovery can potentially happen. Specifically, the transient collapse may severely affect ecosystem services sustained by ecological networks, with large impacts from a management point of view. What is more, several mechanisms we do not consider here could dampen or even prevent the recovery. Low population size may induce adverse ecological (demographic stochasticity, Allee effects) or evolutionary effects (genetic drift) impeding persistence. We also did not model the evolution of primary producers under warming, which may mostly affect other traits than body size (Parmesan, 2006). Empirical evidence highlights for instance temporal mismatches between plants and herbivores resulting from heterogeneous phenological shifts in response to climate warming (Visser & Gienapp, 2019). The consecutive energy losses further threaten the maintenance of diversity within multitrophic networks.

In summary, while evolution has a positive effect on biodiversity maintenance within trophic networks confronted with warming, the impact of warming is nevertheless expected to be dramatic and long lasting, with severe consequences for human populations. Conservation and biodiversity management policies should better integrate evolutionary components to properly address the issues raised by global change.

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AUTHORS' CONTRIBUTIONS

N.L., K.T.A. and Y.Y. conceived the ideas and designed the methodology; The analysis was conducted by A.W. (body mass evolution) and Y.Y. (feeding preference evolution and co-evolution); As for the simulated complex multitrophic networks, K.T.A. developed the code, which was later adapted by Y.Y. to do the simulations; Results analysis was done by N.L., K.T.A. and Y.Y.; Y.Y. wrote the first draft of the manuscript that has been subsequently reviewed and edited by N.L. and K.T.A. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The code used for the simulations (programming language C) is available in the Supporting Information (Appendix S3).

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REFERENCES

- Aljetlawi, A. A., Sparrevik, E., & Leonardsson, K. (2004). Prey-predator size-dependent functional response: Derivation and rescaling to the real world. *Journal of Animal Ecology*, 73. <https://doi.org/10.1111/j.0021-8790.2004.00800.x>
- Allhoff, K. T., Ritterskamp, D., Rall, B. C., Drossel, B., & Guill, C. (2015). Evolutionary food web model based on body masses gives realistic networks with permanent species turnover. *Scientific Reports*, 5(1), 10955. <https://doi.org/10.1038/srep10955>
- Alvarez, S. A., Gibbs, S. J., Bown, P. R., Kim, H., Sheward, R. M., & Ridgwell, A. (2019). Diversity decoupled from ecosystem function and resilience during mass extinction recovery. *Nature*, 574(7777), 242–245. <https://doi.org/10.1038/s41586-019-1590-8>
- Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C. & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471(7336), 51–57. <https://doi.org/10.1038/nature09678>
- Bell, G., & Gonzalez, A. (2009). Evolutionary rescue can prevent extinction following environmental change. *Ecology Letters*, 12(9), 942–948. <https://doi.org/10.1111/j.1461-0248.2009.01350.x>
- Binzer, A., Guill, C., Brose, U., & Rall, B. C. (2012). The dynamics of food chains under climate change and nutrient enrichment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1605), 2935–2944. <https://doi.org/10.1098/rstb.2012.0230>
- Brose, U., Ehnes, R. B., Rall, B. C., Vucic-Pestic, O., Berlow, E. L., & Scheu, S. (2008). Foraging theory predicts predator-prey energy fluxes. *Journal of Animal Ecology*, 77(5), 1072–1078. <https://doi.org/10.1111/j.1365-2656.2008.01408.x>
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7), 1771–1789. <https://doi.org/10.1890/03-9000>
- Buckley, J., Butlin, R. K., & Bridle, J. R. (2012). Evidence for evolutionary change associated with the recent range expansion of the British butterfly, *Aricia agestis*, in response to climate change. *Molecular Ecology*, 21(2), 267–280. <https://doi.org/10.1111/j.1365-294X.2011.05388.x>
- Carlson, S. M., Cunningham, C. J., & Westley, P. A. H. (2014). Evolutionary rescue in a changing world. *Trends in Ecology & Evolution*, 29(9), 521–530. <https://doi.org/10.1016/j.tree.2014.06.005>
- Carroll, S. P., Loye, J. E., Dingle, H., Mathieson, M., Famula, T. R., & Zalucki, M. P. (2005). And the beak shall inherit – Evolution in response to invasion. *Ecology Letters*, 8(9), 944–951. <https://doi.org/10.1111/j.1461-0248.2005.00800.x>
- Colwell, R. K., & Rangel, T. F. (2009). Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences of the United States of America*, 106(Suppl 2), 19651–19658. <https://doi.org/10.1073/pnas.0901650106>
- Dakos, V., Matthews, B., Hendry, A. P., Levine, J., Loeuille, N., Norberg, J., Nosil, P., Scheffer, M., & De Meester, L. (2019). Ecosystem tipping points in an evolving world. *Nature Ecology & Evolution*, 3(3), 355–362. <https://doi.org/10.1038/s41559-019-0797-2>
- Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106(31), 12788–12793. <https://doi.org/10.1073/pnas.0902080106>
- Dieckmann, U., & Law, R. (1996). The dynamical theory of coevolution: A derivation from stochastic ecological processes. *Journal of Mathematical Biology*, 34(5–6), 579–612. <https://doi.org/10.1007/BF02409751>
- Dieckmann, U., Marrow, P., & Law, R. (1995). Evolutionary cycling in predator-prey interactions: Population dynamics and the red queen. *Journal of Theoretical Biology*, 176(1), 91–102. <https://doi.org/10.1006/jtbi.1995.0179>
- Ellner, S. P., & Becks, L. (2011). Rapid prey evolution and the dynamics of two-predator food webs. *Theoretical Ecology*, 4(2), 133–152. <https://doi.org/10.1007/s12080-010-0096-7>
- Englund, G., Öhlund, G., Hein, C. L., & Diehl, S. (2011). Temperature dependence of the functional response. *Ecology Letters*, 14(9), 914–921. <https://doi.org/10.1111/j.1461-0248.2011.01661.x>
- Eshel, I. (1983). Evolutionary and continuous stability. *Journal of Theoretical Biology*, 103(1), 99–111. [https://doi.org/10.1016/0022-5193\(83\)90201-1](https://doi.org/10.1016/0022-5193(83)90201-1)
- Ferriere, R., & Legendre, S. (2012). Eco-evolutionary feedbacks, adaptive dynamics and evolutionary rescue theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1610), 20120081. <https://doi.org/10.1098/rstb.2012.0081>
- Fugère, V., Hébert, M.-P., da Costa, N. B., Xu, C. C. Y., Barrett, R. D. H., Beisner, B. E., Bell, G., Fussmann, G. F., Shapiro, B. J., Yargeau, V., & Gonzalez, A. (2020). Community rescue in experimental phytoplankton communities facing severe herbicide pollution. *Nature Ecology & Evolution*, 4(4), 578–588. <https://doi.org/10.1038/s41559-020-1134-5>
- Fussmann, K. E., Schwarzmüller, F., Brose, U., Jousset, A., & Rall, B. C. (2014). Ecological stability in response to warming. *Nature Climate Change*, 4(3), 206–210. <https://doi.org/10.1038/nclimate2134>
- Geritz, S. A. H., Metz, J. A. J., Kisdi, É., & Meszéna, G. (1997). Dynamics of adaptation and evolutionary branching. *Physical Review Letters*, 78(10), 2024–2027. <https://doi.org/10.1103/PhysRevLett.78.2024>
- Gomulkiwicz, R., & Holt, R. D. (1995). When does evolution by natural selection prevent extinction? *Evolution*, 49(1), 201–207. <https://doi.org/10.1111/j.1558-5646.1995.tb05971.x>
- Hendry, A. P., Farrugia, T. J., & Kinnison, M. T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, 17(1), 20–29. <https://doi.org/10.1111/j.1365-294X.2007.03428.x>
- Koch, H., Frickel, J., Valiadi, M., & Becks, L. (2014). Why rapid, adaptive evolution matters for community dynamics. *Frontiers in Ecology and Evolution*, 2, 17. <https://doi.org/10.3389/fevo.2014.00017>
- Lavergne, S., Mouquet, N., Thuiller, W., & Ronce, O. (2010). Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics*, 41(1), 321–350. <https://doi.org/10.1146/annurev-ecolsys-102209-144628>
- Lindeman, R. (1942). The trophic-dynamic aspect of ecology. *Ecology*, 23(4), 399–417. <https://doi.org/10.2307/1930126>
- Loeuille, N. (2019). Eco-evolutionary dynamics in a disturbed world: Implications for the maintenance of ecological networks. *F1000Research*, 8, 97. <https://doi.org/10.12688/f1000research.15629.1>
- Loeuille, N., & Loreau, M. (2005). Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 102(16), 5761–5766. <https://doi.org/10.1073/pnas.0408424102>
- Macarthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101(921), 377–385. <https://doi.org/10.1086/282505>
- Metz, J. A. J., Nisbet, R. M., & Geritz, S. A. H. (1992). How should we define 'fitness' for general ecological scenarios? *Trends in Ecology & Evolution*, 7. [https://doi.org/10.1016/0169-5347\(92\)90073-K](https://doi.org/10.1016/0169-5347(92)90073-K)
- Naisbit, R. E., Kehrli, P., Rohr, R. P., & Bersier, L. F. (2011). Phylogenetic signal in predator-prey body-size relationships. *Ecology*, 92(12), 2183–2189. <https://doi.org/10.1890/10-2234.1>

- Norberg, J., Urban, M. C., Vellend, M., Klausmeier, C. A., & Loeuille, N. (2012). Eco-evolutionary responses of biodiversity to climate change. *Nature Climate Change*, 2(10), 747–751. <https://doi.org/10.1038/nclimate1588>
- O'Gorman, E. J., Zhao, L., Pichler, D. E., Adams, G., Friberg, N., Rall, B. C., Seeney, A., Zhang, H., Reuman, D. C., & Woodward, G. (2017). Unexpected changes in community size structure in a natural warming experiment. *Nature Climate Change*, 7(9), 659–663. <https://doi.org/10.1038/nclimate3368>
- Olsen, E. M., Heino, M., Lilly, G. R., Morgan, M. J., Bratley, J., Ernande, B., & Dieckmann, U. (2004). Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, 428(6986), 932–935. <https://doi.org/10.1038/nature02430>
- Osmond, M. M., Otto, S. P., & Klausmeier, C. A. (2017). When predators help prey adapt and persist in a changing environment. *The American Naturalist*, 190(1), 83–98. <https://doi.org/10.1086/691778>
- Parnesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual of Ecology, Evolution and Systematics*, 37, 637–669. <https://doi.org/10.2307/annurev.ecolsys.37.091305.30000024>
- Parnesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37–42. <https://doi.org/10.1038/nature01286>
- Pateman, R. M., Hill, J. K., Roy, D. B., Fox, R., & Thomas, C. D. (2012). Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. *Science*, 336(6084), 1028–1030. <https://doi.org/10.1126/science.1216980>
- Pearson, R. G., Dawson, T. P., Berry, P. M., & Harrison, P. A. (2002). SPECIES: A spatial evaluation of climate impact on the envelope of species. *Ecological Modelling*, 154(3), 289–300. [https://doi.org/10.1016/S0304-3800\(02\)00056-X](https://doi.org/10.1016/S0304-3800(02)00056-X)
- Petchey, O. L., McPhearson, P. T., Casey, T. M., & Morin, P. J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature*, 402(6757), 69–72. <https://doi.org/10.1038/47023>
- Peters, R. H. (1983). *The ecological implications of body size*. Cambridge University Press.
- Pounds, J. A., Fogden, M. P. L., & Campbell, J. H. (1999). Biological response to climate change on a tropical mountain. *Nature*, 398, 611–615. <https://doi.org/10.1038/19297>
- Rall, B. C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., & Petchey, O. L. (2012). Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1605), 2923–2934. <https://doi.org/10.1098/rstb.2012.0242>
- Rall, B. Ö. C., Vucic-Pestic, O., Ehnes, R. B., Emmerson, M., & Brose, U. (2010). Temperature, predator-prey interaction strength and population stability. *Global Change Biology*, 16(8), 2145–2157. <https://doi.org/10.1111/j.1365-2486.2009.02124.x>
- Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, 1(8), 401–406. <https://doi.org/10.1038/nclimate1259>
- Singer, M. C., & Parnesan, C. (2018). Lethal trap created by adaptive evolutionary response to an exotic resource. *Nature*, 557(7704), 238–241. <https://doi.org/10.1038/s41586-018-0074-6>
- Smith, T. B., Bruford, M. W., & Wayne, R. K. (1993). The preservation of process: The missing element of conservation programs the preservation of process: The missing element conservation programs. *Biodiversity Letters*, 1(1). Retrieved from <http://www.jstor.org/stable/2999740>
- Stockwell, C. A., Hendry, A. P., & Kinnison, M. T. (2003). Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution*, 18(2), 94–101. [https://doi.org/10.1016/S0169-5347\(02\)00044-7](https://doi.org/10.1016/S0169-5347(02)00044-7)
- Suding, K. N., & Hobbs, R. J. (2009). Threshold models in restoration and conservation: A developing framework. *Trends in Ecology & Evolution*, 24(5), 271–279. <https://doi.org/10.1016/j.tree.2008.11.012>
- Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11(12), 1351–1363. <https://doi.org/10.1111/j.1461-0248.2008.01250.x>
- Uzsko, W., Diehl, S., Englund, G., & Amarasekare, P. (2017). Effects of warming on predator-prey interactions – A resource-based approach and a theoretical synthesis. *Ecology Letters*, 20(4), 513–523. <https://doi.org/10.1111/ele.12755>
- Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution*, 3(6), 879–885. <https://doi.org/10.1038/s41559-019-0880-8>
- Vucic-Pestic, O., Rall, B. C., Kalinkat, G., & Brose, U. (2010). Allometric functional response model: Body masses constrain interaction strengths. *Journal of Animal Ecology*, 79(1), 249–256. <https://doi.org/10.1111/j.1365-2656.2009.01622.x>
- Weinbach, A., Allhoff, K., Thebault, E., Massol, F., & Loeuille, N. (2017). Selective effects of temperature on body mass depend on trophic interactions and network position. *BioRxiv*, 233742. <https://doi.org/10.1101/233742>
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., & Warren, P. H. (2005). Body size in ecological networks. *Trends in Ecology and Evolution*, <https://doi.org/10.1016/j.tree.2005.04.005>
- Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, 96(4), 1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>
- Yamamichi, M., & Miner, B. E. (2015). Indirect evolutionary rescue: Prey adapts, predator avoids extinction. *Evolutionary Applications*, 8(8), 787–795. <https://doi.org/10.1111/eva.12295>
- Yodzis, P., & Innes, S. (1992). Body size and consumer-resource dynamics. *The American Naturalist*, 139(6), 1151–1175. <https://doi.org/10.1086/285380>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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1 **Supporting Information**

2

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4 scenarios

5

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7 analysis summary (A. Trait diversity, B. Species diversity)

8

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10 mass

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16 **Appendix S1:** Eco-evolutionary dynamics of the Consumer-Resource module

17

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21 **Appendix S3:** Simulation Code

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74 **Table S1:** Warming impacts the CR evolutionary dynamics: the 4 possible
 75 scenarios

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 77

Scenario	CR body mass ratio	Consumer body mass	Mathematical significance	Qualitative outcomes (evolution of α)
A	Small	Any	$L \ll L^c(M_1)$	<ul style="list-style-type: none"> One singularity: a CSS that increases with temperature (higher resource consumption)
B	Intermediate	Any	$L < L^c(M_1)$ $L \approx L^c(M_1)$	<ul style="list-style-type: none"> One singularity whose value increases with warming (higher resource consumption) Warming switches the selection regime from disruptive (BP) to stabilizing (CSS) (loss of polymorphism)
C	Big	Small	$L > L^c(M_1)$	<ul style="list-style-type: none"> Three singularities (CSS, Repellor and BP) for low temperatures and only one (CSS) for high temperatures (evolutionary hysteresis)
D		Big		<ul style="list-style-type: none"> One singularity: a CSS that increases with warming (increased resource consumption)

78 **Table S1:** The four possible scenarios with their biological and mathematical significances. $L^c(m_1)$ is the value
 79 of L , determined numerically and m_1 -dependent, at which important features of equation (H) change, leading to
 80 different evolutionary dynamics.

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 82
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86 **Table S2: Diversity persistence in the complex multitrophic networks: statistical**
 87 **analysis summary for trait diversity (A) and species diversity (B)**

88
 89

Mutation rate	Direct effect of evolution		Effect of warming intensity		Interaction term		Adjusted R ²
	δ_2	Effect size	β	Effect size	γ_2	Effect size	
$\mu = 10^{-1}$	0.051	32.3%	-0.029***	11.5%	0.031***	15.6%	58.6 %
$\mu = 10^{-2}$	0.060*	28.4%	-0.024***	30.3%	0.017***	9.5%	67.6%
$\mu = 10^{-3}$	0.062**	39.8%	-0.019***	18.5%	0.017***	13.1%	70.7%

90 **Table S2 (A): Trait diversity persistence.** Outputs of the 3 ANCOVAs. Index 1 corresponds to the level « No
 91 evolution », which serves as a reference ($\delta_1 = \mathbf{0}, \gamma_1 = \mathbf{0}$), while index 2 corresponds to the level « Evolution »
 92 (δ_2, γ_2). All fitted ANCOVAs have a p-value below $2 \cdot 10^{-16}$. Significance code: $<10^{-3}$ '***', $<10^{-2}$ '**', <0.05 '*'

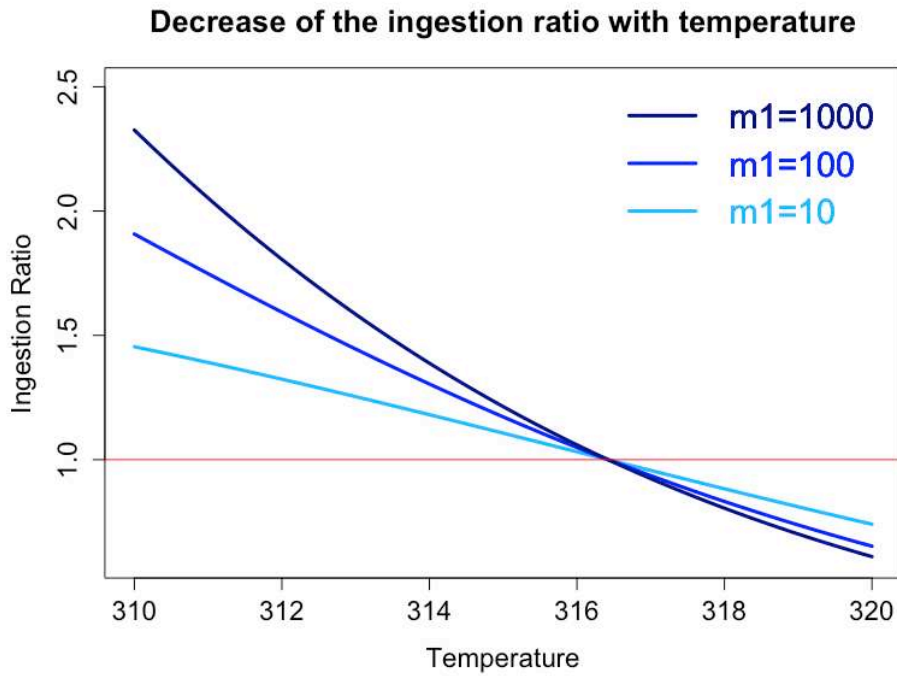
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Mutation rate	Direct effect of evolution		Effect of warming intensity		Interaction term		Adjusted R ²
	δ_2	Effect size	β	Effect size	γ_2	Effect size	
$\mu = 10^{-1}$	-0.026	27.1%	-0.037***	27.9%	0.036***	24.8%	79.4%
$\mu = 10^{-2}$	0.126**	33.4%	-0.035***	22.6%	0.027***	8.9%	64.1%
$\mu = 10^{-3}$	0.196***	37.3%	-0.029***	12.2%	0.023***	5.8%	54.4%

96 **Table S2 (B): Species diversity persistence.** Outputs of the 3 ANCOVAs. Index 1 corresponds to the level « No
 97 evolution », which serves as a reference ($\delta_1 = \mathbf{0}, \gamma_1 = \mathbf{0}$), while index 2 corresponds to the level « Evolution »
 98 (δ_2, γ_2). All fitted ANCOVAs have a p-value below $2 \cdot 10^{-16}$. Significance code: $<10^{-3}$ '***', $<10^{-2}$ '**', <0.05 '*'

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106 **Fig. S1:** The decrease of the ingestion ratio with temperature depends on body
107 mass

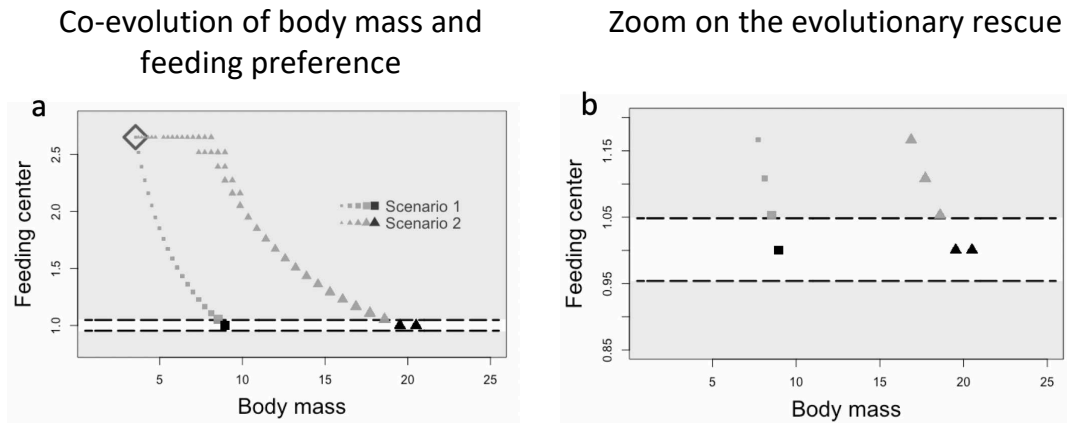


108
109 **Figure S1:** The ingestion ratio (equation (11)) decreases with temperature. Values above one (resp. below) indicate
110 a net energy gain (resp. loss). The bigger the consumer body mass m_1 , the stronger the decrease. Note that the
111 critical temperature $T_c(f_1)$ above which a consumer with feeding preference f_1 cannot survive is independent of
112 its body mass m_1 . Here, we chose $f_1 = m_0 = 1$. All other parameters as in **Table 1**.

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125 **Fig. S2:** Consumer Resource module: the two-trait co-evolution scenario

126



127 **Figure S2: a.** Co-evolution of body mass and feeding preference under two scenarios. **Scenario 1:** body mass and
128 feeding preference evolve at rate $\mu = 10^{-2}$ (squares). **Scenario 2:** body mass evolves at $\mu = 10^{-2}$ while feeding
129 preference evolves at $\mu = 10^{-3}$ (triangles). Unfilled grey diamond: initial conditions. The simulations started at
130 280 K and the increase in symbol size indicates the direction of time. The biggest grey symbols thus correspond
131 to the long-term selected phenotypes at 280 K. Once such a stable evolutionary state is reached, a warming to
132 316.4 K (almost maximal sustainable temperature) occurs. The consumer body mass and feeding preference, which
133 were within the non-viability area at 316.4 K (light grey), evolve in response to warming. The newly selected
134 phenotypes (black symbols) are within the viability area at 316.4 K (white), which indicates an evolutionary rescue
135 process. **b.** Zoom (y-axis) to see the evolutionary rescue consecutive to warming. Note that the selected phenotypes
136 at 280 K were one mutation away from being viable at 316.4 K. Parameter values are in **table 1**.

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150 **Appendix S1: Eco-evolutionary dynamics of the**
 151 **Consumer-Resource module**

152

153 This document is dedicated to present the analytical work supporting the results
 154 presented in the main document on the CR module. The main equations (main document) are
 155 indexed as in the main document while new important ones are indexed by a letter, in order to
 156 avoid confusion. The same applies for figures or tables. This document also serves to present
 157 some complementary side results we feel improve the understanding of our work.

158

159 **A. Ecological dynamics:**

160

161 Population dynamics are given by the following equations:

162

$$\frac{dB_0}{dt} = r \left(1 - \frac{B_0}{K}\right) B_0 - a_{10} B_1 B_0 \quad (9)$$

$$\frac{dB_1}{dt} = e a_{10} B_0 B_1 - (a_{11}(1 - e) + c_{11}) B_1^2 - d_1 B_1 \quad (10)$$

163

164 **1. Ecological equilibria:**

165

166 Ecological equilibria are given by resolving $\frac{dB_0}{dt} = 0$ and $\frac{dB_1}{dt} = 0$ which leads to 4 possible
 167 solutions:

168

$$\{B_0^* = 0 ; B_1^* = 0\}$$

169

$$\{B_0^* = K ; B_1^* = 0\}$$

170

$$\left\{ B_0^* = 0 ; B_1^* = \frac{-d_1}{(a_{11}(1 - e) + c_{11})} \right\}$$

171

$$\left\{ B_0^* = K \left(1 - \frac{r}{K} \frac{a_{10} \left(e a_{10} - \frac{d_1}{K} \right)}{(a_{11}(1 - e) + c_0) + e a_{10}^2} \right) ; B_1^* = \frac{r \left(e a_{10} - \frac{d_1}{K} \right)}{\frac{r}{K} (a_{11}(1 - e) + c_0) + e a_{10}^2} \right\}$$

172

173 The third equilibrium is not reachable because $B_1^* < 0$. The fourth equilibrium is called the
 174 coexistence equilibrium.

175 2. Ingestion ratio and coexistence:

176

177 The coexistence equilibrium is possible when $B_0^* \geq 0$ and $B_1^* \geq 0$.

178 First, we demonstrate: $\forall T \geq 0, B_0^* \geq 0$ at the coexistence equilibrium.

179

180
$$B_0^* > 0 \Leftrightarrow \frac{r}{K}(a_{11}(1-e) + c_{11}) + ea_{10}^2 - a_{10}\left(ea_{10} - \frac{d_1}{K}\right) > 0$$

181
$$\Leftrightarrow \frac{r}{K}(a_{11}(1-e) + c_{11}) + a_{10}\frac{d_1}{K} > 0$$

182

183 The last relation is always true which ends the proof.

184

185 The flux of biomass providing energy from resource to consumer ($ea_{10}B_0^*(T)$) divided by the
186 flux of biomass lost due to metabolic expenditures ($d_1(T)$) corresponds to the ingestion ratio

187 IR .

188

189
$$IR \stackrel{\text{def}}{=} \frac{\text{Ingestion}}{\text{Metabolism}} \stackrel{\text{def}}{=} \frac{ea_{10}B_0^*(T)}{d_1(T)}$$

190 But

191
$$B_0^* = K \left(1 - \frac{a_{10}\left(ea_{10} - \frac{d_1}{K}\right)}{\frac{r}{K}(a_{11}(1-e) + c_0) + ea_{10}^2} \right) = \frac{r(a_{11}(1-e) + c_0) + a_{10}d_1}{\frac{r}{K}(a_{11}(1-e) + c_0) + ea_{10}^2}$$

192 So that:

193

$$IR = \frac{\left[a_{10} + \frac{r}{d_1}(a_{11}(1-e) + c_0) \right] ea_{10}}{\frac{r}{K}(a_{11}(1-e) + c_0) + ea_{10}^2} \quad (11)$$

194

195 Now, we show that the consumer population is viable if and only if its ingestion rate is above
196 one.

197

198 We have:

199
$$0 = \frac{dB_1}{dt} = ea_{10}B_0^*B_1^* - d_1B_1^* - (a_{11}(1-e) + c_{11})B_1^{*2}$$

200 Which implies:

201 $ea_{10}B_0^*B_1^* - d_1B_1^* > 0$

202 Now:

203 $B_1^* > 0 \Leftrightarrow ea_{10}B_0^*(T) > d_1(T) \Leftrightarrow \text{Ingestion} > \text{Metabolism} \Leftrightarrow IR > 1$

204

205 **3. Critical and limit temperature:**

206 We now prove that the ingestion ratio reaches a value of one at a critical temperature above
 207 which, according to the previous section, no consumer population can survive. For
 208 convenience, we introduce the following notations:

209

210 We define M_0, M_1, F_1 by $M_1 \stackrel{\text{def}}{=} \log_{10}(m_1)$ $F_1 \stackrel{\text{def}}{=} \log_{10}(f_1)$

211 $IR \geq 1 \Leftrightarrow B_1^* \geq 0 \Leftrightarrow ea_{10} \geq \frac{d_1}{K} \Leftrightarrow \frac{e}{\sqrt{2\pi}s} \exp\left(-\frac{(F_1 - M_0)^2}{2s^2}\right) \geq \frac{d_0}{K_0} \exp\left(\frac{-2E(T_0 - T)}{kTT_0}\right)$

212 $\Leftrightarrow \frac{(F_1 - M_0)^2}{2s^2} \leq \ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0}$

213

214 $\Leftrightarrow T \leq \frac{2E}{\frac{2E}{T_0} + k \left[\frac{(F_1 - M_0)^2}{2s^2} + \ln\left(\frac{\sqrt{2\pi}sd_0}{eK_0}\right) \right]} \stackrel{\text{def}}{=} T_c(F_1)$

215

216 $T_c(F_1)$ is maximal when its denominator is minimal, that is to say when $F_1 = M_0$. Note that
 217 this is the parametrization used in the case of body mass evolution, feeding center being fixed.

218 It leads to equation (12):

219

$$T_c(f_1) \leq T_{lim} \stackrel{\text{def}}{=} \frac{2E}{\frac{2E}{T_0} + k \left(\ln\left(\frac{\sqrt{2\pi}sd_0}{eK_0}\right) \right)} \quad (12)$$

220

221 With the standard parameter values presented in table 1, $T_{lim} \approx 316.4$ K.

222

223 In the case of feeding preference evolution, the convenient way to express the condition for
 224 coexistence ($B_1^* \geq 0$) is the following (used for the viability areas in the E3 diagrams **Fig. 3**).

225

226
$$\frac{(F_1 - M_0)^2}{2s^2} \leq \ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0}$$

227

228
$$\Leftrightarrow \left(\begin{array}{c} \ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0} \geq 0 \\ -\sqrt{2s^2 \left[\ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0} \right]} \leq F_1 - M_0 \leq \sqrt{2s^2 \left[\ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0} \right]} \end{array} \right)$$

229

$$\left(\begin{array}{c} T \leq \frac{2E}{\frac{2E}{T_0} + k \left(\ln\left(\frac{\sqrt{2\pi}sd_0}{eK_0}\right) \right)} \stackrel{\text{def}}{=} T_{lim} \\ -\sqrt{2s^2 \left[\ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0} \right]} \leq F_1 - M_0 \leq \sqrt{2s^2 \left[\ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0} \right]} \end{array} \right) \quad (A)$$

230

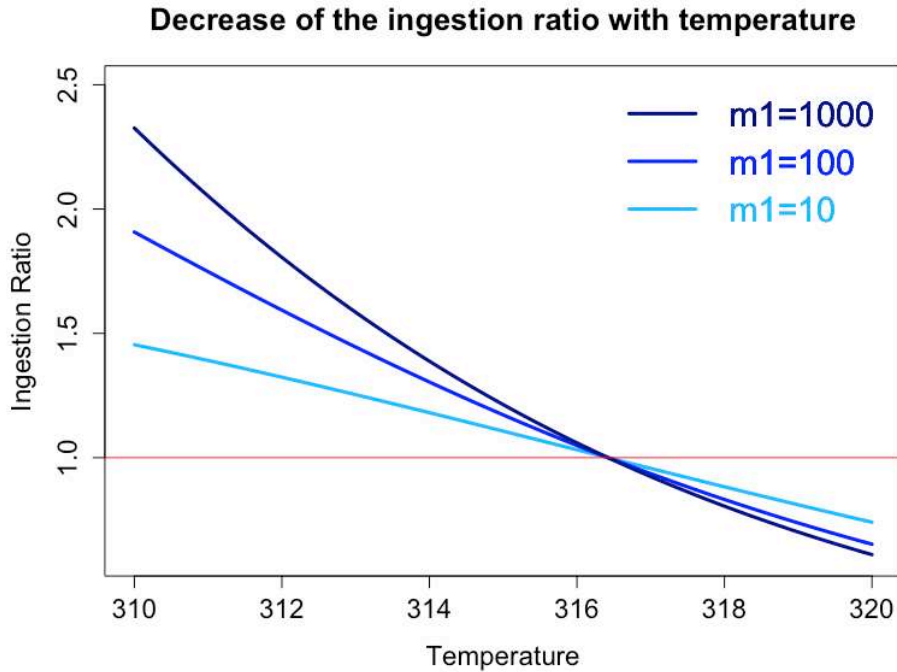
231 4. Ingestion ratio and body mass:

232 We have:

$$IR = \frac{\left[a_{10} + \frac{r}{d_1} (a_{11}(1 - e) + c_0) \right] ea_{10}}{\frac{r}{K} (a_{11}(1 - e) + c_0) + ea_{10}^2} \quad (11)$$

233

234 The only remaining dependence on temperature is due to the relative productivity $\frac{r}{K}$ of the pool
 235 of plants forming the basal resource. It increases exponentially with temperature ($\frac{r}{K} =$
 236 $\frac{r_0}{K_0} \exp\left(\frac{-2E(T_0 - T)}{kTT_0}\right)$) and explains that the ingestion ratio decreases with temperature. It is
 237 interesting to investigate this relationship for different consumer body masses m_1 as bigger
 238 body masses are expected as one goes up the trophic network. **Fig. S1** shows that the ingestion
 239 ratio exhibits a sharper decrease with temperature as the consumer body mass increases.



240

241 **Figure S1:** The ingestion ratio (equation (11)) decreases with temperature. Values above one (resp. below) indicate
 242 a net energy gain (resp. loss). The bigger the consumer body mass m_1 , the stronger the decrease. Note that the
 243 critical temperature $T_c(f_1)$ above which a consumer with feeding preference f_1 cannot survive is independent of
 244 its body mass m_1 . Here, we chose $f_1 = m_0 = 1$. All other parameters as in **Table 1**.

245

246 This result indicates that upper trophic levels, that are associated with bigger sizes (**Fig. 2c&f**),
 247 are likely to suffer more from warming than lower trophic levels. We would like to point out
 248 that the ranking of ingestion ratios with body masses observed in the CR module
 249 ($IR(m_1 = 1000) > IR(m_1 = 100) > IR(m_1 = 10)$) do not contradict the fact that upper
 250 trophic levels are likely to be initially closer to their critical ingestion ratio. Indeed, the
 251 argument relies on the trophic distance from the basal resource, each trophic interaction being
 252 associated with losses ($e < 1$). Here (**Fig. S1**), the three consumer populations differ in body
 253 mass but have the same trophic level (= 1).

254

255 **B. Evolutionary dynamics:**

256

257 1. The adaptive dynamics framework

258 In the case of body mass (m_1) evolution, the invasion fitness $w(m_1^{mut}, m_1^{res})$ of a rare
 259 mutant corresponds to its relative growth rate in the resident population:

$$w(m_1^{mut}, m_1^{res}) = \left[\frac{1}{B_1^{mut}} \frac{dB_1^{mut}}{dt} \right]_{B_0^*, B_1^*, B_1^{mut} \ll B_1^*} \quad (\text{B})$$

260 The sequence of trait substitutions describes the evolutionary dynamics of the system and can
 261 be approximated by the canonical equation (Dieckmann & Law, 1996) that links the trait
 262 dynamics to the selection gradient:

$$\frac{dm_1}{dt} = CN_1^* \mu \sigma^2 \underbrace{\left[\frac{\partial w(m_1^{mut}, m_1^{res})}{\partial m_1^{mut}} \right]_{m_1^{mut} = m_1^{res} = m_1}}_{\text{selection gradient}} \quad (\text{C})$$

263 where C, N_1^*, μ, σ are respectively a homogenizing constant, the equilibrium resident population
 264 density, the mutation rate and the amplitude of mutations. The zeros of equation (C) are
 265 evolutionary singularities, m_1^* , satisfying:

$$\left[\frac{\partial w(m_1^{mut}, m_1^{res})}{\partial m_1^{mut}} \right]_{m_1^{mut} = m_1^{res} = m_1} = 0 \quad (\text{D})$$

266

267 The convergence and invasibility properties of an evolutionary singularity are determined via
 268 the second derivatives of the invasion fitness function as detailed in section B.2.d.

269

270 2. How does the selected body mass depend on temperature?

271 Reminder: we define M_0, M_1, F_1 by $M_0 \stackrel{\text{def}}{=} \log_{10}(m_1)$ $F_1 \stackrel{\text{def}}{=} \log_{10}(f_1)$

272 a. Fitness of invasion

273 Here, we expose the whole approach to determine the invasion fitness function in the adaptive
 274 dynamics' framework:

275 We consider a rare mutant 1' appearing in the resident population 1, given the population
 276 dynamics equations, we have:

277

$$278 \quad \frac{1}{B_{1'}} \frac{dB_{1'}}{dt} = \underbrace{ea_{1'0}B_0}_{\text{ressource}} - \overbrace{(c_{1'1'}B_{1'} + c_{1'1}B_1)}^{\text{competition}} + \underbrace{(ea_{1'1}B_1 - a_{11'}B_1 - (1-e)a_{1'1'}B_{1'})}_{\text{consumption interaction between 1 and 1'}} - d_{1'}$$

279

280

281 Given 1 and 1' have the same feeding preference, we have $c_{1'1'} = c_{1'1} = c_0$ and $a_{11'} = a_{1'1}$.

282 Also, $B_{1'} \ll B_1$ (rare mutant). Hence: $c_{1'1'}B_{1'} \ll c_{1'1}B_1$ and $(1-e)a_{1'1'}B_{1'} \ll a_{11'}B_1$

283 All in all, we deduce:

$$284 \quad \frac{1}{B_{1'}} \frac{dB_{1'}}{dt} = ea_{1'0}B_0 - c_0B_1 - a_{11'}B_1 + ea_{1'1}B_1 - d_{1'}$$

285 Which leads to:

286

$$287 \quad w(M_{1'}, M_1) \stackrel{\text{def}}{=} \left[\frac{1}{B_{1'}} \frac{dB_{1'}}{dt} \right]_{\substack{B_{1'} \ll B_1 \\ B_0^*, B_1^*}} = ea_{1'0}B_0^* - c_0B_1^* - a_{11'}B_1^* + ea_{1'1}B_1^* - d_{1'}$$

288

289 b. Evolutionary singularities

290 We first need to determine the derivative of the fitness invasion function with respect to the

291 mutant body mass (first variable):

292

$$293 \quad \frac{\partial w(M_{1'}, M_1)}{\partial M_{1'}} = eB_0^* \frac{\partial a_{1'0}}{\partial M_{1'}} - \underbrace{\frac{\partial c_0 B_1^*}{\partial M_{1'}}}_0 - B_1^* \frac{\partial a_{11'}}{\partial M_{1'}} + eB_1^* \frac{\partial a_{1'1}}{\partial M_{1'}} - \frac{\partial d_{1'}}{\partial M_{1'}}$$

$$294 \quad = -\frac{\ln(10)}{4} ea_{1'0}B_0^* - \frac{(F_1 - M_{1'})}{S^2} a_{11'} - \frac{\ln(10)}{4} ea_{1'1}B_1^* - \frac{\ln(10)}{4} d_{1'}$$

295

296 Thus:

$$297 \quad \left[\frac{\partial w(M_{1'}, M_1)}{\partial M_{1'}} \right]_{M_{1'}=M_1} = -\frac{\ln(10)}{4} (ea_{10}B_0^* + ea_{11}B_1^* - d_1) - \frac{(F_1 - M_1)}{S^2} a_{11}B_1^*$$

298

299 At ecological equilibrium $\frac{dB_1}{dt} = 0$ gives $ea_{10}B_0^* + ea_{11}B_1^* - d_1 = c_0B_1^* + a_{11}B_1^*$ and hence:

300

$$301 \quad \left[\frac{\partial w(M_{1'}, M_1)}{\partial M_{1'}} \right]_{M_{1'}=M_1} = B_1^* \left(-\frac{\ln(10)}{4} (c_0 + a_{11}) - \frac{(F_1 - M_1)}{S^2} a_{11} \right)$$

302

303 Evolutionary singularities occur when the selection gradient vanishes:

304

$$\begin{aligned} 305 \quad \left[\frac{\partial w(M_{1'}, M_1)}{\partial M_{1'}} \right]_{M_{1'}=M_1} &= 0 \Leftrightarrow -\frac{\ln(10)}{4} (c_0 + a_{11}) - \frac{(F_1 - M_1^*)}{s^2} a_{11} = 0 \\ 306 \quad &\Leftrightarrow c_0 + a_{11} \left(1 - \frac{4(M_1 - F_1)}{s^2 \ln(10)} \right) = 0 \end{aligned}$$

307 Noting explicitly the dependence of a_{11} on M_1 , we deduce evolutionary singularities M_1^* verify:

308

$$c_0 + a_{11}(M_1^*) * \left(1 - \frac{4(M_1^* - F_1)}{s^2 \ln(10)} \right) = 0 \quad (E)$$

309

310 Temperature does not influence any parameter of equation (E) indicating that warming has no
311 effect on the evolutionary dynamics of body mass here.

312

313 3. How does the selected feeding preference depend on temperature?

314 a. Fitness of invasion

315

316 Here, the evolving trait is f_1 or equivalently F_1 . As we did before, we consider the appearance
317 of a new morph 1' issued from 1 by a random small mutation.

318 Given our model, its biomass follows the equation (note that $d_1 = d_{1'}$):

319

$$320 \quad \frac{1}{B_{1'}} \frac{dB_{1'}}{dt} = ea_{1'0}B_0 + ea_{1'1}B_1 - (1 - e)a_{1'1'}B_{1'} - a_{1'1}B_1 - c_{1'1'}B_{1'} - c_{1'1}B_1 - d_1$$

321

322 Using $B_{1'} \ll B_1$ and $F_1 \approx F_{1'}$ (small mutation hypothesis), we find:

323

$$324 \quad \frac{1}{B_{1'}} \frac{dB_{1'}}{dt} = ea_{1'0}B_0 + (ea_{1'1} - a_{1'1'})B_1 - c_{1'1}B_1 - d_1$$

325

326 When considered at ecological equilibrium, the previous expression gives the invasion fitness
327 function:

328

$$329 \quad w(F_{1'}, F_1) \stackrel{\text{def}}{=} \left[\frac{1}{B_{1'}} \frac{dB_{1'}}{dt} \right]_{B_{1'} \ll B_1} = ea_{1'0}B_0^* + (ea_{1'1} - a_{11'})B_1^* - c_{11'}B_1^* - d_1$$

330

331 *b. Evolutionary singularities:*

332 When the selection gradient vanishes:

333

$$334 \quad \left[\frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1} = 0 \Leftrightarrow \left[eB_0^* \frac{\partial a_{1'0}}{\partial F_{1'}} + eB_1^* \frac{\partial a_{1'1}}{\partial F_{1'}} - B_1^* \frac{\partial a_{11'}}{\partial F_{1'}} - B_1^* \frac{\partial c_{11'}}{\partial F_{1'}} - \frac{\partial d_1}{\partial F_{1'}} \right]_{F_{1'}=F_1} = 0$$

$$335 \quad \Leftrightarrow \frac{-eB_0^*}{s^2} a_{10}(F_1 - M_0) - \frac{eB_1^*}{s^2} a_{11}(F_1 - M_1) + \frac{B_1^*}{2s^2} \underbrace{(F_1 - F_1)}_0 c_0 = 0$$

336

337

338 So that evolutionary singularities F_1^* satisfy:

339

$$(M_1 - F_1^*)a_{11}B_1^* - (F_1^* - M_0)a_{10}B_0^* = 0 \quad (\text{F})$$

340

341

342 *Proof of the existence of at least one singularity:*

343

344 Here, we prove that equation (F) has at least one solution and that all solutions F_1^* verify: $M_0 <$

345 $F_1^* < M_1$. For convenience we define:

$$346 \quad \alpha \text{ such as : } F_1 = \alpha M_0 + (1 - \alpha)M_1 \quad \text{ie: } \alpha \stackrel{\text{def}}{=} \frac{M_1 - F_1}{M_1 - M_0}$$

347

$$348 \quad L \stackrel{\text{def}}{=} \frac{M_1 - M_0}{s}$$

349 Equation (F) can be rewritten with these new notations, by noting that $M_1 - M_0 > 0$

350 (hypothesis of the model):

$$\alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right) B_1^*(\alpha, T, M_1, L) - (1 - \alpha) \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right) B_0^*(\alpha, T, M_1, L) = 0 \quad (\text{G})$$

351 We define:

$$352 \quad z(\alpha, T, M_1, L) \stackrel{\text{def}}{=} \alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right) B_1^*(\alpha, T, M_1, L) - (1 - \alpha) \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right) B_0^*(\alpha, T, M_1, L)$$

353

354 We have, $z(0, T, M_1, L) < 0, z(1, T, M_1, L) > 0$ and, given T, M_1, L $z_\alpha : \alpha \rightarrow z(\alpha, T, M_1, L)$
 355 is a continuous function. So, by the Intermediate Value Theorem, there exists α^* such that
 356 $z_\alpha(\alpha^*) = z(\alpha, T, M_1, L) = 0$. This is equivalent to say that equation (D) or (16) has at least one
 357 solution. Moreover, under coexistence (i.e. $B_0^* > 0$ and $B_1^* > 0$), if $\alpha \leq$
 358 0 then $z(\alpha, T, M_1, L) < 0$ and if $\alpha \geq 1$ then $z(\alpha, T, M_1, L) > 0$ so that we have necessarily
 359 $0 < \alpha^* < 1$. This is equivalent to $M_0 < F_1^* < M_1$. This ends the proof.

360

361 *c. Effect of warming on feeding preference evolution and emergence of 4*

362 *scenarios:*

363

364 Since $B_0^*(T)$ and $B_1^*(T)$ do depend on the temperature, equation (F) indicates temperature
 365 has an impact on the singularities and consequently on evolutionary dynamics. In order to go
 366 further, we rewrite (F) replacing B_0^* and B_1^* by their explicit expressions and isolating the
 367 temperature from the evolutionary singularity:

368 equation (F) \Leftrightarrow equation (G) $\Leftrightarrow \frac{B_1^*(\alpha, T, M_1, L)}{B_0^*(\alpha, T, M_1, L)} = \frac{(1 - \alpha) \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right)}{\alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right)}$

369 $\Leftrightarrow \frac{e a_{10} - \frac{d_\infty 10^{-\frac{M_1}{4}}}{K_\infty} \exp\left(\frac{-2E}{kT}\right)}{a_{11}(1 - e) + c_0 + \frac{d_\infty 10^{-\frac{M_1}{4}}}{R_\infty} a_{10}} = \frac{(1 - \alpha) \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right)}{\alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right)}$

370 $\Leftrightarrow e \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right)$

371 $-\frac{\sqrt{2\pi} s d_\infty}{K_\infty} \exp\left(\frac{-2E}{kT}\right)$

372 $= \left[(1 - e) \exp\left(\frac{-\alpha^2 L^2}{2}\right) + \sqrt{2\pi} s c_0 10^{\frac{M_1}{4}} \right]$

373 $+\frac{d_\infty 10^{-\frac{M_1}{4}}}{R_\infty} \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right) \left[\frac{(1 - \alpha) \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right)}{\alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right)} \right]$

374

$$\begin{aligned}
375 \quad & \Leftrightarrow e \exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right) - \frac{\sqrt{2\pi} s d_\infty}{K_\infty} \exp\left(\frac{-2E}{kT}\right) \\
376 \quad & = (1-e) \frac{(1-\alpha)}{\alpha} \exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right) + \sqrt{2\pi} s c_0 10^{\frac{M_1}{4}} \frac{(1-\alpha)}{\alpha} \exp\left(\frac{-(1-2\alpha)L^2}{2}\right) \\
377 \quad & + \frac{(1-\alpha) d_\infty 10^{\frac{-M_1}{4}}}{R_\infty} \exp\left(\frac{-(2(1-\alpha)^2 - \alpha^2)L^2}{2}\right)
\end{aligned}$$

378

379 We define $C(M_1) = \sqrt{2\pi} s c_0 10^{\frac{M_1}{4}}$ and have the equivalence with:

$$\begin{aligned}
380 \quad & \frac{\sqrt{2\pi} s d_\infty}{K_\infty} \exp\left(\frac{-2E}{kT}\right) \\
381 \quad & = \frac{-1}{\alpha} \left[(1-\alpha) C(M_1) \exp\left(\frac{-(1-2\alpha)L^2}{2}\right) \right. \\
382 \quad & \left. + (1-\alpha) \frac{d_\infty 10^{\frac{-M_1}{4}}}{R_\infty} \exp\left(\frac{-(2(1-\alpha)^2 - \alpha^2)L^2}{2}\right) \right. \\
383 \quad & \left. + \left[(-\alpha e + (1-e)(1-\alpha)) \exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right) \right] \right]
\end{aligned}$$

384

$$\begin{aligned}
385 \quad & \Leftrightarrow \frac{\sqrt{2\pi} s d_\infty}{K_\infty} \exp\left(\frac{-2E}{kT}\right) \\
386 \quad & = \frac{-1}{\alpha} \left[(1-\alpha) C(M_1) \exp\left(\frac{-(1-2\alpha)L^2}{2}\right) + (1-e-\alpha) \exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right) + (1 \right. \\
387 \quad & \left. - \alpha) \frac{d_\infty 10^{\frac{-M_1}{4}}}{R_\infty} \exp\left(\frac{-(2(1-\alpha)^2 - \alpha^2)L^2}{2}\right) \right]
\end{aligned}$$

388

$\Leftrightarrow Q(T) = G(\alpha, M_1, L)$	(H)
--	-----

389

390 Where the functions $Q(T)$ and $G(\alpha, M_1, L)$ are defined by:

391

$$392 \quad Q(T) \stackrel{\text{def}}{=} \frac{\sqrt{2\pi} s d_\infty}{K_\infty} \exp\left(\frac{-2E}{kT}\right)$$

393

394
$$G(\alpha, M_1, L) \stackrel{\text{def}}{=} \frac{-1}{\alpha} \left[(1 - \alpha) C(M_1) \exp\left(\frac{-(1 - 2\alpha)L^2}{2}\right) + (1 - e - \alpha) \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right) + (1 - \alpha) \frac{d_\infty 10^{-\frac{M_1}{4}}}{R_\infty} \exp\left(\frac{-(2(1 - \alpha)^2 - \alpha^2)L^2}{2}\right) \right]$$

395

396

397 To investigate the effect of temperature on the evolutionary dynamics, we analyze the
 398 functions:

399

$$T \rightarrow Q(T)$$

400

$$\alpha \rightarrow G(\alpha, M_1, L)$$

401

402 Q captures the temperature component of selection while G captures the biotic components of
 403 selection that depend on the consumer feeding preference (α), body mass (M_1) and consumer
 404 to resource body mass ratio (L).

405

406 Study of Q as a function of T:

407 Q is increasing with the temperature T and has the following variation table:

408

T	0	$+\infty$
$Q(T)$	0	$\frac{\sqrt{2\pi} s d_\infty}{K_\infty}$

409

Table A: Table of variation of $Q(T)$. Note that $Q(T)$ is always positive.

410

411

412 Study of G as a function of α , M_1 and L seen as parameters:

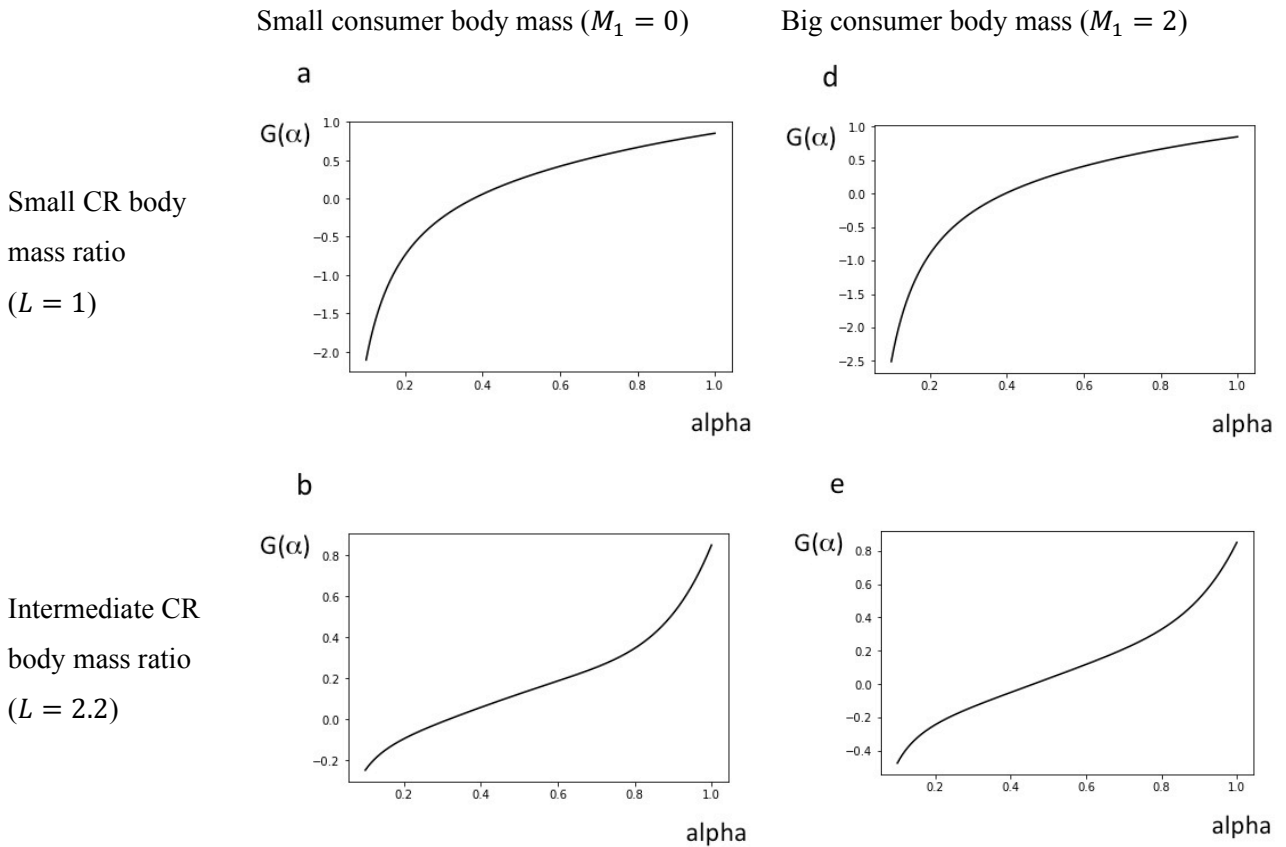
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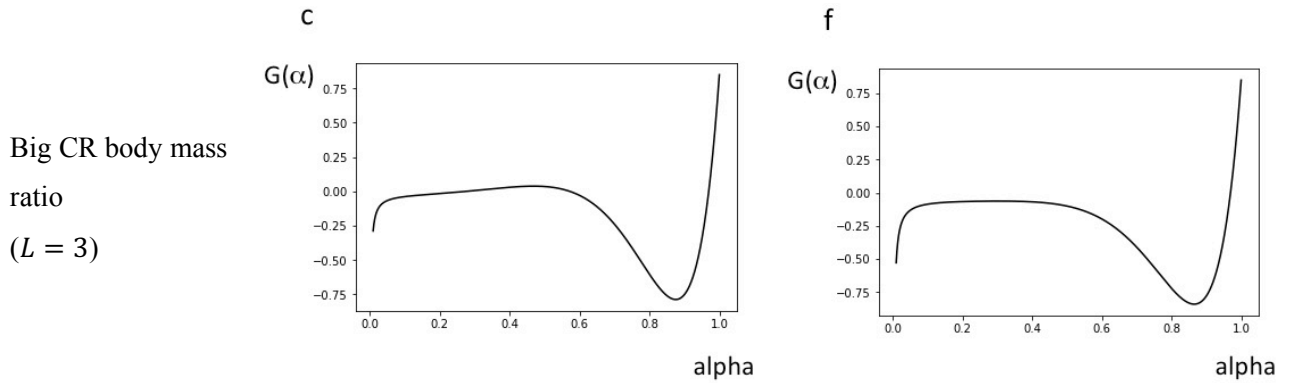
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Analytically we cannot determine all the possible behaviors of G. Thus, we used the
 software Python to investigate its variation. **Fig. B** shows the shape of G for different values
 of Consumer to Resource (CR) body mass ratios.

415

416 For small CR body mass ratios, G is increasing with α (**Fig. B a&d**). For big CR body
 417 mass ratios, G is not monotonous anymore (**Fig. B c&f**). There is a value of the parameter L ,
 418 M_1 -dependant, we refer to as $L^c(M_1)$, around which the switch of behavior from monotonous
 419 to not monotonous occurs. We can show by studying the derivative $\frac{\partial G}{\partial \alpha}$ that $\forall M_1 \in \mathbb{R}, L^c(M_1) \geq$
 420 $\sqrt{2}$. Its value is around 2.2 for the values of M_1 we investigated ($M_1 = 0$ and $M_1 = 2$). In
 421 addition, just before the change of behavior occurs, the curvature of G changes (**Fig. B b&e**)
 422 meaning its second derivative switches sign. This can have consequences on the nature of the
 423 singularities as this nature depends on the second derivatives of the fitness gradient. This led us
 424 to consider scenarios with an intermediate CR body masses ratio.
 425
 426
 427





428 **Fig. B:** Plots of $G(\alpha)$ for various values of L and M_1 .

429 From the previous analysis, we deduce the following table of variation for G :

430

Case	α	0	$\alpha_1(M_1, L)$	$\alpha_2(M_1, L)$	1
$L \leq L^*(M_1)$	$G(\alpha)$				
$L > L^*(M_1)$	$G(\alpha)$				

431 **Table B:** Variation table of function G according to the value of L

432 If the consumer to resource body mass ratio is small, G is strictly increasing with α so that there
433 is necessarily only one singularity.

434 If the ratio between consumer and resource body mass is big, the behavior of G indicates
435 the existence of up to three singularities. The coexistence condition on temperature (T_{lim})
436 implies $Q(T) < e$ so that it is impossible to have two singularities (except one degenerate case)
437 Hence, in this case, there is one or three singularities, depending on
438 $G(\alpha_1(M_1, L)), G(\alpha_2(M_1, L))$ and T .

439 Finally, while there is no qualitative difference between the case of a small consumer
440 body mass and a big one when the CR body mass ratio is either small (**Fig. A a&d**) or
441 intermediate (**Fig. A b&e**), there is one in the case it is big. In that case, when the consumer

442 body mass is small, $G(\alpha_1) > 0$ (**Fig. A c**), while when the consumer body mass is big, $G(\alpha_1) <$
 443 0 (**Fig. A f**). This is important since $Q(T)$ is always positive (see Table A). This means there
 444 can potentially be 3 singularities in the case of a small consumer body mass while there is only
 445 one in the case of a big consumer body mass.

446

447 All this analysis of equation (H) leads to distinguish 4 scenarios that differ in the impact
 448 of warming on feeding preference evolution: small CR body mass ratio (**scenario A**),
 449 intermediate CR body mass ratio (**scenario B**), big CR body mass ratio and small consumer
 450 body mass (**scenario C**), big CR body mass ratio and big consumer body mass (**scenario D**).
 451 These scenarios emerge through the technical analysis of the classical equation of adaptive
 452 dynamics (equation D) but are ecologically consistent as they differ in parameters known to be
 453 important for trophic interactions, namely body masses and body mass ratios ($M_1, L \stackrel{\text{def}}{=} \frac{M_1 - M_0}{s}$).
 454 These scenarios are presented in the following **table S1**, with their ecological meaning
 455 and evolutionary dynamics.

456

457 Warming impacts the CR evolutionary dynamics: the 4 possible scenarios

458

459

Scenario	CR body mass ratio	Consumer body mass	Mathematical significance	Qualitative outcomes (evolution of α)
A	Small	Any	$L \ll L^c(M_1)$	<ul style="list-style-type: none"> One singularity: a CSS that increases with temperature (higher resource consumption)
B	Intermediate	Any	$L < L^c(M_1)$ $L \approx L^c(M_1)$	<ul style="list-style-type: none"> One singularity whose value increases with warming (higher resource consumption) Warming switches the selection regime from disruptive (BP) to stabilizing (CSS) (loss of polymorphism)

C	Big	Small	$L > L^c(M_1)$	<ul style="list-style-type: none"> Three singularities (CSS, Repellor and BP) for low temperatures and only one (CSS) for high temperatures (evolutionary hysteresis)
D		Big		<ul style="list-style-type: none"> One singularity: a CSS that increases with warming (increased resource consumption)

460 **Table S1:** The four possible scenarios with their biological and mathematical significances. $L^c(M_1)$ is the value
461 of L , determined numerically and M_1 -dependent, around which important features of equation (H) change, leading
462 to different evolutionary dynamics.

463

464 *d. Nature of the evolutionary singularities*

465

466 Let F_1^* be the evolutionary singularity.

467 Non-invasibility corresponds mathematically to:

468

469
$$\left[\frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1=F_1^*} < 0$$

470 Moreover, we have the following expression obtained by derivation:

471

472
$$\left[\frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1} = \frac{e}{s^2} a_{10} B_0^* ((1 - \alpha)^2 L^2 - 1) + \frac{e}{s^2} a_{11} B_1^* (\alpha^2 L^2 - 1) + \frac{B_1^* c_{11}}{2s^2}$$

473 We used this expression to determine numerically trough Python software the invasibility
474 properties.

475

476 Convergence corresponds mathematically to:

477
$$\left[\frac{d}{dF_1} \left[\frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1} \right]_{F_1=F_1^*} < 0$$

478 In the case of one singularity F_1^* , it can be shown without calculation that the singularity will
479 be convergent stable.

480 *Proof:*

481 Let $F < M_0$ and $0 < \varepsilon < \frac{M_0 - F}{2}$, we have $w(F + \varepsilon, F) > 0$ because the mutant with trait ($F +$
 482 ε) has better attack rates on both the resource and the resident F and experiences less
 483 competition with the resident F than experienced by the resident ($c_{11} = c_0$).

484 Hence, $\left[\frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1, F_1=F} > 0$.

485 In the same way, we have: $\forall F > M_1, \left[\frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1, F_1=F} < 0$

486 Moreover, the function:

487 $\mathbb{R} \rightarrow \mathbb{R}$
 488 $F_1 \mapsto \left[\frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1}$

489

490 is continuous and only vanishes at $F = F_1^* \in]M_0, M_1[$.

491 Hence, $\forall F < F_1^*, \left[\frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1, F_1=F} > 0$, $\forall F > F_1^*, \left[\frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1, F_1=F} < 0$ and

492 $\left[\frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1, F_1=F_1^*} = 0$ thus: $\left[\frac{d}{dF_1} \left[\frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1} \right]_{F_1=F_1^*} < 0$

493

494 In the case of three singularities $F_1^* < F_2^* < F_3^*$, with the same kind of arguments, we know at
 495 least one singularity is convergent stable. It appears numerically that F_1^* and F_3^* are convergent
 496 stable while F_2^* is not. This analysis gives the qualitative outcomes of warming for each scenario
 497 presented in **Table S1**.

498

499

500 *e. Robustness check: variation of the conversion efficiency*

501

502 The conversion efficiency is likely to vary with the feeding mode, with overall smaller values
 503 for herbivores and larger values for carnivores, as estimated by Yodzis & Innes (1992). We
 504 propose here to investigate the effect of warming on the consumer's evolutionary dynamics
 505 (trait α) for a value of conversion efficiency that corresponds to herbivory ($e = 0.45$).

506

507 Value of T_{lim} :

508

509 The critical temperature value above which the consumer population cannot survive anymore
 510 increases with the conversion efficiency as indicated by equation (B).

511

Conversion efficiency	Limit Temperature
$e = 0.85$	$T_{lim} = 316.4$
$e = 0.45$	$T_{lim} = 312.3$

512

513 Evolutionary dynamics:

514 Fig. B (akin Fig. 3) shows the evolutionary dynamics of the trait α according to temperature
 515 for the four scenarios (Table 1).

516

517

	E³-diagrams	Comparison with Fig. 3
<p>Scenario A Small consumer to resource mass ratio ($L = 1$)</p>		<p>Similar to Scenario A presented in Fig. 3 a</p>
<p>Scenario B Intermediate consumer to resource mass ratio ($L = 2.2$)</p>		<p>Different from Scenario B presented in Fig. 3 c: <i>Branching does not occur anymore for low temperature values (Fig. 3c)</i></p>
<p>Scenario C Big consumer to resource mass ratio ($L = 2.8$) Small consumer body mass ($m_1 = 1$)</p>		<p>Different from Scenario C presented in Fig. 3 f: <i>We do not have two additional singularities (Branching Point and Repellor) for low temperature values. Consequently,</i></p>

		<i>evolutionary hysteresis is no longer possible.</i>
<p>Scenario D</p> <p>Big consumer to resource mass ratio ($L = 2.8$)</p> <p>Big consumer body mass ($m_1 = 100$)</p>		<p>Similar to Scenario D presented in Fig.3 h</p>

518 **Figure C:** E^3 diagrams corresponding respectively to scenarios A, B, C and D (**Table S1**). Grey areas are non-
519 viability regions; the curves indicate the evolutionary singularities with the type of lines indicating their nature. **a.**
520 Thin black arrows indicate the direction of evolution and the big white arrow indicates potential evolutionary
521 rescue. Note that there is potential for evolutionary rescue in all scenarios although it is illustrated only in **a.**

522 This analysis reveals that some of the results observed for a higher value of conversion
523 efficiency hold while others do not.

Consistent results	Non-consistent results
<ul style="list-style-type: none"> • All scenarios are characterized by an increasing CSS with warming: in order to cope with higher metabolic demands, the consumer population has to increase its attack rate on the basal resource. The ingestion ratio has to stay above the critical value of one. • Above a critical temperature T_{lim}, the consumer population cannot survive anymore whatever the trait α. • For temperature below T_{lim}, evolutionary rescue is always 	<ul style="list-style-type: none"> • The four scenarios do not differ in their evolutionary dynamics anymore. • Whatever the scenario and the temperature, branching is not possible any more. Consequently, we do not observe warming reducing polymorphism (scenario B) nor evolutionary hysteresis (scenario C).

possible as illustrated by the white arrow in Fig. C a .	
--	--

524

525 All in all, this robustness check confirms that evolutionary rescue is a potential mechanism by
526 which evolution can impede the consumer population extinction given the temperature stays
527 below a critical value T_{lim} . However, some of our results, such as the potential for warming to
528 dampen diversification processes (Scenario B, Fig. 3) seem to only apply for higher value of
529 conversion efficiency. This can be interpreted as additional evidence that higher trophic levels
530 are more vulnerable to warming (e.g. Binzer et al., 2012).

531

532

533 4. The co-evolution of body mass and feeding preference

534 The separation between body mass and feeding preference evolution implemented so far
535 may only be justified if one trait evolves much faster than the other (e.g. asymmetries in
536 heritabilities). In other conditions, the two traits coevolve. We simulated two co-evolutionary
537 scenarios that differ in mutation rates (10^{-2} for both traits in scenario 1 and 10^{-2} (resp. 10^{-3})
538 for body mass (resp. feeding preference) in scenario 2). Warming goes from 280 to 316.4K
539 (from 7 to 43°C, slightly below T_{lim}). Evolutionary trajectories are shown on **Fig. S2**.
540 Evolutionary rescue occurs and enables food chain persistence. Note two important results.
541 First, the two scenarios yield different evolutionary trajectories. The relative speed of evolution
542 between the two evolving traits therefore affect evolutionary dynamics, possibly constraining
543 evolutionary rescue. Second, while warming does not affect body mass when only body mass
544 is allowed to evolve (equation (E), **Fig. 3**), it does under co-evolution. Here, warming exerts a
545 selective pressure on the consumer feeding preference (see equation E) whose evolution, in
546 turn, exerts a selective pressure on the consumer body mass. Consequently, both body mass and
547 feeding preference are affected by warming (squares and triangles trajectories in **Fig. S1a**).
548 Evolutionary rescue trajectories (**Fig. S1b**) then involve the effective evolution of both traits.

549

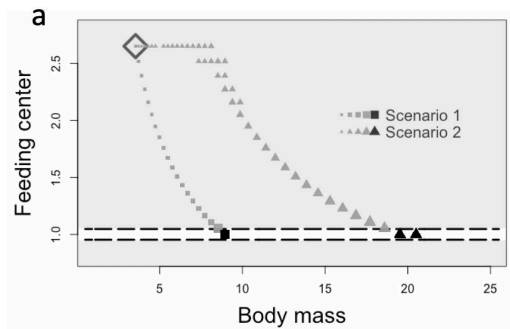
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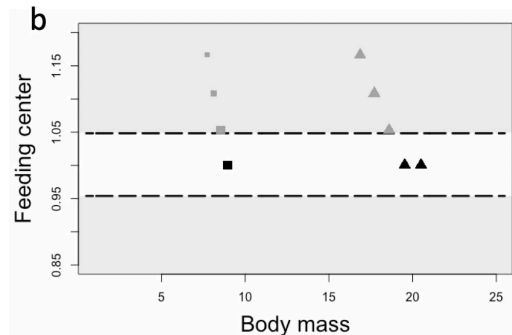
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553

Co-evolution of body mass and feeding preference



Zoom on the evolutionary rescue



554 **Figure S2:** **a.** Co-evolution of body mass and feeding preference under two scenarios. **Scenario 1:** body mass and
555 feeding preference evolve at rate $\mu = 10^{-2}$ (squares). **Scenario 2:** body mass evolves at $\mu = 10^{-2}$ while feeding
556 preference evolves at $\mu = 10^{-3}$ (triangles). Unfilled grey diamond: initial conditions. The simulations started at
557 280 K and the increase in symbol size indicates the direction of time. The biggest grey symbols thus correspond
558 to the long-term selected phenotypes at 280 K. Once such a stable evolutionary state is reached, a warming to
559 316.4 K (almost maximal sustainable temperature) occurs. The consumer body mass and feeding preference, which
560 were within the non-viability area at 316.4 K (light grey), evolve in response to warming. The newly selected
561 phenotypes (black symbols) are within the viability area at 316.4 K (white), which indicates an evolutionary rescue
562 process. **b.** Zoom (y-axis) to see the evolutionary rescue consecutive to warming. Note that the selected phenotypes
563 at 280 K were one mutation away from being viable at 316.4 K. Parameter values are in **table 1**.

564

565 This result indicates that the eco-evolutionary dynamics within the complex multi-trophic
566 network, where both traits coevolve, is likely to exhibit complex patterns not captured within
567 the CR module. This complexity arises from the indirect interactions at play. Indirect
568 interactions correspond for instance to interactions between the two evolving traits, as
569 illustrated in this section. The many indirect ecological interactions occurring at the network
570 scales also explain this additional complexity.

571

572 **References:**

573 Binzer, A., Guill, C., Brose, U., & Rall, B. C. (2012). The dynamics of food chains under
574 climate change and nutrient enrichment. *Philosophical Transactions of the Royal Society
575 B: Biological Sciences*, 367(1605), 2935–2944. doi:10.1098/rstb.2012.0230

576

577 Yodzis, P., & Innes, S. (1992). *Body Size and Consumer-Resource Dynamics*. Source: *The
578 American Naturalist* (Vol. 139).

579

Appendix S2: Complex multitrophic network model

Our community evolution model starts with a consumer feeding on the basal resource. The evolution of the consumer body mass and feeding preference follows a mutation/selection process leading to the emergence of a complex multi-trophic network of approximately 30 to 40 morphs and 4 to 5 trophic levels. A morph corresponds to an adaptive phenotype, that is to say, a couple (*body mass, feeding preference*).

A. Definition of species diversity:

At first, we only have one straightforward diversity measure: the trait diversity (i.e. the number of morphs in the trophic network at a given time). Because our model ignores genetic details and focuses on phenotypes, the definition of species is notoriously tricky. For lack of better criteria, we define species as clusters in the phenotypic space. The silhouette method (Rousseeuw, 1987) is used to determine the best number of clusters on the k-means clustering algorithm applied on the set of body masses and feeding preferences (m_i, f_i) corresponding to the trait diversity. The number of clusters gives what we define as species diversity.

We consider a set of observations and a clustering. For each observation i , we note C_i the cluster to which i is affected. For each observation i , the silhouette width $S(i)$ is a measure of how much the observation is close to its cluster C_i in comparison with other clusters. It is defined as follow:

$$S(i) = \frac{b(i) - a(i)}{\max(a(i), b(i))}$$

Where:

- $a(i)$ is the average dissimilarity between i and the other observations in C_i
- $b(i)$ is the average dissimilarity between i and the observations in the closest cluster to i , C , with $C \neq C_i$ (ie $b(i) = \min_C d(i, C)$)

$S(i)$ is between -1 and 1 and the more it is close to 1, the better is the affectation of i in the clustering. We use $\text{mean}_i S(i)$ as a measure of the performance of a given clustering. We compare the different clustering obtained by the k-means algorithm for different values of k.

612

613 We implemented the algorithm in R-software using the packages “Cluster” by Martin
614 Maechler, Peter Rousseeuw Anja Struyf, Mia Hubert, Kurt Hornik, Pierre Roudier, Juan
615 Gonzalez (2017).

616

617 **B. Simulations:**

618 **Random draw of mutant’s traits**

619 Proportionally to the population densities distribution, a parent morph is chosen
620 randomly at each mutation event. Mutant traits are then drawn from log-normal distributions
621 centered on the parent’s traits. More precisely, mutant j ’s traits $\log_{10}(m_j)$ (resp. $\log_{10}(f_j)$) are
622 randomly selected from a normal distribution of mean $\log_{10}(m_i)$ (resp. $\log_{10}(f_i)$) and variance
623 σ^2 . The value of σ (0.25) allows occasional big mutational steps: 5% of the mutations result in
624 $m_j < \frac{m_i}{3}$ or $m_j > 3m_i$.

625

626 **Transition criterion**

627 According to the scenario, each simulation follows a sequence of events.

628

629 • Scenarios NE: (1) the network is built up with a mutation rate μ ; (2) evolution stops
630 ($\mu = 0$); (3) warming occurs; (4) simulation stops.

631

632 • Scenarios E: (1) the network is built up with a mutation rate μ ; (2) warming occurs; (3)
633 simulation stops.

634

635 Each transition is triggered once the transient dynamics are over. We consider these transient
636 dynamics to be over when the ratio between the trait diversity standard deviation and mean
637 (coefficient of variation) over a time window of $2 \cdot 10^6$ mutation events is below 0.045.

638 This translates into:

639

$$640 \text{ Coefficient of Variation over time} \stackrel{\text{def}}{=} \frac{\sigma_{\text{trait diversity}}}{\varphi_{\text{trait diversity}}} < 0.045$$

641

642 Where $\sigma_{trait\ diversity}$ is the standard deviation of the trait diversity over a time window of $2 \cdot 10^6$
 643 mutation events and $\varphi_{trait\ diversity}$ is the trait diversity mean over the same time period. Such
 644 a criterion allows for at least 95% of the observed trait diversity over this time window to be
 645 within the range of $\pm 10\%$ of the observed trait diversity mean over the same period.

646

647 **Diversity before and after warming (persistence):**

648 Due to the constant mutation/extinction events, diversity is subject to stochastic
 649 variation while we would like to have exactly one measure of diversity before and after
 650 warming to assess performance. Therefore, we take the diversity before (resp. after) as the
 651 average diversity over the time window of $2 \cdot 10^6$ mutation events that satisfied the transition
 652 criterion before (resp. after) warming ($\varphi_{trait\ diversity}$). Each simulation gives a diversity
 653 maintenance measure we call “persistence”, either calculated for trait or species diversity.

654

$$655 \quad DiversityPersistence = \frac{\varphi_{diversity}(after\ warming)}{\varphi_{diversity}(before\ warming)}$$

656

657

658 **C. Statistical analysis:**

659 We want to compare the diversity response to warming within our multi-trophic network
 660 with and without evolution.

661

662 For trait and species diversity, three models were fitted ($\mu = 10^{-1}, 10^{-2}, 10^{-3}$) in order
 663 to contrast diversity persistence for different evolutionary scenarios (scenario E μ against
 664 scenario NE μ). 6 ANCOVAs were fitted with evolution as factor (two levels: “evolution”
 665 versus “no evolution”) and intensity of warming as quantitative variable (0, 2, 4, 6, 8, 10, 20K).
 666 The model is written as follows:

667

$$668 \quad \text{Model: } DiversityPersistence_{ij} = \mu + \delta_i + (\beta + \gamma_i) * WarmingIntensity_{ij} + \varepsilon_{ij}$$

669 As indicated in **table S2**, index 1 (resp. index 2) corresponds to the level “no evolution” (resp.
 670 “evolution”). The level “no evolution” serves as a reference ($\delta_1 = 0, \gamma_1 = 0$). Therefore, δ_2
 671 corresponds to the direct effect of evolution, while γ_2 corresponds to the interaction term
 672 between evolution and warming or indirect effect of evolution. β describes the direct effect of
 673 warming.

Mutation rate	Direct effect of evolution		Effect of warming intensity		Interaction term		Adjusted R ²
	δ_2	Effect size	β	Effect size	γ_2	Effect size	
$\mu = 10^{-1}$	0.051	32.3%	-0.029***	11.5%	0.031***	15.6%	58.6 %
$\mu = 10^{-2}$	0.060*	28.4%	-0.024***	30.3%	0.017***	9.5%	67.6%
$\mu = 10^{-3}$	0.062**	39.8%	-0.019***	18.5%	0.017***	13.1%	70.7%

674 **Table S2 (A): Trait diversity persistence.** Outputs of the 3 ANCOVAs. Index 1 corresponds to the level « No
675 evolution », which serves as a reference ($\delta_1 = \mathbf{0}$, $\gamma_1 = \mathbf{0}$), while index 2 corresponds to the level « Evolution »
676 (δ_2 , γ_2). All fitted ANCOVAs have a p-value below $2 \cdot 10^{-16}$. Significance code: $<10^{-3}$ '***', $<10^{-2}$ '**', <0.05 '*'

677
678
679

Mutation rate	Direct effect of evolution		Effect of warming intensity		Interaction term		Adjusted R ²
	δ_2	Effect size	β	Effect size	γ_2	Effect size	
$\mu = 10^{-1}$	-0.026	27.1%	-0.037***	27.9%	0.036***	24.8%	79.4%
$\mu = 10^{-2}$	0.126**	33.4%	-0.035***	22.6%	0.027***	8.9%	64.1%
$\mu = 10^{-3}$	0.196***	37.3%	-0.029***	12.2%	0.023***	5.8%	54.4%

680 **Table S2 (B): Species diversity persistence.** Outputs of the 3 ANCOVAs. Index 1 corresponds to the level « No
681 evolution », which serves as a reference ($\delta_1 = \mathbf{0}$, $\gamma_1 = \mathbf{0}$), while index 2 corresponds to the level « Evolution »
682 (δ_2 , γ_2). All fitted ANCOVAs have a p-value below $2 \cdot 10^{-16}$. Significance code: $<10^{-3}$ '***', $<10^{-2}$ '**', <0.05 '*'

683

684 An additional ANCOVA was fitted in order to compare the diversity persistence
685 according to the mutation rate μ . Here, diversity persistence is explained by the mutation rate
686 ($\mu = 10^{-1}, 10^{-2}, 10^{-3}$) as a three-level factor and the intensity of warming (0, 2, 4, 6, 8, 10,
687 20 K) as a quantitative variable. The model is written as follows (but results are not shown
688 because not significant):

689

690 Model: $DiversityPersistence_{ij} = \mu + \delta_i + (\beta + \gamma_i) * WarmingIntensity_{ij} + \varepsilon_{ij}$

691 A graphical visualization showed all hypothesis for ANCOVA were verified for each
692 fitted model. All statistical analyses were conducted using R-software (version 3.5.2). The
693 “Anova” function of the R-package “car” was also used.

694

695 **References:**

696 Rousseeuw, P. J. (1987). Silhouettes: A graphical aid to the interpretation and validation of
697 cluster analysis. *Journal of Computational and Applied Mathematics*, 20, 53–65.
698 doi:10.1016/0377-0427(87)90125-7

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721 **Appendix S3: Simulation code**

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723 The C code given as supporting information (file: SimulationCode.c) corresponds to the
724 code simulating complex multi-trophic networks for scenarios NE (i.e. without evolution). In
725 order for the code to work, the folder where it is launched has to contain a folder with a correct
726 path (see variable “path” L75 & input data L 149). In addition to this variable “path”, 3 other
727 inputs are necessary (see L 149-152 of the code): a seed, a new temperature and a deltaTm (i.e.
728 $1/\mu$, μ being the mutation rate).

729

730 In order to simulate scenarios E (with evolution), the following 2 changes are necessary:

731

732 (1): L 301: **while** (t<tend && S<Smax && S>0 && state<3)

733

734 Has to be replaced by:

735

736 **while** (t<tend && S<Smax && S>0 && state<2)

737

738

739 (2) L341-344:

740

741 **if**(state==1)

742 {

743 pattern=0;

744 }

745

746 Has to be replaced by:

747

748 **if**(state==1)

749 {

750 temperature=newtemperature;

751 }

752

753

754

755

Abstract

Eco-evolutionary dynamics of mutualistic-antagonistic systems Implications for plant-pollinator-herbivore communities

Ecological communities consist of multiple species interacting in diverse ways. Yet, the diversity of ecological interactions has often been ignored as most studies focus on a single type - antagonism, mutualism, or competition - of interaction. Studies of communities combining several interaction kinds should significantly improve our understanding of the mechanisms supporting biodiversity in natural communities because (1) most species get simultaneously involved in a diversity of interaction networks, and (2) the eco-evolutionary processes within such communities may differ from the linear combination of the processes at play within single-interaction-type communities. Playing a key role in the functioning of terrestrial ecosystems, plant-pollinator-herbivore communities are in addition crucial for agricultural production. Moreover, a large number of empirical studies documents the complex coevolutionary dynamics that may arise from the interplay of pollination and herbivory. At the core of the present PhD thesis, studying the eco-evolutionary dynamics of plant-pollinator-herbivore communities is thus of high applied relevance while offering the opportunity to gain new conceptual insights into the functioning of mutualistic-antagonistic communities.

We formulate a model describing the population dynamics of a plant-pollinator-herbivore community in which the strengths of plant-animal interactions depend on the trait-matching between plant and animal phenotypes. When evolution is not accounted for, we show that stable coexistence requires a balance between the strengths of pollination and herbivory. When evolution is accounted for, we show that the diversification of the plant phenotype may arise from the interplay of pollination and herbivory. This result is particularly important as several empirical works report the role of such an interplay in the maintenance of plant polymorphism. Studying animal evolution, we show that pollinator evolution fosters competitive exclusion among plant species, while herbivore evolution favors the maintenance of a diverse plant community. We also find that coevolutionary dynamics may significantly differ from the dynamics arising from the sole evolution of one animal species.

All in all, our work shed light on several key mechanisms underlying the eco-evolutionary dynamics of mutualistic-antagonistic communities, plant-pollinator-herbivore in particular. For instance, our results unravel two distinct processes that could explain the ubiquity of shared pollinator and herbivore preferences for plant phenotypes. But first and foremost, our study advocates in favor of accounting for both evolution and the multispecies community context in which species are embedded to better grasp the processes supporting biodiversity in natural ecosystems

Keywords: pollination, herbivory, multispecies coexistence, diversification, eco-evolutionary feedback, adaptive dynamics, evolutionary rescue

Résumé

Dynamique éco-évolutive des systèmes mutualiste-antagoniste

Implications pour les communautés plantes-pollinisateurs-herbivores

Les communautés écologiques se composent de multiples espèces qui interagissent de diverses manières. La diversité des interactions écologiques a néanmoins souvent été ignorée, la plupart des études se concentrant sur un seul type d'interaction - antagonisme, mutualisme ou compétition. L'étude des communautés combinant plusieurs types d'interactions devrait pourtant grandement améliorer notre compréhension des mécanismes supportant le maintien de la biodiversité dans les communautés naturelles pour au moins deux raisons. D'une part, la grande majorité des espèces sont simultanément impliquées dans divers réseaux d'interactions. D'autre part, les processus éco-évolutifs au sein de ces communautés peuvent différer de la combinaison linéaire des processus en jeu dans les communautés à interaction unique. Jouant un rôle clé dans le fonctionnement des écosystèmes terrestres, les communautés plantes-pollinisateurs-herbivores sont en outre cruciales pour la production agricole. De plus, un grand nombre d'études empiriques documentent la dynamique co-évolutive complexe qui peut résulter de l'interaction entre pollinisation herbivorie. Au cœur de la présente thèse de doctorat, l'étude de la dynamique éco-évolutive des communautés de plantes-pollinisateurs-herbivores présente donc un intérêt appliqué majeur tout en offrant l'opportunité d'acquérir de nouvelles connaissances conceptuelles sur le fonctionnement des communautés mutualistes-antagonistes.

Nous formulons un modèle décrivant la dynamique de population d'une communauté plantes-pollinisateurs-herbivores dans laquelle la force des interactions plante-animal dépend de l'adéquation entre le phénotype de la plante et celui des animaux. Lorsque l'évolution n'est pas prise en compte, nous montrons que la coexistence stable nécessite un équilibre entre les forces de pollinisation et d'herbivorie. Lorsque l'évolution est prise en compte, nous montrons que l'interaction entre pollinisation et herbivorie peut conduire à la diversification du phénotype de la plante. Ce résultat est particulièrement important car plusieurs travaux empiriques démontrent le rôle de l'interaction entre pollinisation et herbivorie dans le maintien du polymorphisme chez les plantes. En étudiant l'évolution animale, nous montrons que l'évolution des pollinisateurs favorise l'exclusion compétitive au sein de la communauté de plantes, tandis que l'évolution des herbivores favorise le maintien d'une communauté de plante diversifiée. Nous constatons également que la dynamique co-évolutive peut différer de manière significative de la dynamique découlant de la seule évolution d'une espèce animale.

Dans l'ensemble, nos travaux mettent en lumière plusieurs mécanismes importants sous-jacents la dynamique éco-évolutive des communautés mutualistes-antagonistes, notamment plantes-pollinisateurs-herbivores. Par exemple, nos résultats mettent en évidence deux processus distincts pouvant expliquer la tendance largement répandue de préférences similaires entre pollinisateurs et herbivores pour les phénotypes de plantes. Mais d'abord et avant tout, notre étude plaide en faveur de la prise en compte simultanée de l'évolution et du contexte de communauté multi-spécifique afin de mieux comprendre les processus qui supportent le maintien de la biodiversité dans les écosystèmes naturels.

Mots clés : pollinisation, herbivorie, coexistence multi-spécifique, diversification, boucle de rétroaction éco-évolutive, dynamique adaptative, sauvetage évolutif

The end :p