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

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Running headline

Plant evolution: pollination vs. herbivory

Statement of authorship

N.L. and Y.Y. conceived the ideas. The analytical and numerical 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.

Keywords

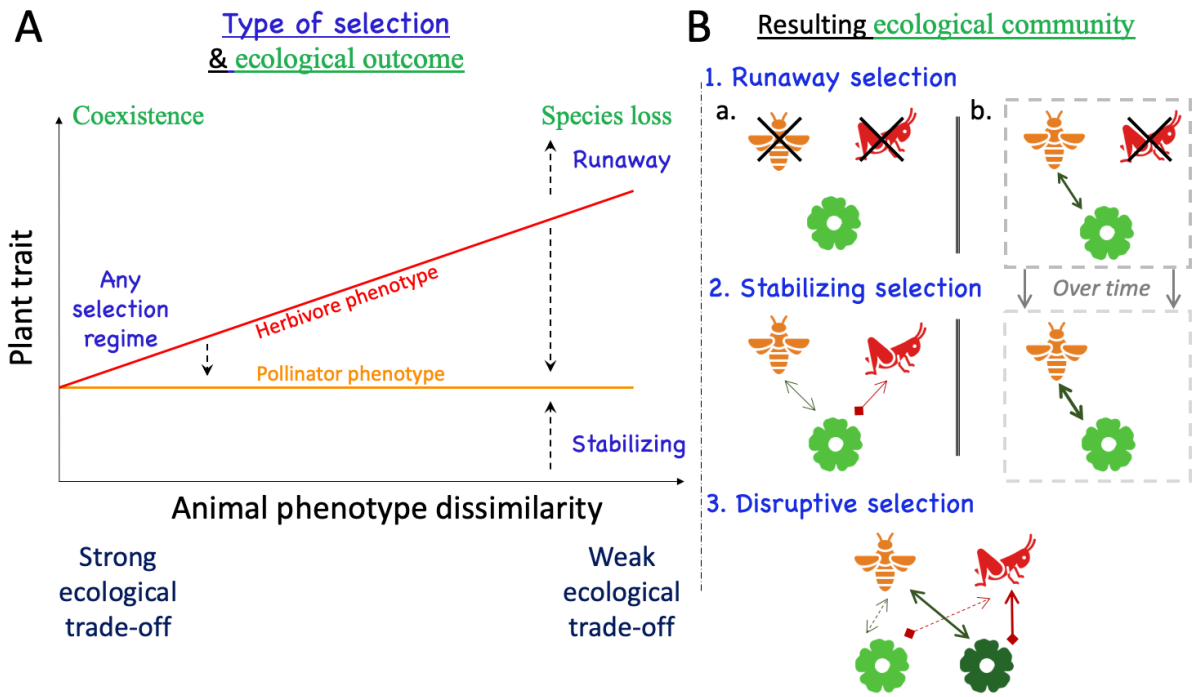
adaptive dynamics, pollination, herbivory, plant evolution, trait matching, diversification

Abstract

Many plant traits are subject to an ecological trade-off between attracting pollinators and escaping herbivores. The interplay of both plant-animal interaction types determines their evolution. As most studies focus on either pollination or herbivory, how they jointly affect the eco-evolutionary dynamics of plant-animal communities is often left unknown. Within a plant-pollinator-herbivore community where interaction strengths depend on trait matching, we consider the evolution of a plant trait involved in both plant-animal interactions. Using adaptive dynamics, we uncover when stabilizing, runaway (i.e. directional) or disruptive selection emerges and its consequences for multispecies coexistence. We find that strong pollination relative to herbivory favors stabilizing selection and coexistence. Strong herbivory relative to pollination fosters runaway selection and threatens coexistence. Importantly, given balanced interactions, joint effects may lead to disruptive selection, allowing the emergence of plant dimorphism. The strength of the ecological trade-off largely explains the occurrence of these contrasting eco-evolutionary dynamics. In particular, plant diversification requires strong trade-offs, with the strongest trade-offs allowing long-term polymorphism. We discuss how our results relate to various empirical cases where the interplay of pollination and herbivory maintains plant polymorphism. Beyond maintenance, our work suggests that it might also have fueled the diversification process itself.

Graphical Abstract:

Eco-evolutionary dynamics resulting from the evolution of plant phenotype under ecological trade-off



A. Typical eco-evolutionary landscape. The type of selection and the ecological outcome depend on the dissimilarity between animal phenotypes (i.e. preferences for plant phenotype), which is a proxy for the strength of the ecological trade-off. **B. The long-term community composition** depends on the type of selection. **(1)** Runaway selection leads to the extinction of a first animal species as the plant phenotype is diverging. **(a)** Pollinators are lost first so that runway selection continues until herbivores are also lost. **(b)** Herbivores are lost first so that selection turns stabilizing over time, leading to a perfect plant-pollinator matching. **(2)** Stabilizing selection can enable the maintenance of coexistence. **(3)** Disruptive selection leads to the emergence of plant dimorphism.

53 # Introduction

54 Flowering plants (i.e. angiosperms) are the most diverse and successful plant clade in
55 terrestrial ecosystems, representing almost 90% of the species described (Hernández-
56 Hernández & Wiens 2020). Most of them rely on animals for pollination (Ollerton *et al.* 2011).
57 Because animal pollination can favor reproductive isolation, it has been proposed early as an
58 important diversity driver among angiosperms (Grant 1949). Plant-herbivore interactions have,
59 however, also been identified as potentially fostering diversification due to the ensuing
60 evolutionary arms race between interacting antagonists (Ehrlich & Raven 1964). These two
61 non-mutually exclusive hypotheses are supported by several phylogenetic investigations. Plant-
62 pollinator coevolution explains higher diversification rates within angiosperms (Hodges &
63 Arnold 1995; Sargent 2004; Hernández-Hernández & Wiens 2020), but plant-herbivore
64 coevolution also spurs plant diversification as a result of defense-counterdefense innovations
65 (Farrell *et al.* 1991; Becerra *et al.* 2009). Plant phylogenies reveal that plant-pollinator and
66 plant-herbivore coevolution are often inextricably intertwined (e.g. Armbruster 1997), which
67 advocates for an integrative framework accounting for both interaction types (Fontaine *et al.*
68 2011). From an ecological perspective, the positive or negative outcome of many interactions
69 is often context-dependent (Chamberlain *et al.* 2014), varying for instance with the phenotype
70 of interacting individuals (e.g. larvae vs. adult of nursery pollinators, Hahn and Brühl 2016).
71 This dynamic nature of interactions along a mutualistic-antagonistic continuum (Thompson
72 1988; Gómez *et al.* 2023) further highlights the relevance of such an integrative framework.
73
74 A large number of plant traits are notably under conflicting selection due to the interplay
75 between pollination and herbivory (Strauss & Irwin 2004), floral traits in particular (Strauss &
76 Whittall 2006). Conflicting selection pressures can emerge from several mechanisms acting
77 either in isolation or synergistically. Herbivory-induced changes in plant chemistry potentially

78 reduce pollinator visitations (e.g. Kessler *et al.* 2011). Many plant traits acting on the plant
79 visibility (size, phenology, floral display, volatile compounds) may increase herbivory
80 (apparency hypothesis, Feeny 1976) while also attracting allies (e.g. Brody 2008). Genetic
81 correlation can also exist between two plant traits, each involved in one plant-animal interaction
82 (Strauss *et al.* 2004). A decisive consequence is that the selection pressures in the absence of
83 either one animal species would be modified in the presence of both animal groups (Ramos &
84 Schiestl 2019). Conflicting selection is very often due to shared preferences for plant
85 phenotypes between pollinators and herbivores, a pattern that is largely widespread in nature
86 (Strauss & Whittall 2006) and that promotes the stable coexistence of the community (Yacine
87 & Loeuille 2022). This preference pattern indicates that plant species are subject to an
88 ecological trade-off between attracting pollinators and escaping herbivores (Strauss *et al.* 2002).
89 In other words, an increase in the strength of pollination (e.g. investment in attraction) comes
90 at the cost of an increase in the strength of herbivory, while a decrease in the strength of
91 herbivory (e.g. production of defenses) comes at the cost of a decrease in the strength of
92 pollination. This trade-off has interestingly been shown to support the maintenance of a flower-
93 color polymorphism in the wild radish *Raphanus sativus* (Irwin *et al.* 2003), which suggests
94 that the interplay between pollination and herbivory could also lead to disruptive selection and
95 promote diversification.
96
97 Conflicting selection arises because pollination and herbivory exert opposite pressures
98 on plant traits (Thompson 2009), with contrasting implications in terms of diversification
99 potential (Yoder & Nuismer 2010). These differences are especially prominent under the
100 assumption that interaction strengths increase with the matching between plant and animal
101 phenotypes (i.e. trait-matching). Such an assumption seems reasonable as it has been reported
102 to apply in various instances, including flower color (Irwin *et al.* 2003) or flower display (Galen

103 & Cuba 2001) matching animal preferences, chemical volatiles (Theis *et al.* 2014) matching
104 animal detection abilities, or plant phenology matching that of animals (Brody 2008). As fitness
105 increases with the strength of a mutualistic interaction, plants are selected to better match their
106 pollinator phenotype and vice versa (e.g. spur length and pollinator tongue, Whittall & Hodges
107 2007) so that stabilizing selection is expected (e.g. Kiester *et al.* 1984). Pollination-induced
108 stabilizing selection has been empirically characterized several times (e.g. Parachnowitsch and
109 Kessler 2010; Sahli and Conner 2011; De Jager and Peakall 2019). It disfavors extreme
110 phenotypes, thus reducing the potential for disruptive selection (Kopp & Gavrilets 2006; Yoder
111 & Nuismer 2010; Maliet *et al.* 2020). Conversely, predation reduces prey fitness so that plants
112 are selected to escape herbivore preferences (e.g. chemical defenses and herbivore tolerance,
113 Becerra *et al.* 2009). Such arms race dynamics (Ehrlich & Raven 1964; Dawkins & Krebs 1979)
114 expose the plant species to runaway selection, as observed in empirical systems (e.g. Mauricio
115 and Rausher 1997; Becerra et al. 2009; Griese et al. 2021). Because apparent competition (Holt
116 1977) imposes a cost on phenotype matching between conspecific plants, herbivory also favors
117 increased plant phenotypic divergence thereby enhancing disruptive selection (Kopp &
118 Gavrilets 2006; Yoder & Nuismer 2010; Maliet *et al.* 2020). Note finally that conflicting
119 selection may have far-reaching ecological implications. The relative interaction strength of
120 pollination vs. herbivory has been shown to determine coexistence within plant-pollinator-
121 herbivore communities (Mougi & Kondoh 2014; Sauve *et al.* 2016a; Yacine & Loeuille 2022).
122 A balance between the strength of interactions makes coexistence more likely. Because
123 interaction strengths are the result of plant-animal coevolution, the evolution of plant traits
124 under conflicting selection may have important consequences for multispecies coexistence.
125
126 In the present paper, our goals are to determine how the interplay of pollination and
127 herbivory drives the evolution of plant traits involved in both interactions, and how, in turn,

such an evolution affects the maintenance of coexistence. We model a community – a plant species interacting simultaneously with a pollinator and a herbivore species - in which plant-animal interactions depend on a plant trait involved in both interactions. Assuming that each interaction increases in strength with the matching of plant and animal phenotypes (trait-matching), we study the eco-evolutionary dynamics resulting from the evolution of the plant phenotype using the adaptive dynamics framework (Metz *et al.* 1992; Dieckmann & Law 1996). We are particularly interested in understanding how these dynamics depend on an ecological trade-off to which the plant might be subject. An ecological trade-off is here defined as a positive covariation between the strengths of pollination and herbivory, i.e. stronger pollination (resp. weaker herbivory) comes at the cost of stronger herbivory (resp. weaker pollination). We first show that under our trait-matching assumption, variations in plant phenotype intrinsically entail an ecological trade-off whose strength depends on the dissimilarity between animal phenotypes (details in Methods, **Fig. 1**). Manipulating animal phenotype dissimilarity, we investigate how the strength of this ecological trade-off affects the type of selection on the plant trait and the maintenance of coexistence. When animal phenotypes are highly dissimilar (weak trade-off), interaction strengths are intrinsically unbalanced making the plant essentially interacting with one animal species so that we expect selection to be stabilizing close to the pollinator phenotype, and runaway close to the herbivore phenotype. Coexistence should then be frequently disrupted as a previous purely ecological study of the three-species population dynamics (i.e. ignoring all evolutionary aspects) showed that stable coexistence requires the plant-animal interaction strengths to be of similar magnitudes (Yacine & Loeuille 2022). When animal phenotypes are fairly similar (strong trade-off), the balance between interaction strengths should, in contrast, favor the maintenance of coexistence. The potential for disruptive selection to occur in such instances, and the maintenance of the ensuing polymorphism, is one of the key questions of the present study.

Model & Methods

Model

Population dynamics

We model the dynamics of a plant-pollinator-herbivore module (P, M, H respectively) using a Lotka-Volterra framework:

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

Plants are assumed to have a positive intrinsic growth rate ($r_p > 0$), while both pollinator ($r_m < 0$) and herbivore growth rates ($r_h < 0$) are assumed negative. 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. All interacting species undergo negative (quadratic) density-dependence. These terms are here interpreted as intraspecific competition. The plant competition rate (c_p) would notably encompass the competition for space, water or nutrients (Craine & Dybzinski 2013). Animal competition rates (c_m, c_h) would essentially coincide with interference (e.g. Thébault and Fontaine 2010). Note however that these terms might be more generally considered as any negative regulation not explicitly accounted for in our model (e.g. other predators or resources, diseases….). The per-capita strengths of interspecific interactions are 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.

Without evolution, stable coexistence occurs when the strengths of pollination (a_{pm}) and herbivory (a_{ph}) are balanced (Yacine & Loeuille 2022). The analytical expression of the coexistence equilibrium (P^*, M^*, H^*) is given in Appendix A.I (see Supporting Information). Here, we investigate how the relative strength of pollination vs. herbivory influences plant evolution, and how such evolution, in turn, affects the maintenance of multispecies coexistence.

Plant-animal interactions depend on trait matching

We assume plant-animal interactions to intensify as the matching between plant (t_p) and animal phenotypes – pollinator (t_m) or herbivore (t_h) – increases (equations 2). Interactions are maximal when traits perfectly match (i.e. $|t_p - t_m| = 0$, resp. $|t_p - t_h| = 0$), and weaken when trait-matching is reduced (i.e. $|t_p - t_m| \nearrow$, resp. $|t_p - t_h| \nearrow$). Examples include the color of plant flowers (t_p) and associated animal preferences (t_m, t_h) (e.g. Irwin *et al.* 2003) or phenological traits (e.g. Brody 2008) such as the date of flowering (t_p) and of animal activity (t_m, t_h).

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

$$a_{ph}(t_p) = \frac{a_{ph0}}{\sqrt{2\pi\sigma_{Her}^2}} \exp\left[-\frac{(t_p - t_h)^2}{2\sigma_{Her}^2}\right] \quad (2)$$

As σ_{Pol} controls how quickly the strength of pollination decreases with plant-pollinator phenotype dissimilarity, it corresponds to the pollination-niche width, which depends on the generalism of both species. Likewise, σ_{Her} embodies the herbivory-niche width. a_{pm0} and a_{ph0} correspond to basal interaction rates. See table 1 for details.

Table 1: List of all model parameters and variables with their biological definitions, values and dimensions.

Variables and parameters		Biological definition	Value	Dimension
Variables	P	Plant biomass density		$mass.length^{-2}$
	M	Pollinator biomass density		$mass.length^{-2}$
	H	Herbivore biomass density		$mass.length^{-2}$
	t_p	Plant phenotype		*Dimensionless*
Animal phenotypes	t_m	Pollinator phenotype	0	*Dimensionless*
	t_h	Herbivore phenotype	[0,3]	*Dimensionless*
Interspecific interaction parameters	$t_h - t_m$	Animal phenotype dissimilarity Proxy for the strength of the ecological trade-off (see Methods)	[0,3]	*Dimensionless*
	a_{pm0}	Basal pollination rate (per capita)	[3,9]	$(M.L^{-2})^{-1}.t^{-1}$
	a_{ph0}	Basal herbivory rate (per capita)	[3,9]	$(M.L^{-2})^{-1}.t^{-1}$
	σ_{Pol}	Pollination niche width	[1.5,3]	*Dimensionless*
	σ_{Her}	Herbivory niche width	[1.5,3]	*Dimensionless*
Other ecological parameters	r_p	Plant intrinsic growth rate	10	$time^{-1}$
	r_m	Pollinator intrinsic growth rate	-1	$time^{-1}$
	r_h	Herbivore intrinsic growth rate	-4 (or -1)	$time^{-1}$
	c_p	Plant intra-specific competition rate	0.6	$[(mass.length^{-2}).time]^{-1}$
	c_m	Pollinator intra-specific competition rate	0.5 (or 0.4)	$[(mass.length^{-2}).time]^{-1}$
	c_h	Herbivore intra-specific competition rate	0.4	$(M.L^{-2})^{-1}.t^{-1}$
	e_m	Plant to pollinator conversion efficiency	0.2	*Dimensionless*
	e_h	Plant to herbivore conversion efficiency	0.3 (or 0.2)	*Dimensionless*
Numerical simulations	μ	Mutation probability (per unit of time and plant biomass density)	2.10^{-7}	$[(mass.length^{-2}).time]^{-1}$
	σ	Mutation amplitude (standard deviation)	0.02	*Dimensionless*
	ε	Extinction threshold	2.10^{-6}	$mass.length^{-2}$

Methods

Definition and emergence of an ecological trade-off

An ecological trade-off between attracting pollinators and escaping herbivory is defined as a positive covariation between the strengths of pollination and herbivory, i.e. both increasing or decreasing. As our focal plant trait is involved in both plant-animal interactions (equation 2), its variation affects both interaction strengths (e.g. **Fig. 1b**). Because of our trait-matching hypothesis, the induced covariation between the strengths of pollination and herbivory is positive when the plant phenotype is outside the phenotypic interval $[t_m, t_h]$. Variation in plant phenotype there entails an ecological trade-off (**Fig. 1b**, **solid line**). Within the interval $[t_m, t_h]$, there is no ecological trade-off (**Fig. 1b, dotted line**).

We consider the dissimilarity between animal phenotypes $(t_h - t_m)$ to be a proxy for the strength of the ecological trade-off that emerges within our framework. There are two reasons for that. First, as animal phenotype similarity increases (**Fig. 1, a vs. b vs. c**), the phenotypic region over which plant phenotype variation induces an ecological trade-off increases in size. Second, over this region, in the case of very dissimilar animal phenotypes (i.e. $t_m \ll t_h$, **Fig. 1a**), plant phenotype variations affect much more one interaction than the other, depending on the closest animal phenotype. In contrast, over the same region but in the case of similar phenotypes (i.e. $t_m \approx t_h$, **Fig. 1c**), any variation of the plant phenotype has an effect of comparable magnitude on the strength of both interactions. All in all, the ecological trade-off between attracting pollinators and escaping herbivores gets stronger as animal dissimilarity decreases (**Fig. 1**).

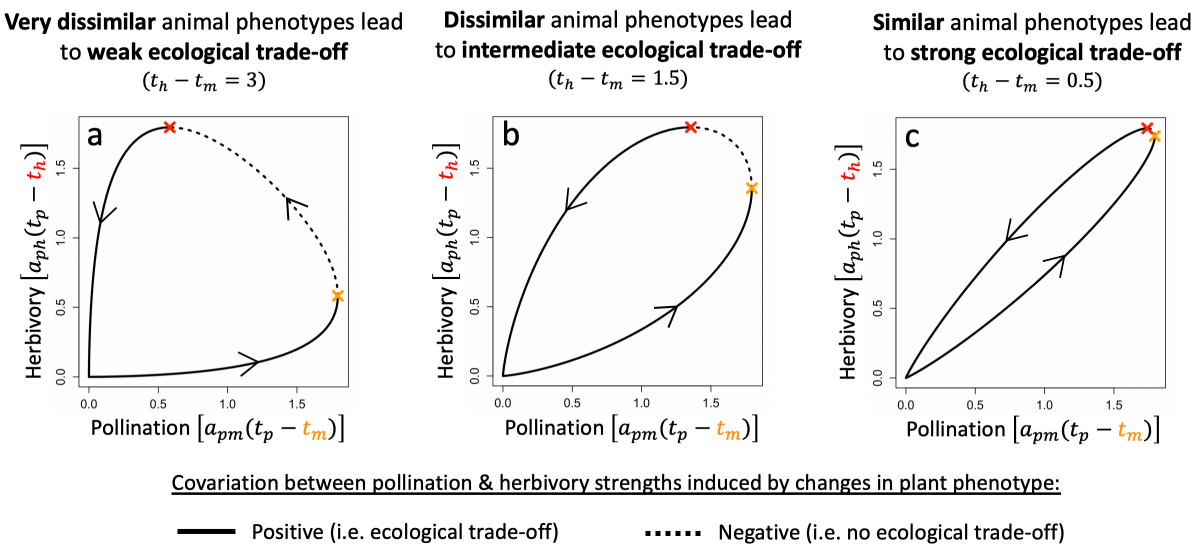


Fig. 1: Animal phenotype dissimilarity determines the strength of the ecological trade-off. Each graph shows the covariation between the strength of plant-animal interactions resulting from varying plant phenotype (t_p varies from -10 to 10 in the direction indicated by the arrows, the orange (resp. red) point indicates when $t_p = t_m$ (resp. $t_p = t_h$)). **a. b. c. Increasing strength of ecological trade-off with increasing similarity between animal phenotypes (i.e. decreasing dissimilarity).** 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 ($t_m = 0, a_{pm0} = a_{ph0} = 9, \sigma_{Pol} = \sigma_{Her} = 2$).

Adaptive dynamics and type of selection

Within a monomorphic plant population with phenotype t_p (resident), we investigate whether a mutant with a new phenotype $t_p{}'$ can invade. Invasion fitness $w(t_p{}', t_p)$ is computed as the per capita growth rate of that mutant, when rare and in the environment (P^*, M^*, H^*) set by the resident population (Metz *et al.* 1992, see appendix A.II). When a mutant invades (i.e. $w(t_p{}', t_p) > 0$), it replaces the resident population, thus becoming the new resident. The sequence of trait substitutions defines the long-term evolutionary dynamics. Assuming small and rare mutational steps, the variation of phenotype t_p is proportional to the selection gradient (equation (3)), i.e. the derivative of invasion fitness with respect to the mutant's trait (Dieckmann & Law 1996). Evolutionary singularities t_p^* correspond to phenotypes that nullify the selection gradient.

239 The type of selection – stabilizing, disruptive, or runaway – acting on the plant trait
240 depends on (1) the properties of the evolutionary singularities, and (2) the position of the plant
241 phenotype relative to these singularities. Two independent properties - convergence and
242 invasibility – characterize evolutionary singularities (criteria in appendix A.II). Convergence
243 indicates whether the trait evolves toward the singularity in its vicinity. Two types of
244 singularities are convergent – the non-invasible continuously stable strategy (, Eshel, 1983) and
245 the invasible branching point (Geritz *et al.* 1997). Invasibility specifies whether the singularity
246 may be invaded by nearby mutants (i.e. ESS, Maynard Smith & Price 1973). CSS phenotypes
247 correspond to cases of stabilizing selection (e.g. Fig. 2B.a). Selection is thus considered
248 stabilizing in the basin of attraction of a CSS. Plant-pollinator-herbivore coexistence is notably
249 maintained if a CSS is reached while the three species coexist. In contrast, a branching point
250 yields the emergence of plant dimorphism due to disruptive selection (e.g. Fig. 2B.d).
251 Accordingly, selection is considered disruptive in the basin of attraction of a branching point.
252 Finally, phenotypes that are not in the basin of attraction of a convergent singularity are under
253 runaway selection. This is possible in the presence of a non-convergent singularity, i.e. a
254 repellor. For the sake of simplicity, we will refer to this set of phenotypes as the basin of
255 attraction associated with runaway selection. Runaway selection should always disrupt plant-
256 pollinator-herbivore coexistence (e.g. Fig. 2B.b). We illustrate how the proportion of
257 phenotypic space under each type of selection is calculated in Appendix B.II.1.
258

259 ## Numerical simulations of community eco-evolutionary dynamics

260 This framework is completed by numerical simulations starting from a monomorphic
261 plant population (t_p) interacting with a pollinator (t_m) and a herbivore (t_h) population.
262 Mutations are randomly generated following a Poisson process characterized by a mutation
263 probability per unit of time and plant biomass density $\mu = 2.10^{-7}$. Proportionally to phenotype

abundances, a parent phenotype is randomly chosen at each mutation event. The mutant phenotype is drawn from a Gaussian distribution centered around the parent phenotype with standard deviation $\sigma = 0.02$. Its initial density is set to a small value ε, taken from the parent population. Symmetrically, populations falling below ε are removed from the system (extinction).

Workflow

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). Parameters directly affecting plant-animal interactions – i.e. the interspecific parameter set ($t_h - t_m, a_{pm0}, a_{ph0}, \sigma_{Pol}, \sigma_{Her}$) – are at the core of our investigation. Thanks to the model simplicity, several analytical results uncovering various aspects of evolutionary dynamics (e.g. equation (3)) are possible. For aspects that cannot be mathematically investigated, we provide numerical resolutions characterizing the variation of eco-evolutionary dynamics along the gradient of trade-off intensity (E3-diagrams, e.g. Fig. 2A). To broaden our understanding of possible evolutionary dynamics, we undertake Monte Carlo experiments (details in appendix B.II). We let interspecific parameters vary independently within their interval ranges (table 1), which were chosen to explore a wide range of pollination and herbivory intensities (Appendix B.I). Remaining parameters ($r_p, r_m, r_h, c_p, c_m, c_h, e_m, e_h$) are fixed, but the experiments were conducted for two different sets to assess their robustness. The different Monte Carlo experiments are presented directly in the Result section when needed. Our approach is finally complemented by numerical simulations of the community eco-evolutionary dynamics. Such simulations are used to investigate the emergence of plant dimorphism in the case of disruptive selection.

Results

A typical example of eco-evolutionary dynamics

Eco-evolutionary dynamics qualitatively depend on the strength of the ecological trade-off (Fig. 2). These dynamics are characterized by stabilizing or disruptive selection when trade-offs are strong. They then allow the coexistence of all species. Such a coexistence is, however, often lost in the case of weak trade-offs, where runaway selection is much more common. As developed later on (Fig. 4A), these variations are more general than the specific example we introduce here (Fig. 2A). On Fig. 2A, the plant phenotype always converges towards a CSS phenotype under very strong trade-offs (region I) so that selection is stabilizing. As the trade-off weakens (region II), both stabilizing (Fig. 2B.a) and disruptive selection (Fig. 2B.e) become possible depending on the initial plant phenotype. Stabilizing (resp. disruptive) selection is observed over the basin of attraction of the CSS (black line) (resp. branching point, blue line). These basins of attraction (see arrows) are separated by the repellor (grey line). At weaker trade-offs (region III), the basin of attraction of the CSS covers the whole coexistence area (white) so that selection is always stabilizing (Fig. 2B.b). In region IV, eco-evolutionary dynamics are qualitatively similar to those of region II. For even weaker trade-offs (region V), runaway selection is observed whenever the initial plant phenotype is above the repellor (Fig. 2B.c). Associated eco-evolutionary dynamics lead first to the extinction of pollinators, then of herbivores. Below the repellor, selection stabilizes at the CSS phenotype. For even weaker trade-offs (region VI), the CSS exits the coexistence area so that only runaway selection remains possible. It provokes the extinction of both animal species when starting above the repellor, and that of herbivores when starting below the repellor. The extinction of herbivores then leads to a perfectly matched plant-pollinator community (Fig. 2B.d).

The ecological dynamics induced by each type of selection qualitatively differ (Fig. 2B). Coexistence is always maintained in the case of stabilizing selection. It is always disrupted in

the case of runaway selection due to the weakening of one or both plant-animal interactions. Disruptive selection allows the emergence of plant dimorphism. The two plant phenotypes diverge, one leading to stronger plant-animal interactions, the other to weaker plant-animal interactions. Dimorphism can be temporary (Fig. 2B.e) or permanently maintained (Fig. 2B.f). An example of eco-evolutionary landscape associated with permanent dimorphism is given in Fig. S1 (Supporting Information), while the landscape presented in Fig. 2A typically leads to temporary branchings. In addition to trade-off intensity, other interspecific parameters can thus be responsible for qualitative changes in eco-evolutionary dynamics. Most of such (qualitative) variation is covered by the simulations in Fig. 2B.

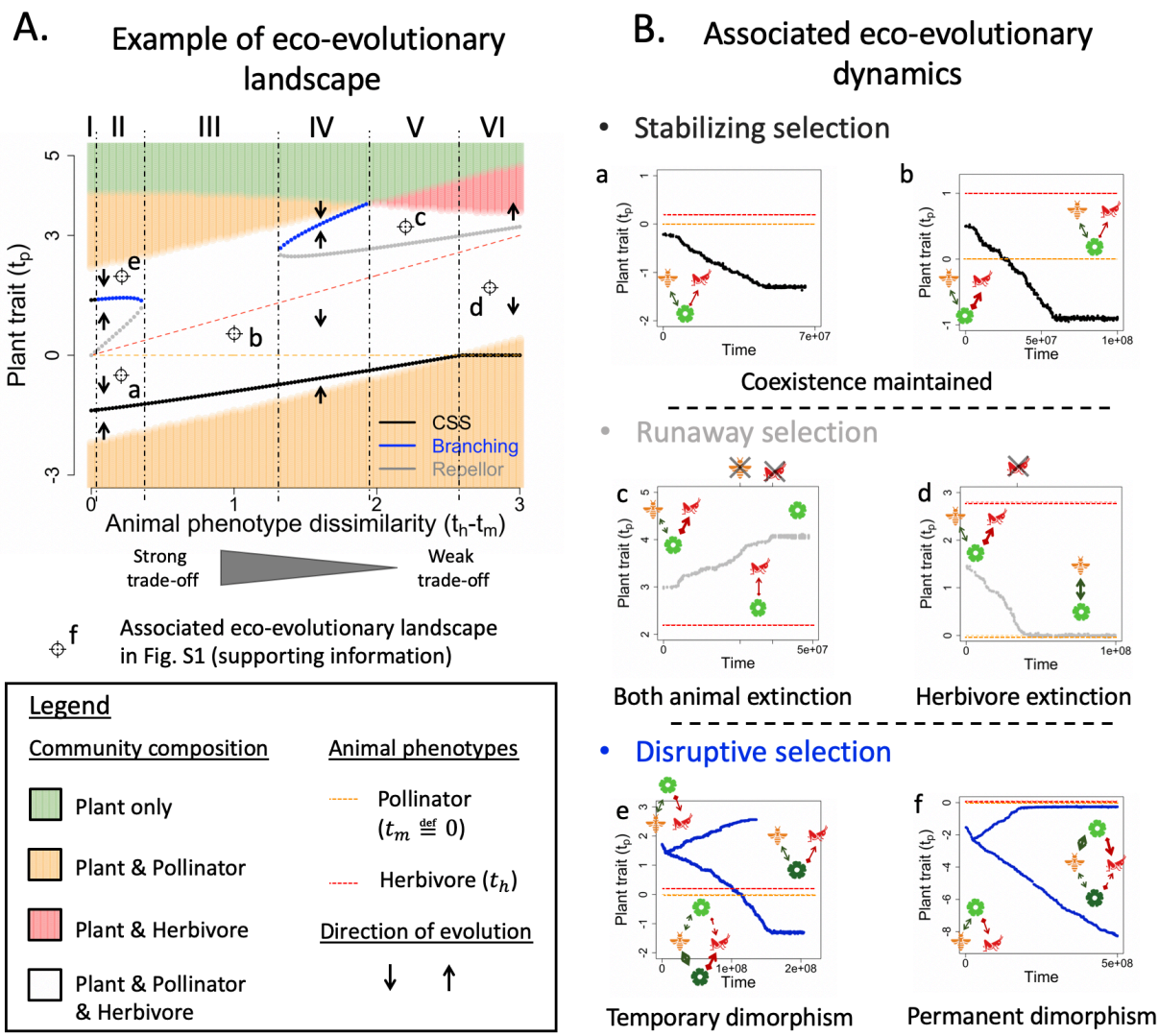


Fig. 2: Typical examples of eco-evolutionary dynamics with their associated eco-evolutionary landscape. A. Eco-evolutionary landscape. The points labelled by letters indicate the initial conditions of the simulations presented in B. Ecological parameter set: $(r_p = 10, r_m = -1, r_h = -4, c_p = 0.6, c_m = 0.5, c_h = 0.4, e_m =$

$0.2, e_h = 0.3$). Interspecific parameter set ($a_{pm0} = 5, a_{ph0} = 7, \sigma_{Pol} = 3, \sigma_{Her} = 2.8$) **B. Simulated eco-evolutionary dynamics associated with each type of selection. a-b. Stabilizing selection enables the maintenance of coexistence** ($t_h = 0.2$ & 1 respectively). **c-d. Runaway selection leads to coexistence loss** ($t_h = 2.8$ & 2.2 respectively). **e-f. Disruptive selection allows the emergence of plant dimorphism** ($t_h = 0.2$ & 0.1 respectively). Note that for f, the interspecific parameter set is modified ($a_{pm0} = 5, a_{ph0} = 9, \sigma_{Pol} = 1.7, \sigma_{Her} = 2$). The associated landscape is given in **Fig. S1**. In B, pictograms depict the community composition, with arrow thickness correlating to interaction strengths.

Opposite effects of pollination vs herbivory on the (local) selection gradient

The selection gradient (equation (3)) shows that plant evolution is under two contrasting selective forces (i.e. opposite sign).

$$\frac{dt_p}{dt} \propto \begin{matrix} Selection \\ gradient \end{matrix} = -\underbrace{\frac{a_{pm}(t_p)M^*}{\sigma_{Pol}^2}}_{pollination}(t_p - t_m) + \underbrace{\frac{a_{ph}(t_p)H^*}{\sigma_{Her}^2}}_{herbivory}(t_p - t_h) \tag{3}$$

Pollination selects for plant phenotypes that are closer to that of pollinators (negative sign). Herbivory selects for phenotypes that are further away from that of herbivores (positive sign). These two selective forces act synergistically when the plant phenotype is within $[t_m, t_h]$ so that evolution enables a simultaneous increase in pollination and decrease in herbivory. In contrast, these two forces become antagonistic when the plant phenotype is outside $[t_m, t_h]$. Pollination selects for stronger plant-animal trait matchings, while herbivory selects for weaker trait matchings. Such conflicting selection captures the ecological trade-off with which plants are confronted.

Pollination and herbivory have also an opposite effect on the evolutionary stability – i.e. non-invasibility – of evolutionary singularities t_p^*. Singularities are invasible if inequality (4) is satisfied (proof and expression of $f(t_p^*)$ in Appendix A.II.2).

$$Invasibility \Leftrightarrow -\underbrace{a_{pm}(t_p^*)M^*}_{pollination}\left[1 + \frac{f(t_p^*)^2}{\sigma_{Pol}^2}\right] + \underbrace{a_{ph}(t_p^*)H^*}_{herbivory}\left[1 + \frac{f(t_p^*)^2}{\sigma_{Her}^2}\right] > 0 \tag{4}$$

Invasibility is thus favored by herbivory and disfavored by pollination. Convergence being however not analytically tractable, we rely on a first Monte Carlo experiment (MC1, details in appendix B.II.2) to investigate the relationship between selection type and plant-animal interactions. We sampled 10 000 interspecific parameter sets and analyzed the nature of all evolutionary singularities allowing ecological coexistence, as well as interaction strengths and animal densities at these singularities. The resulting dataset thereby links the ratio of pollination to herbivory at the singularity $\left(\left[\frac{a_{pm}M^*}{a_{ph}H^*}\right]_{t_p^*}\right)$ to the type of selection. Stabilizing, runaway and disruptive selections are characterized by contrasting pollination to herbivory ratios (**Fig. 3**), whose variation explains around two-thirds of the variance in selection type (Kruskal-Wallis).

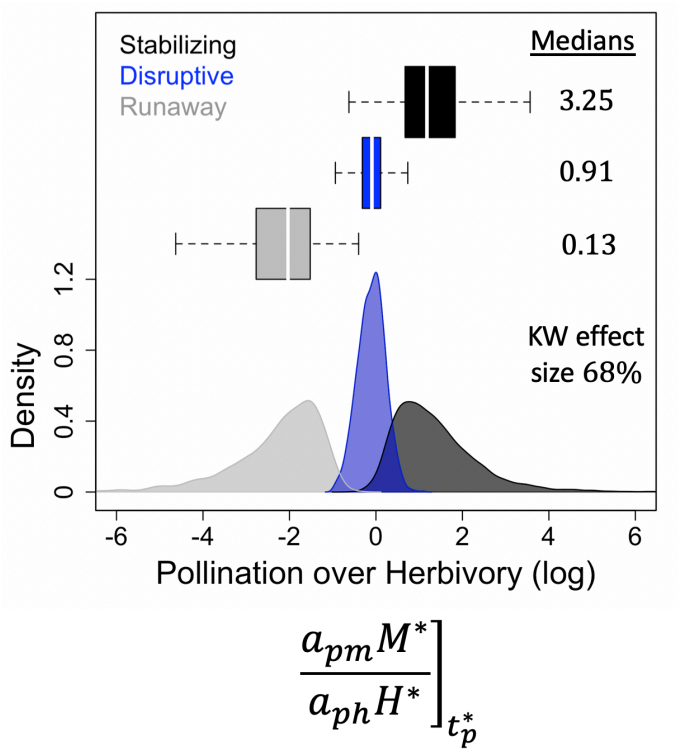


Fig. 3: Distribution of pollination to herbivory ratios depending on the type of selection. The ratio is measured at the corresponding evolutionary singularity. The medians indicated correspond to absolute values (no log). The effect size of the Kruskal-Wallis test ($p_{value} < 2.10^{-16}$) is also indicated. Ecological parameter set: ($r_p = 10, r_m = -1, r_h = -4, c_p = 0.6, c_m = 0.5, c_h = 0.4, e_m = 0.2, e_h = 0.3$). Results are from our first Monte Carlo experiment (MC1, appendix B.II.2), with 10 000 interspecific parameter sets sampled.

High pollination relative to herbivory is associated with stabilizing selection (Fig. 3). High herbivory relative to pollination is associated with runaway selection (Fig. 3). When

369 pollination and herbivory are balanced, selection turns disruptive (Fig. 3). The association of
370 stabilizing, runaway and disruptive selection with respectively high, low and balanced
371 pollination to herbivory ratios implies that the convergence of evolutionary singularities (i.e.
372 convergence stability, Eshel 1983) is favored by pollination and disfavored by herbivory.
373 Disruptive selection requires a balance between pollination and herbivory because strong
374 herbivory relative to pollination fosters invasibility (inequality (4)), but convergence is lost
375 when herbivory is too strong, leading to runaway dynamics (Fig. 3). Note finally that simpler
376 ratios measuring the strength of pollination vs. herbivory (e.g. interaction strengths $\left.\frac{a_{pm}}{a_{ph}}\right]_{t_p^*}$ or
377 animal densities $\left.\frac{M^*}{H^*}\right]_{t_p^*}$) also have a large – but inferior – power in explaining the nature of
378 selection (table S1, Supporting Material). These key results derived from our Monte Carlo
379 experiment are robust to the modification of the ecological parameter set (Appendix C.I).
380

381 ## Effects of interspecific parameters on selective landscapes

382 Beyond local selection at evolutionary singularities, we now investigate the effect of
383 plant-animal interactions on the selective landscape at large, i.e. the distribution of basins of
384 attraction associated with each type of selection (e.g. Fig. 2A). We build a second Monte Carlo
385 experiment (MC2, details in Appendix B.II.3). For each focal interspecific parameter, we divide
386 the potential range of that parameter (table 1) into six equal intervals to sample from, the
387 sampling of the other interspecific parameters remaining unconstrained. For each sampling (6
388 x 1000), we calculate the proportion of phenotypic space associated with each type of selection
389 (i.e. basin of attraction, see Appendix B.II.1 for details). We thereby estimate the effect of
390 varying (1) the strength of ecological trade-off (Fig. 4A) and (2) the intensity and generalism
391 of pollination and herbivory (Fig. 4B) on the selective landscape.
392

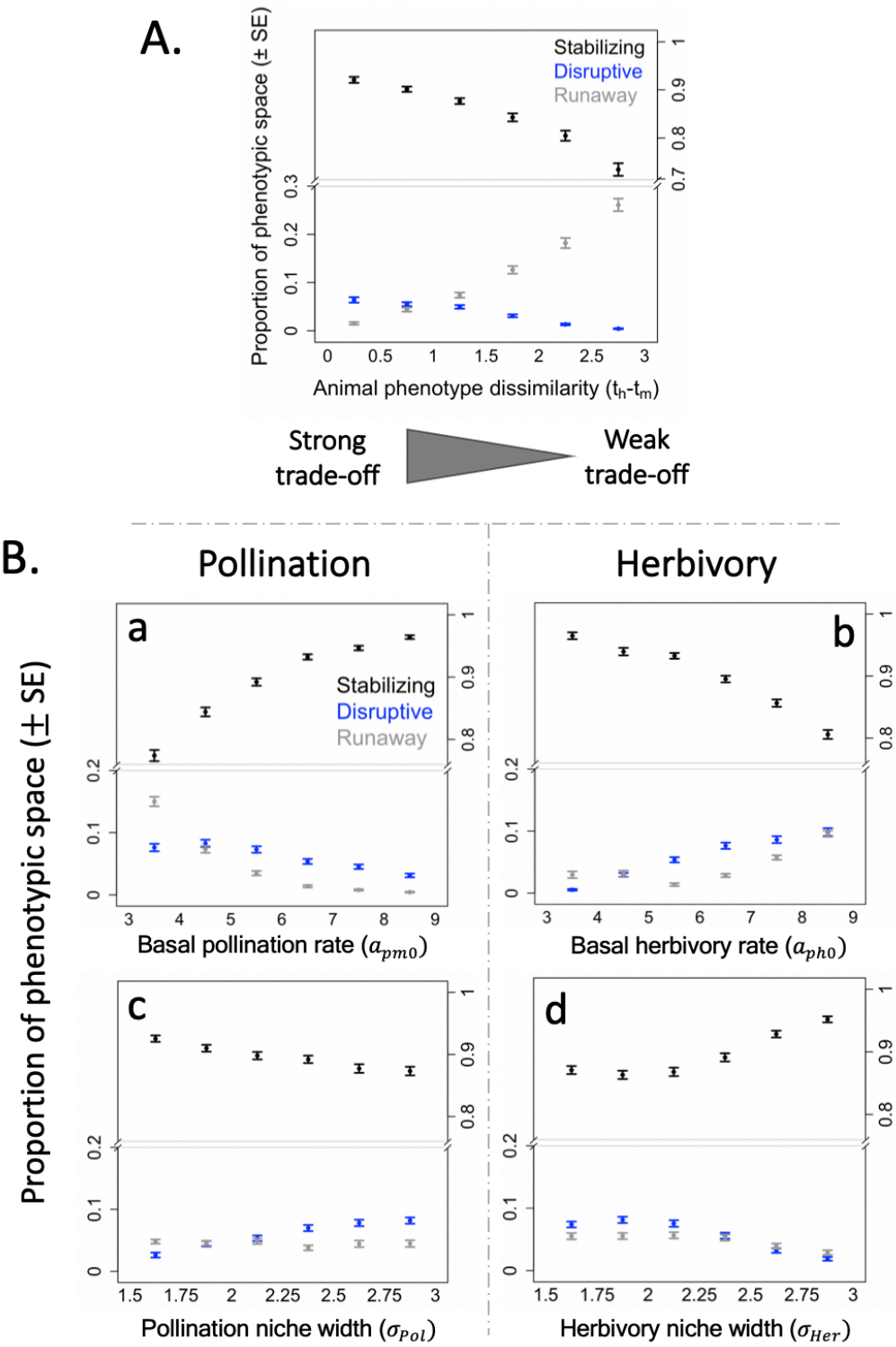


Fig. 4: Effect of interspecific parameters on the selective landscape. A. The selective landscape depends on trade-off intensity. B. Opposite effects of pollination and herbivory on selection. a. b. Variations in basal interaction rates. c. d. Variations in niche widths. Results are from our second Monte Carlo experiment (MC 2, appendix B.II.3), with 1000 interspecific parameter sets sampled at each point. Y-axes indicate the normalized size of the basins of attraction (Mean ± SE) associated with each type of selection (see appendix B.II.1). 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. C2 (Appendix C.II) for robustness.

401 Stabilizing selection dominates the selective landscape (Fig. 4), indicating that
402 evolutionary dynamics usually tend to maintain plant-animal coexistence. This result is robust
403 to the modification of the ecological parameter set (Appendix C.II).

404 Disruptive selection is possible at strong trade-offs, but not at weak trade-offs that
405 typically lead to stabilizing or runaway selection (Fig 4A). Disruptive selection indeed requires
406 a balance between pollination and herbivory (Fig. 3). Such a balance has to be achieved over a
407 phenotypic region outside $[t_m, t_h]$ for a branching point to occur. Phenotypes within $[t_m, t_h]$
408 are continuously selected toward the pollinator phenotype and away from the herbivore one so
409 that no singularity is possible between the two animal traits (see equation 3). When the trade-
410 off is strong, balanced interactions naturally emerge as animal phenotypes are similar. When
411 animals have very dissimilar phenotypes, pollination to herbivory ratios are either large or small
412 outside $[t_m, t_h]$, depending on which animal phenotype is closer to the plant phenotype. As a
413 result, selection is either stabilizing or runaway at weak trade-offs. Note finally that disruptive
414 selection is seldom observed with our second ecological parameter set (Fig. C2.A, Appendix
415 C.II), and that it again does not occur at weak trade-offs.

416

417 The reported opposite influence of pollination and herbivory on local selection extends
418 in a consistent manner to the selective landscape (Fig. 4B). More precisely, the distribution of
419 basins of attraction associated with each type of selection shifts towards a higher prevalence of
420 stabilizing selection with stronger pollination, and a higher prevalence of runaway selection
421 with stronger herbivory.

422 Increasing the basal rate of pollination (a_{pm0}) favors stabilizing selection at the expense
423 of disruptive and runaway selection (Fig. 4B.a). On the contrary, higher herbivory rates (a_{ph0})
424 favor disruptive and runaway selection at the expense of stabilizing selection (Fig. 4B.b). These
425 results suggest that the prevalence of disruptive selection is restricted by strong pollination and

426 fostered by strong herbivory (Fig 4B. a vs. b). A narrower pollination niche width (σ_{Pol})
427 increases the prevalence of stabilizing selection at the expense of disruptive selection (Fig.
428 4B.c). In contrast, disruptive and runaway selection become more frequent as the herbivory
429 niche width (σ_{Her}) gets narrower (Fig. 4B.d). Variations are, however, less pronounced for
430 niche widths (σ) than for interaction rates (a_0). Moreover, only in the case of interaction rates
431 are these patterns robust to the variation of the ecological parameter set (Appendix C.II). While
432 basal rate variations have a consistent effect on interaction strength across the phenotypic space,
433 niche width variations increase or decrease interaction strength depending on plant-animal trait
434 matching (i.e. $t_p - t_m, t_p - t_h$) , likely explaining such a difference.
435
436 Changes in the niches of pollination and herbivory modify community eco-evolutionary
437 dynamics, but these modifications are mainly driven by changes in evolutionary dynamics at
438 strong trade-offs, and changes in ecological dynamics at weak trade-offs (Fig. 5 & S2,
439 Supporting Material).
440 At weak trade-offs, varying interaction basal rates (Fig. 5) or niche widths (Fig. S2)
441 mainly affects the composition and stability of the ecological communities, i.e. background
442 colors in Fig. 5 & S2. The selective landscape, characterized by stabilizing vs. runaway
443 selection close the pollinator vs. herbivore phenotype (as in Fig. 2A), remains essentially
444 unaltered. In particular, increasing the basal rate of pollination eventually selects for phenotypes
445 leading to unstable community dynamics (e.g. Fig. 5a vs. 5b). Increasing the rate of herbivory
446 restores stability (e.g. Fig. 5b vs. 5d). Note also the narrower set of plant phenotypes allowing
447 coexistence when herbivory becomes more specialized (e.g. Fig. S2a vs. S2c). Close to the
448 herbivore phenotype, the resulting increase in herbivory strength (equation 2) reduces plant
449 density so that pollinators no longer survive. Close to the pollinator phenotype, the resulting
450 decrease in herbivory strength impedes herbivore survival. Plant evolution within the three-

species community then provokes the extinction of herbivores. More specialized pollination can restore coexistence, but exposes the community to unstable dynamics (Fig. S2c vs. S2d).

At strong trade-offs, basal rates or niche widths variations primarily modify the selective landscape – i.e. evolutionary singularities in Fig. 5 & S2 – while the ecological context remains essentially unaffected. Evolutionary dynamics may utterly change. For instance, increasing herbivory can shift the selection regime from stabilizing to disruptive (Fig. 5a vs. 5c), due to the modification of the number of singularities (one vs. three), and of their type (a CSS becoming a branching point). The plant-animal community is significantly modified by the emergence of plant dimorphism, maintained in this case. Modifications of the position of singularities, CSSs in particular, can also have far-reaching implications for the maintained community. A stronger herbivory displaces CSS phenotypes closer to animal extinction thresholds (e.g. Fig. 5a vs. 5c), which implies a fragile coexistence. Given small animal densities, coexistence is indeed vulnerable to perturbations or stochasticity. Stronger pollination, in contrast, displaces the CSS phenotypes away from extinction boundaries (e.g. Fig. 5c vs. 5d).

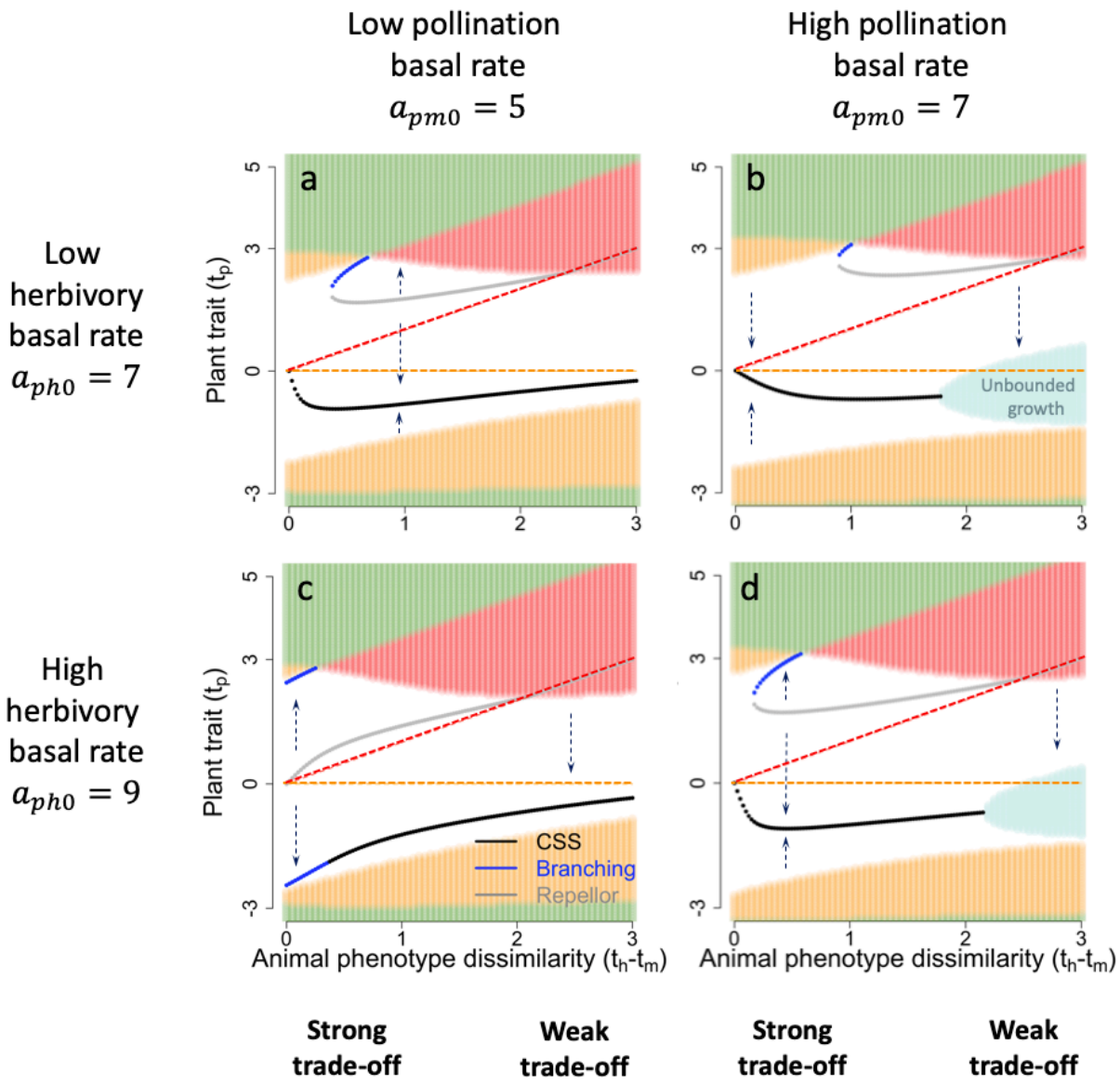


Fig. 5: Effect of the basal rates of plant-animal interactions on community eco-evolutionary dynamics. At strong trade-offs, eco-evolutionary dynamics are primarily altered by changes affecting evolutionary singularities. At weak trade-offs, the alteration is mainly mediated by changes in the composition of the ecological community (i.e. background colors). Orange and red dotted lines indicate the pollinator and herbivore phenotype. Arrows indicate evolutionary trajectories and background colors indicate community composition as in Fig. 2A, with light blue figuring unstable population dynamics corresponding to unbounded growth. 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: $\sigma_{Pol} = 1.7$, $\sigma_{Her} = 2$.

Maintenance of plant dimorphism arising from disruptive selection

Disruptive selection on the plant phenotype arises from the interplay of pollination and herbivory. The resulting dimorphism is often temporary, but stable dimorphism is possible in

481 the case of strong trade-offs. Simulating the eco-evolutionary dynamics following the 676
482 branching points encountered during our second Monte Carlo experiment when constraining
483 the sampling of trade-off intensity, we indeed find that dimorphism is maintained in only 6%
484 of the cases, all occurring at very strong trade-offs ($t_h - t_m \leq 0.5$). At such trade-offs,
485 however, the maintenance of dimorphism is relatively frequent, representing around 27% of the
486 cases (details in appendix D). Interestingly, we find that the ratio of pollination to herbivory at
487 branching $\left(i.e.\ \left.\frac{a_{pm}M^*}{a_{ph}H^*}\right]_{t_p^*}\right)$ again largely explains the maintenance of dimorphism at these
488 strongest trade-offs (Wilcoxon test, $p_{value} < 10^{-10}$ & $effect_{size} \approx 50\%$, see Fig. 6A).
489 Dimorphism maintenance is associated with stronger herbivory than pollination, which
490 suggests a decisive role of herbivory in the process. We finally show that even a slight amount
491 of similarity-dependent competition suffices to maintain dimorphism in the cases where it is
492 lost (Fig. 6B). To do this, we reformulate our model assumptions to make intraspecific plant
493 competition depend on the phenotypes of competing plant individuals (equation 5).
494 Competition between two plant phenotypes (t_{p1}, t_{p2}) now declines as their niche-overlap (i.e.
495 $t_{p1} - t_{p2}$) decreases, (5)α_c and σ_c being the input parameters controlling the proportion and
496 shape of similarity-dependent competition, respectively.

$$c_p \rightarrow c_p(t_{p1}, t_{p2}) = (1 - \alpha_c)c_p + \alpha_c e^{\frac{-(t_{p1}-t_{p2})^2}{2\sigma_c{}^2}} c_p \qquad (5)$$

497

498 Five percent of similarity-dependence can enable the maintenance of dimorphism (Fig. 6B. a
499 vs. b). Ten percent of similarity-dependence can lead to secondary branching events and the
500 emergence of plant polymorphism (Fig. 6B.c), which suggests a potential role of the interplay
501 between pollination, herbivory and associated niche-overlap competition in the diversification
502 of flowering plant species.

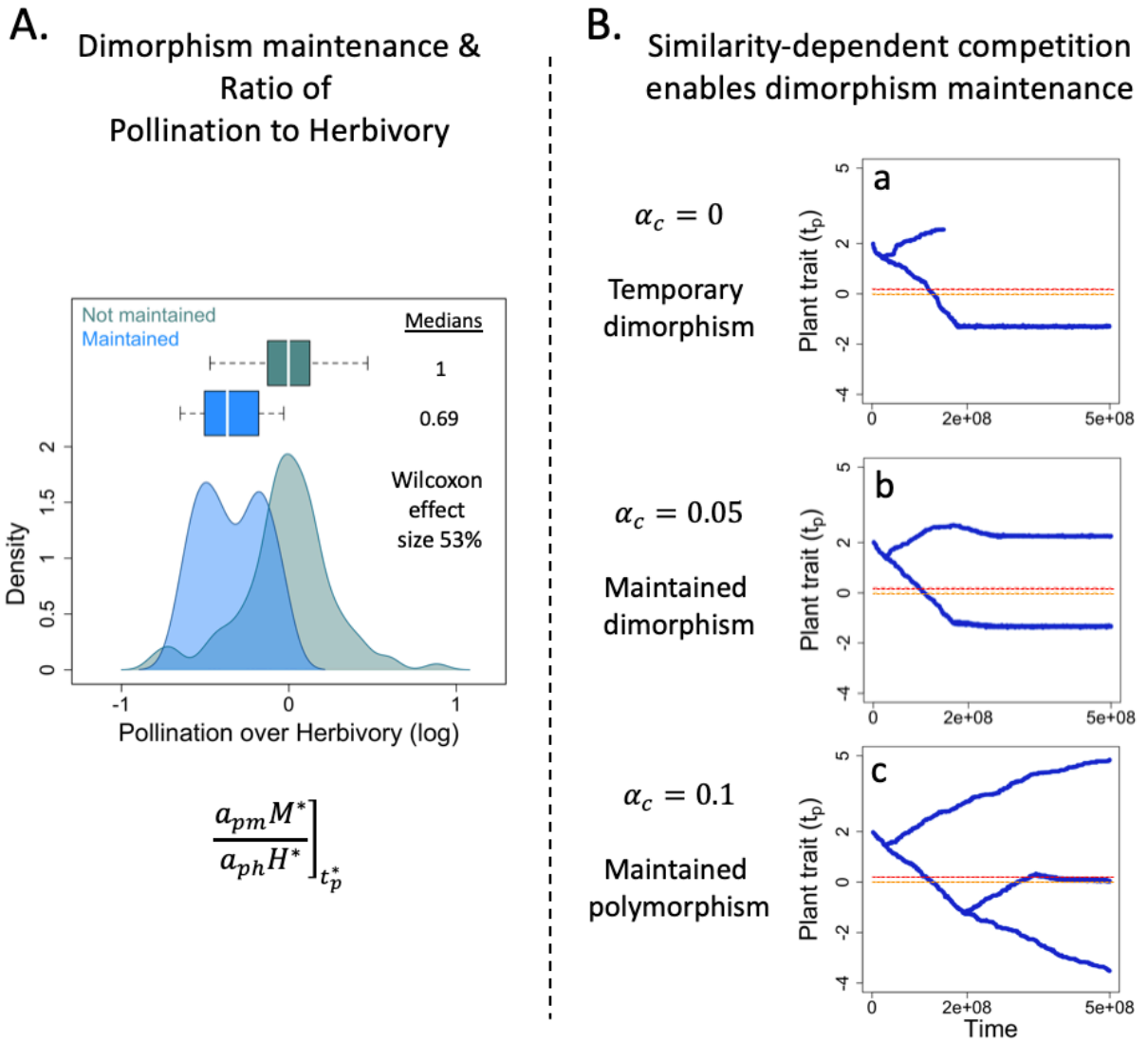


Fig. 6: The maintenance of plant dimorphism. A. Ratio of pollination and herbivory at branching explains the maintenance of plant dimorphism. The branchings considered here are those occurring at very strong trade-offs ($t_h - t_m \leq 0.5, 154/676$), given that dimorphism maintenance is only possible at such strong trade-offs. Wilcoxon $p_{value} < 10^{-10}$. **B. Emergence and maintenance of polymorphism are favored by similarity-dependent competition. a. No similarity-dependent competition.** The branching corresponds to that presented in **Fig. 2B.e**. **b. Five percent of similarity-dependent competition** enables the maintenance of plant dimorphism. **c. Ten percent of similarity-dependent competition** enables secondary branchings, leading to a polymorphic plant population. Ecological parameter set: ($r_p = 10, r_m = -1, r_h = -4, c_p = 0.6, c_m = 0.5, c_h = 0.4, e_m = 0.2, e_h = 0.3$). Interspecific parameter set: ($a_{pm0} = 5, a_{ph0} = 7, \sigma_{Pol} = 3, \sigma_{Her} = 2.8$). Animal phenotypes are indicated with orange (pollinator) and red (herbivore) dotted lines: ($t_m = 0, t_h = 0.2$).

517 # Discussion

518 In this article, we investigate how the eco-evolutionary dynamics of plant-pollinator-
519 herbivore communities are driven by the evolution of plant traits under conflicting selection.
520 Conflicting selection arises from the ecological trade-off between attracting pollinators and
521 escaping herbivores which naturally emerges in a trait-matching framework. We find that
522 stronger pollination makes stabilizing selection more prevalent and facilitates coexistence.
523 Stronger herbivory increases the prevalence of runaway selection and threatens coexistence.
524 Importantly, joint selection may be disruptive, leading to plant diversification. Such a
525 diversification requires strong trade-offs, with the strongest trade-offs allowing its long-term
526 maintenance. At weak trade-offs, coexistence is threatened as runaway dynamics are more
527 frequent. Stabilizing selection can still maintain coexistence, but the intrinsic imbalance of
528 plant-animal interactions makes it vulnerable to perturbations. The strength of the ecological
529 trade-off appears as a structuring determinant of community eco-evolutionary dynamics.
530

531 We find that pollination fosters the convergence toward the pollinator phenotype – i.e.
532 stabilizing selection – while herbivory favors the divergence from the herbivore phenotype –
533 i.e. runaway selection. Such opposite selection pressures have notably been found acting on
534 flower color (Irwin *et al.* 2003; Frey 2004), shape (Galen & Cuba 2001) or display (Gómez
535 2005), nectar quantity (Adler & Bronstein 2004) and flowering phenology (Brody 2008; Ehrlén
536 & Münzbergová 2009). Conceptually, all traits that make the discovery of a plant species easier
537 for interacting species – i.e. more "apparent" (Feeny 1976), e.g. high abundance, large size,
538 wide phenology… – may experience ecological trade-offs as they facilitate the discovery by
539 both allies and enemies. A consequence of such trade-offs is that plant phenotypes deviate from
540 optima favored by pollinators (CSSs $\neq t_m$ in Fig. 5), as illustrated by Ramos & Schiestl (2019).
541 Using experimental evolution, the authors show that plants that evolved in the presence of both

542 pollinators and herbivores were less attractive to pollinators than those that evolved with only
543 pollinators, but still more attractive than plants that evolved with hand-pollination, with or
544 without herbivores. The presence of pollinators thus selected toward plant-pollinator trait
545 matching, but the presence of herbivores reduced such matching by adding a runaway
546 component to selection (equation (3)).
547
548 Recent data have highlighted the occurrence of vast insect declines (Hallmann *et al.*
549 2017; Outhwaite *et al.* 2022). Such declines may be accompanied by changes in the relative
550 frequency of antagonistic vs mutualistic interactions (e.g. herbivores vs pollinators). Given
551 massive pollinator declines (Potts *et al.* 2010) for instance, plant-animal interactions could
552 become increasingly biased towards antagonism. Given our results, this should favor runaway
553 selection thereby leading to plant phenotypes maladapted to pollinators, further accelerating
554 their declines (see also Weinbach et al. 2022). Herbivore extinctions are also expected as a
555 result of more frequent runaway dynamics. Contrary to our assumption of being fixed, animal
556 phenotypes also evolve to match their resource phenotype in natural settings (e.g. Berenbaum
557 and Zangerl 1998; Muchhala 2006). Runaway dynamics are therefore not expected to
558 systematically provoke the extinction of one or both animals, but their ecological outcome will
559 rather depend on the relative speed of evolution of the different species (e.g. evolutionary
560 rescue, Gomulkiewicz and Holt 1995).
561
562 More generally, several assumptions that simplify the evolutionary process are made
563 within our modeling framework. The assumption of fixed animal phenotypes might prove to be
564 relevant for some specific communities in which the plant evolves at a much faster rate than
565 the animals owing to higher mutation rates, standing genetic variation, reproduction rates or
566 lifespans. Animal morphologies, preferences, detection abilities or phenologies may however

567 coevolve with plant phenotypes in natural communities (Thompson 2009). Results of this
568 coevolution will depend on the relative speeds of evolution of all interactors, which may lead
569 to many different scenarios whose analyses go beyond the scope of this article. Our work aims
570 at developing an in-depth analytical understanding of the dynamics resulting from the sole plant
571 evolution, before more complex coevolutionary scenarios are studied. We acknowledge that it
572 is not straightforward to extend our results to these scenarios as a higher trait dimensionality
573 can substantially alter evolutionary dynamics (Kisdi 2006; Débarre *et al.* 2014). Another
574 assumption of our framework is that plant evolution has no other costs than those ensuing from
575 pollination and herbivory. We used this assumption to better highlight the direct implications
576 of ecological trade-offs. This might be a reasonable approximation for specific traits whose
577 selective pressures essentially arise from these plant-animal interactions (e.g. presumably
578 flower color in *Raphanus sativus,* Irwin et al. 2003), but plant traits are highly multifunctional
579 in general. They are indeed often also involved in other types of interactions (Strauss & Whittall
580 2006) or processes such as stress tolerance (Sack & Buckley 2020). A direct consequence is
581 that phenotypes are usually constrained within an ecologically viable space, which notably sets
582 a limit to runaway dynamics, mitigating the likelihood of extinctions.
583
584 In line with the empirical evidence so far (Strauss *et al.* 2002; Strauss & Irwin 2004),
585 our study identifies the strength of ecological trade-off as a key driver of plant-animal eco-
586 evolutionary dynamics. We underline that trade-off intensity affects the maintenance of
587 coexistence, as well as the nature of joint selection, in particular the potential for disruptive
588 selection and plant diversification.
589 We find that coexistence is fragile or destroyed at weak trade-offs. Runaway dynamics
590 are more frequent (Fig. 4A). Evolutionary-induced unstable dynamics become possible (Fig.
591 5b&d). In the vicinity of the pollinator phenotype, the plant phenotype is more likely to stabilize

592 after the extinction of herbivores, as indicated by the CSSs leaving the coexistence area (Fig.
593 2A). When stabilizing selection occurs before herbivore extinction, their low density makes
594 them vulnerable to demographic stochasticity, Allee effects or external disturbances. Because
595 weak ecological trade-offs are associated with fragile plant-pollinator-herbivore coexistence,
596 they should be seldom encountered in natural communities. Accordingly, shared animal
597 preferences for plant phenotype are most often reported in the empirical literature (Adler &
598 Bronstein 2004; Strauss & Whittall 2006).

599 Selection can turn disruptive under stronger ecological trade-offs. We stress that
600 disruptive selection here arises from the joint selection of pollination and herbivory. In the
601 absence of either one interaction, branching is not possible here, as evolutionary dynamics
602 would run away from the herbivore phenotype in the absence of pollination, and would stabilize
603 at the pollinator phenotype in the absence of herbivory. Diversification we uncover here is thus
604 fundamentally different from the one uncovered in previous trait-matching models that consider
605 the two interactions separately (e.g. Yoder and Nuismer 2010; Maliet et al. 2020). While
606 dimorphism can only be maintained when the trade-off is sufficiently strong, long-term
607 maintenance is frequent in such instances. Polymorphism then yields two contrasted
608 phenotypes: one that has many allies and enemies, while the other one has few interactions.
609 Interestingly, such a pattern has been frequently reported in the empirical literature. In *Primula*
610 *farinosa,* the fitness advantage of long-scaped phenotypes resulting from higher pollinator
611 visitation rates is balanced by higher levels of fruit predation, allowing the maintenance of
612 dimorphism in scape length (Ehrlén *et al.* 2002). The maintenance of color dimorphism in
613 *Raphanus sativus* (Irwin *et al.* 2003) and *Claytonia virginica* (Frey 2004) is similarly supported
614 by animal species preferentially interacting with the same plant phenotype. Field studies of
615 tripartite networks also report a positive correlation between the number (Sauve *et al.* 2016b)
616 or strength (Melián *et al.* 2009) of plant-pollinator and plant-herbivore interactions of plant

617 species, indicating a rather widespread pattern. This mechanism of diversification under
618 balanced interaction strengths may also apply on longer evolutionary timescales. Using a
619 phylogenetic analysis on 32 *Nicotiana* species, Adler *et al.* (2012) show that variations in
620 nicotine defenses among species are largely negatively correlated to pollinator reliance. These
621 tobacco species are therefore either well-defended with few pollinators, or lowly defended and
622 relying on pollination.
623
624 We find that disruptive selection requires a local balance between pollination and
625 herbivory (Fig 3), while its prevalence within the selective landscape increases with the
626 strength of herbivory (Fig. 4B). This is not contradictory as those aspects describe selection at
627 two different scales. To put it simply, disruptive selection can be expected in any three-species
628 community when plant-animal interactions are well-balanced, but communities in which
629 herbivores are more ravenous ($a_{ph0} \nearrow$) will more likely exhibit such evolutionary dynamics.
630 Dimorphism is also more likely to be permanent with stronger herbivory (Fig. 6A), further
631 emphasizing its decisive role in diversification processes. Previous theoretical works that
632 contrast interaction types but one at a time have also highlighted the crucial role of antagonisms
633 for diversification (Kopp & Gavrilets 2006; Yoder & Nuismer 2010; Maliet *et al.* 2020). Given
634 these results, we note that observed declines in the diversity and abundances of herbivore
635 species (Sánchez-Bayo & Wyckhuys 2019; Atwood *et al.* 2020) may have far-reaching
636 consequences if they lead to future reductions in diversification rates.
637
638 Overall, dimorphism is often temporary within our framework. While we assume
639 constant competition rates in order to focus on how trophic vs mutualistic interactions shape
640 eco-evolutionary dynamics, similarity-dependent competition is likely to occur in natural
641 communities (Macarthur & Levins 1967). Here, similar plants would share pollinators, which

642 could lead to strong pollination niche-overlap competition for instance due to the dilution of
643 pollen between plant species (Morales & Traveset 2008; Mitchell *et al.* 2009). Similarly, shared
644 herbivores would increase apparent competition. Plant traits can also be simultaneously
645 involved in both competitive and plant-animal interactions, either directly (e.g. phenological
646 traits, Schwinning & Kelly 2013) or due to genetic correlations (e.g. plant size, Carmona *et al.*
647 2011). Accounting for a small amount of niche-overlap competition suffice to maintain
648 dimorphism in our model, and enhances the potential for further diversification (Fig. 6B).
649 Reproductive isolation may then evolve as the morph that interacts weakly with animal species
650 acquires new pollinators species (Baack *et al.* 2015), or evolves self-fertilization (Bodbyl Roels
651 & Kelly 2011). Disruptive selection from the interplay of pollination, herbivory and niche-
652 overlap competition can therefore be construed as a first step toward modeling the evolutionary
653 emergence of plant-pollinator-herbivore networks, which would allow new insights into the
654 eco-evolutionary processes supporting the diversity of natural communities.
655

656 # Supporting information

657 Supplementary details, notably including the derivation of mathematical expressions and
658 demonstrations, are provided online (directly on BioRxiv, or on Zenodo via
659 https://doi.org/10.5281/zenodo.10497716). It consists of 2 additional figures (S1, S2), one table
660 (S1) and 4 appendices (A, B, C & D).
661

662 # Data availability statement

663 The codes used to conduct the Monte Carlo numerical experiments, as well as that used to
664 simulate the community eco-evolutionary dynamics, are available in Zenodo
665 (https://doi.org/10.5281/zenodo.10497716).

Conflict of interest disclosure

The authors declare they have no conflict of interest relating to the content of this article.

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