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 their joint effect constrains 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.

Introduction

Flowering plants (i.e. angiosperms) are the most diverse and successful plant clade in terrestrial ecosystems, representing almost 90% of the species described (Hernández-Hernández and Wiens 2020). Most of them rely on animals for pollination (Ollerton et al. 2011). Because animal pollination can favor reproductive isolation, it has been proposed early as an important diversity driver among angiosperms (Grant 1949). Plant-herbivore interactions have, however, also been identified as potentially fostering diversification due to the ensuing evolutionary arms race between interacting antagonists (Ehrlich and Raven 1964). These two non-mutually exclusive hypotheses are supported by several phylogenetic investigations. Plant-pollinator coevolution explains higher diversification rates within angiosperms (Hodges and Arnold 1995; Sargent 2004; Hernández-Hernández and Wiens 2020), but plant-herbivore coevolution also spurs plant diversification as a result of defense-counterdefense innovations (Farrell et al. 1991; Becerra et al. 2009). Plant phylogenies reveal that plant-pollinator and plant-herbivore coevolution are 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 due to the interplay between pollination and herbivory (Strauss and Irwin 2004), floral traits in particular (Strauss and Whittall 2006). Conflicting selection pressures can emerge from several mechanisms acting either in isolation or synergistically. Herbivory-induced changes in plant chemistry potentially reduce pollinator visitations (e.g. Kessler *et al.* 2011). Many plant traits acting on the plant visibility (size, phenology, floral display, volatile compounds) may increase herbivory (apparency hypothesis, Feeny 1976) while also attracting allies (e.g. Brody 2008). Genetic correlation can also exist between two plant traits, each involved in one plant-animal interaction

(Strauss *et al.* 2004). A decisive consequence is that the selection pressures in the absence of either one animal species would be modified in the presence of both animal groups (Ramos and 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 and Whittall 2006) and that promotes the stable coexistence of the community (Yacine and Loeuille 2022). 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 also lead to disruptive selection and promote diversification.

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

As stronger mutualism increases fitness, plants are selected to better match their pollinator phenotype and vice versa (e.g. spur length and pollinator tongue, Whittall & Hodges 2007) so that stabilizing selection is expected (e.g. Kiester *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 and Gavrilets 2006; Yoder and Nuismer 2010; Maliet et al. 2020).

Conversely, predation reduces prey fitness so that plants are selected to escape herbivore preferences (e.g. chemical defenses and herbivore tolerance, Becerra *et al.* 2009). Such arms race dynamics (Ehrlich and Raven 1964; Dawkins and Krebs 1979) expose the plant species to runaway selection, as observed 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 thereby enhancing disruptive selection (Kopp and Gavrilets 2006; Yoder and Nuismer 2010; Maliet et al. 2020).

The ecological implications of such conflicting selection are far-reaching. The relative interaction strength of pollination vs. herbivory has been shown to constrain coexistence within plant-pollinator-herbivore communities (Mougi and Kondoh 2014; Sauve et al. 2016*a*; Yacine and Loeuille 2022). A balance between the two interactions is expected to foster coexistence. Because interaction strengths are the result of plant-animal coevolution, the evolution of plant traits under conflicting selection may have important consequences for multispecies coexistence.

In the present paper, our goals are (1) to determine how the interplay of pollination and herbivory drives the evolution of plant traits involved in both interactions, (2) to understand the consequences for multispecies coexistence, and (3) to assess how ecological trade-offs may lead to stabilizing vs. disruptive selection. We model 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 increases in strength with the matching of plant and animal phenotypes. 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 or detection abilities. Phenological matching (e.g. Brody 2008) would also fit our framework well. Using adaptive dynamics (Metz et al. 1992; Dieckmann and Law 1996), we determine how the coupling of pollination and herbivory determine plant evolutionary dynamics, and in turn, how such evolution affects coexistence maintenance.

In particular, we modulate the strength of the trade-off by manipulating the dissimilarity between animal phenotypes (x-axis in Fig. 1A). An important dissimilarity allows plants to escape herbivory while paying little cost in terms of pollination, or conversely to match pollinators while paying little cost in terms of herbivory. The ecological trade-off is therefore weak. In such instances (Fig. 1A-right), we expect selection to favor plant phenotypes away from the herbivore phenotype. Such runaway dynamics may either lead away from the pollinator phenotype, resulting in the loss of both animals (Fig. 1B.1a), or towards the pollinator phenotype around which they eventually stabilize before herbivores are lost (Fig. 1B.2). If herbivores are lost, stabilizing selection provided by pollinators eventually prevails (temporality, Fig. 1B.1b). In general, because interactions are unbalanced under weak trade-offs, we expect coexistence to be rarely favored. In contrast, when animal phenotypes are very similar, any plant evolution toward more pollinator attraction directly increases herbivory, and any escape from herbivory comes with a direct cost in pollination. The ecological trade-off is thus strong. In such cases (Fig. 1A-left), interactions are intrinsically correlated, so that coexistence should be more systematically observed. As herbivory and pollination selection effects are more balanced, selection regimes may vary from stabilizing to disruptive depending on parameter scenarios. In the latter case, stable plant dimorphism may emerge (Fig. 1B.3).

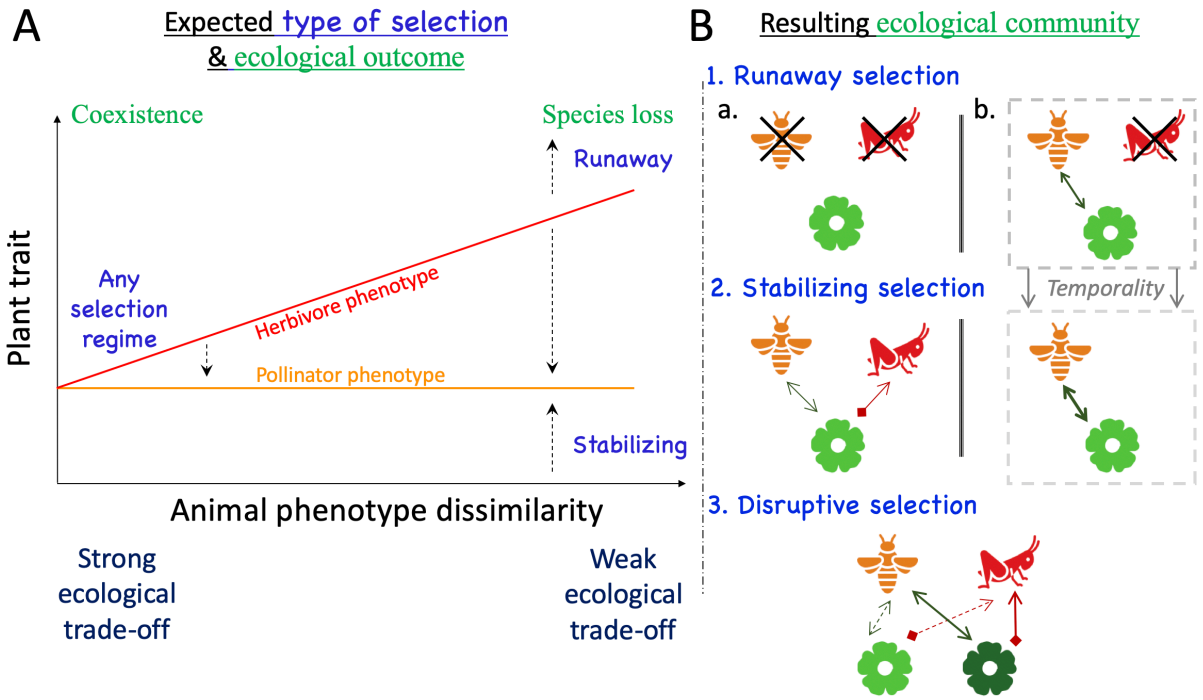


Fig. 1: Expected eco-evolutionary dynamics within the plant-pollinator-herbivore community. A. The type of selection and the ecological outcome depend on the dissimilarity between animal phenotypes (i.e. preferences), which is a proxy for the strength of the ecological trade-off. **B.** The long-term 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 (i.e. temporality), 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.

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 ($r_p > 0$, 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.

Without evolution, stable coexistence occurs when the strengths of pollination and herbivory are balanced (Yacine and Loeuille 2022). The analytical expression of the coexistence equilibrium (P^*, M^*, H^*) is given in Appendix A.I. Here, we investigate how the interaction balance (i.e. pollination vs. herbivory) affects plant evolution, and how such evolution, in turn, constrains 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)). 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 (***M*** for mass, ***L*** for length and ***t*** for time).

Variables and parameters		Biological definition	Value	Dimension
Variables	P	Plant biomass density		$M.L^{-2}$
	M	Pollinator biomass density		$M.L^{-2}$
	H	Herbivore biomass density		$M.L^{-2}$
	t_p	Plant phenotype		Dimensionless
Animal phenotypes	t_m	Pollinator phenotype	0	Dimensionless
	t_h	Herbivore phenotype	[0,3]	Dimensionless

Interspecific interaction parameters	$t_h - t_m$	Strength of ecological trade-off	[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	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	$(M.L^{-2})^{-1}.t^{-1}$
	c_m	Pollinator intra-specific competition rate	0.5 $(or\ 0.4)$	$(M.L^{-2})^{-1}.t^{-1}$
	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}	$(M.L^{-2})^{-1}.t^{-1}$
	σ	Mutation amplitude (standard deviation)	0.02	Dimensionless
	ε	Extinction threshold	2.10^{-6}	$M.L^{-2}$

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). 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. In particular, the dissimilarity between animal phenotypes ($t_h - t_m$) constrains the strength of the ecological trade-off affecting plant evolution (Fig. 1A). The trade-off gets stronger as animal phenotypes get similar (details in Appendix B.I).

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. 1A, Fig. 2A). To broaden our understanding of possible evolutionary dynamics, we undertake Monte Carlo experiments (details in appendix B.III). 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.II). 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 (code available in Dryad). Such simulations are used to investigate the emergence of plant dimorphism in the case of disruptive selection.

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

232 (Dieckmann and Law 1996). Evolutionary singularities t_p^* correspond to phenotypes that nullify
233 the selection gradient.

234 The type of selection – stabilizing, disruptive, or runaway – acting on the plant trait
235 depends on (1) the properties of the evolutionary singularities, and (2) the position of the plant
236 phenotype relative to these singularities. Two independent properties - convergence and
237 invasibility – characterize evolutionary singularities (criteria in appendix A.II). Convergence
238 indicates whether the trait evolves toward the singularity in its vicinity. Two types of
239 singularities are convergent – the non-invasible continuously stable strategy (CSS, Eshel, 1983)
240 and the invasible branching point (Geritz *et al.* 1997). Invasibility specifies whether the
241 singularity may be invaded by nearby mutants (i.e. ESS, Maynard Smith & Price 1973). CSS
242 phenotypes correspond to cases of stabilizing selection (e.g. Fig. 2B.a). Selection is thus
243 considered stabilizing in the basin of attraction of a CSS. Plant-pollinator-herbivore coexistence
244 is notably maintained if a CSS is reached while the three species coexist (Fig. 1B.2). In contrast,
245 a branching point yields the emergence of plant dimorphism (Fig. 1B.3) due to disruptive
246 selection (e.g. Fig. 2B.d). Accordingly, selection is considered disruptive in the basin of
247 attraction of a branching point. Finally, phenotypes that are not in the basin of attraction of a
248 convergent singularity are under runaway selection. This is possible in the presence of a non-
249 convergent singularity, i.e. a repellor. For the sake of simplicity, we will refer to this set of
250 phenotypes as the basin of attraction associated with runaway selection. Runaway selection
251 should always disrupt plant-pollinator-herbivore coexistence (Fig. 1B.1, e.g. Fig. 2B.b). We
252 illustrate how the proportion of phenotypic space under each type of selection is calculated in
253 Appendix B.III.1.

254 This framework is completed by numerical simulations starting from a monomorphic
255 plant population (t_p) interacting with a pollinator (t_m) and a herbivore (t_h) population.
256 Mutations are randomly generated following a Poisson process characterized by a mutation

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).

Results

As expected (Fig. 1), 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 favor 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.

282 For even weaker trade-offs (region VI), the CSS exits the coexistence area so that only runaway
283 selection remains possible. It provokes the extinction of both animal species when starting
284 above the repellor, and that of herbivores when starting below the repellor. The extinction of
285 herbivores then leads to a perfectly matched plant-pollinator community (Fig. 2B.d).

286 The ecological consequences (Fig. 2B) associated with each type of selection also match
287 our predictions (Fig. 1B). Coexistence is always maintained in the case of stabilizing selection.
288 It is always disrupted in the case of runaway selection due to the weakening of one or both
289 plant-animal interactions. Disruptive selection allows the emergence of plant dimorphism. The
290 two plant phenotypes diverge, one leading to stronger plant-animal interactions, the other to
291 weaker plant-animal interactions. Dimorphism can be temporary (Fig. 2B.e) or permanently
292 maintained (Fig. 2B.f). An example of eco-evolutionary landscape associated with permanent
293 dimorphism is given in Fig. S1 (Supporting Material), while the landscape presented in Fig. 2A
294 typically leads to temporary branchings. In addition to trade-off intensity, other interspecific
295 parameters can thus be responsible for qualitative changes in eco-evolutionary dynamics. Most
296 of such (qualitative) variation is covered by the simulations in Fig. 2B.

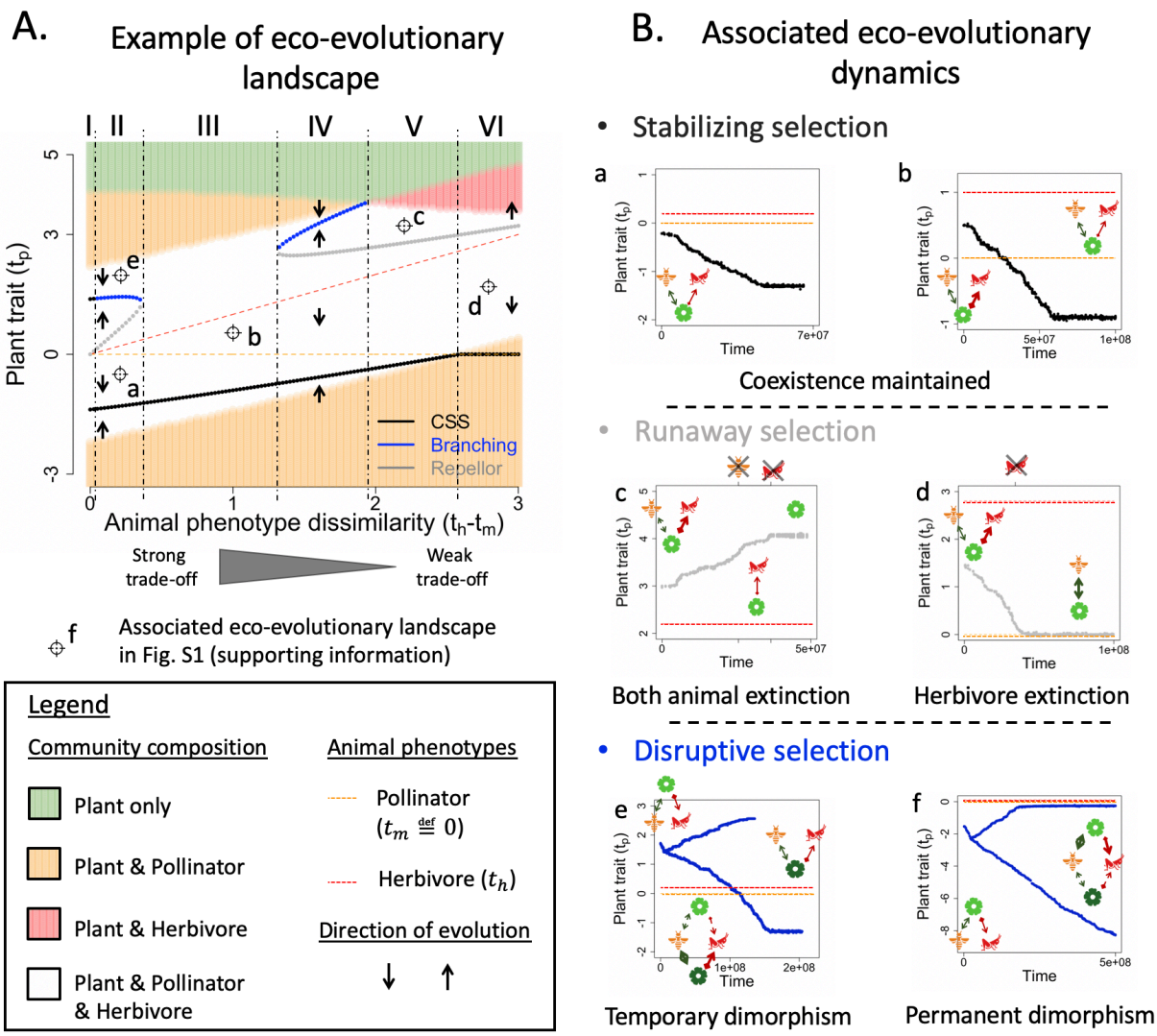


Fig. 2: Typical examples of eco-evolutionary dynamics with their associated eco-evolutionary landscape. A. Eco-evolutionary landscape. The points labelled by letters indicate the initial conditions of the simulations presented in B. Ecological parameter set: ($r_p = 10, r_m = -1, r_h = -4, c_p = 0.6, c_m = 0.5, c_h = 0.4, e_m = 0.2, e_h = 0.3$). 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.

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

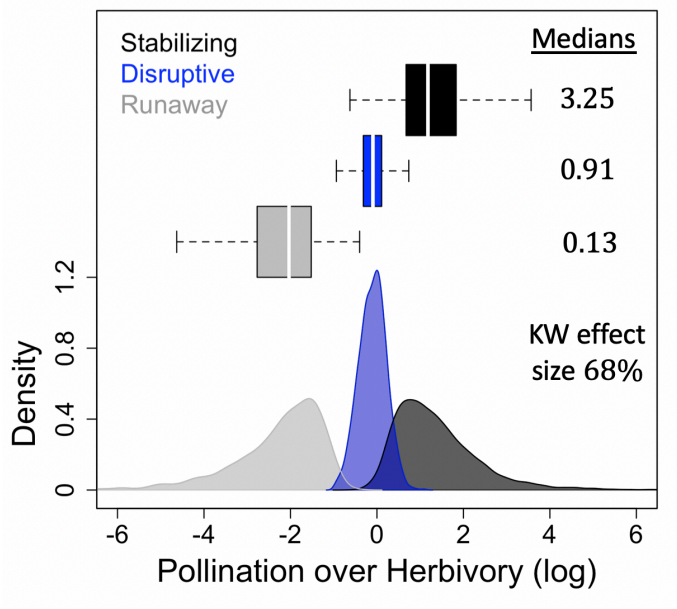
$$\frac{dt_p}{dt} \propto \begin{matrix} Selection \\ gradient \end{matrix} = \underbrace{-\frac{a_{pm}(t_p)M^*}{\sigma_{Pol}^2}}_{pollination}(t_p - t_m) + \underbrace{\frac{a_{ph}(t_p)H^*}{\sigma_{Her}^2}}_{herbivory}(t_p - t_h) \qquad (3)$$

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).

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

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.III.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).



$$\left.\frac{a_{pm}M^*}{a_{ph}H^*}\right]_{t_p^*}$$

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.III.2), with 10 000 interspecific parameter sets sampled.

High pollination relative to herbivory is associated with stabilizing selection. High herbivory relative to pollination is associated with runaway selection. When pollination and herbivory are balanced, selection turns disruptive. The association of stabilizing, runaway and disruptive selection with respectively high, low and balanced pollination to herbivory ratios implies that the convergence of evolutionary singularities (i.e. convergence stability, Eshel 1983) is favored by pollination and disfavored by herbivory. Disruptive selection requires a balance between pollination and herbivory because strong herbivory relative to pollination fosters invasibility (inequality (4)), but convergence is lost when herbivory is too strong, leading to runaway dynamics (Fig. 3). Note finally that simpler ratios measuring the strength of pollination vs. herbivory (e.g. interaction strengths $\left.\frac{a_{pm}}{a_{ph}}\right]_{t_p^*}$ or animal densities $\left.\frac{M^*}{H^*}\right]_{t_p^*}$) also have a large – but inferior – power in explaining the nature of selection (table S1, Supporting

351 Material). These key results derived from our Monte Carlo experiment are robust to the
352 modification of the ecological parameter set (Appendix C.I).
353
354 Beyond local selection at evolutionary singularities, we now investigate the effect of
355 plant-animal interactions on the selective landscape at large, i.e. the distribution of basins of
356 attraction associated with each type of selection (e.g. Fig. 2A). We build a second Monte Carlo
357 experiment (MC2, details in Appendix B.III.3). For each focal interspecific parameter, we
358 divide the potential range of that parameter (table 1) into six equal intervals to sample from, the
359 sampling of the other interspecific parameters remaining unconstrained. For each sampling (6
360 x 1000), we calculate the proportion of phenotypic space associated with each type of selection
361 (i.e. basin of attraction, see Appendix B.III.1 for details). We thereby estimate the effect of
362 varying (1) the strength of ecological trade-off (Fig. 4A) and (2) the intensity and generalism
363 of pollination and herbivory (Fig. 4B) on the selective landscape.
364

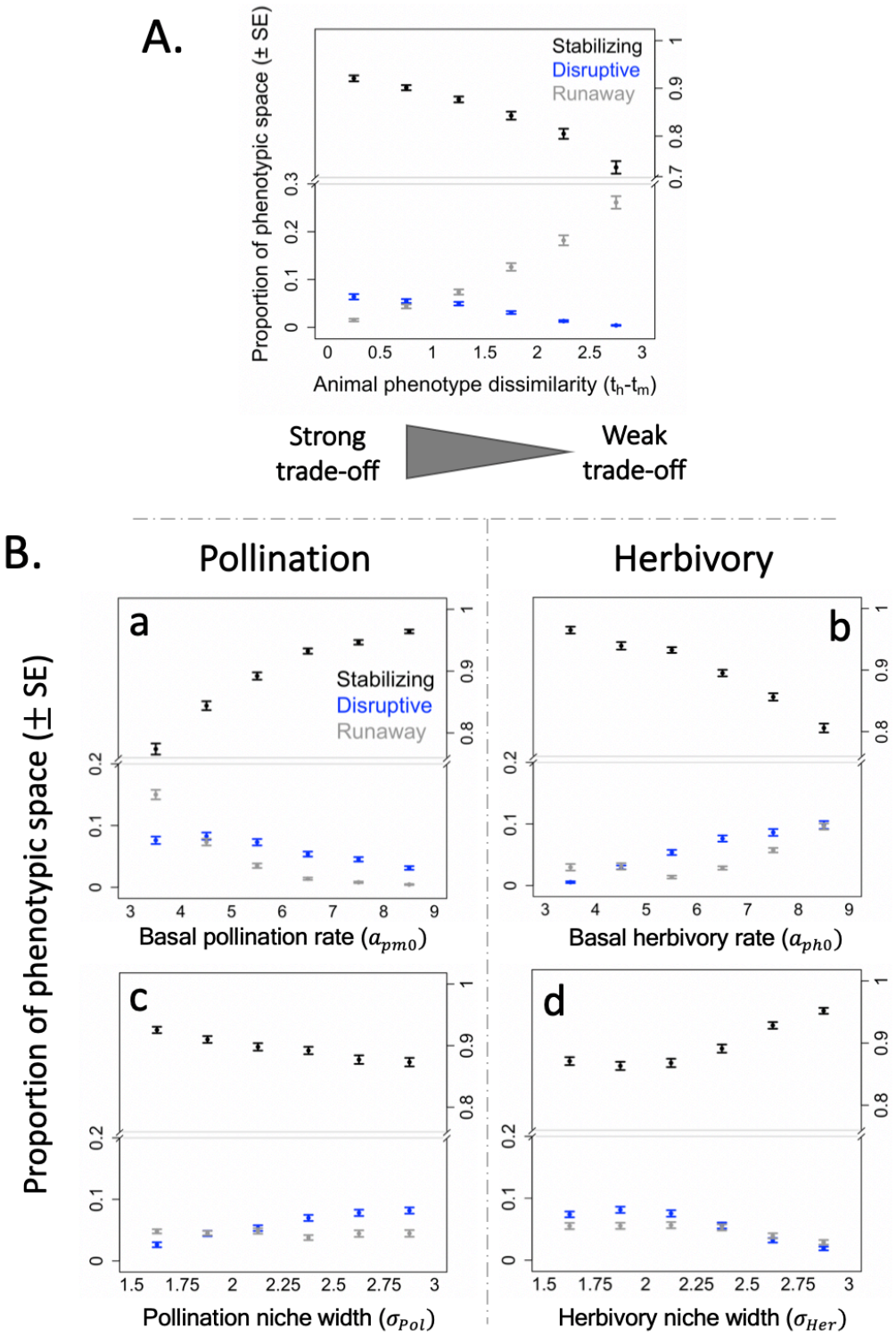


Fig. 4: Effect of interspecific parameters on the selective landscape. A. The selective landscape depends on trade-off intensity. B. Opposite effects of pollination and herbivory on selection. a. b. Variations in basal interaction rates. c. d. Variations in niche widths. Results are from our second Monte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

373 Stabilizing selection dominates the selective landscape (Fig. 4), indicating that
374 evolutionary dynamics usually tend to maintain plant-animal coexistence. This result is robust
375 to the modification of the ecological parameter set (Appendix C.II).
376 Disruptive selection is possible at strong trade-offs, but not at weak trade-offs that
377 typically lead to stabilizing or runaway selection (Fig 4A). Disruptive selection indeed requires
378 a balance between pollination and herbivory (Fig. 3). Such a balance has to be achieved over a
379 phenotypic region outside $[t_m, t_h]$ for a branching point to occur. Phenotypes within $[t_m, t_h]$
380 are continuously selected toward the pollinator phenotype away from the herbivore one so that
381 no singularity is possible between the two animal traits (see equation 3). When the trade-off is
382 strong, balanced interactions naturally emerge as animal phenotypes are similar. When animals
383 have very dissimilar phenotypes, pollination to herbivory ratios are either large or small outside
384 $[t_m, t_h]$, depending on which animal phenotype is closer to the plant phenotype. As a result,
385 selection is either stabilizing or runaway at weak trade-offs. Note finally that disruptive
386 selection is seldom observed with our second ecological parameter set (Fig. C2.A, Appendix
387 C.II), and that it again does not occur at weak trade-offs.
388
389 The reported opposite influence of pollination and herbivory on local selection extends
390 in a consistent manner to the selective landscape (Fig. 4B). More precisely, the distribution of
391 basins of attraction associated with each type of selection shifts towards a higher prevalence of
392 stabilizing selection with stronger pollination, and a higher prevalence of runaway selection
393 with stronger herbivory.
394 Increasing the basal rate of pollination (a_{pm0}) favors stabilizing selection at the expense
395 of disruptive and runaway selection (Fig. 4B.a). On the contrary, higher herbivory rates (a_{ph0})
396 favor disruptive and runaway selection at the expense of stabilizing selection (Fig. 4B.b). These
397 results suggest that the prevalence of disruptive selection is restricted by strong pollination and

398 fostered by strong herbivory (Fig 4B. a vs. b). A narrower pollination niche width (σ_{Pol})
399 increases the prevalence of stabilizing selection at the expense of disruptive selection (Fig.
400 4B.c). In contrast, disruptive and runaway selection become more frequent as the herbivory
401 niche width (σ_{Her}) gets narrower (Fig. 4B.d). Variations are, however, less pronounced for
402 niche widths (σ) than for interaction rates (a_0). Moreover, only in the case of interaction rates
403 are these patterns robust to the variation of the ecological parameter set (Appendix C.II). While
404 basal rate variations have a consistent effect on interaction strength across the phenotypic space,
405 niche width variations increase or decrease interaction strength depending on plant-animal trait
406 matching (i.e. $t_p - t_m, t_p - t_h$) , likely explaining such a difference.
407
408 Changes in the niches of pollination and herbivory modify community eco-evolutionary
409 dynamics, but these modifications are mainly driven by changes in evolutionary dynamics at
410 strong trade-offs, and changes in ecological dynamics at weak trade-offs (Fig. 5 & S2,
411 Supporting Material).
412 At weak trade-offs, varying interaction basal rates (Fig. 5) or niche widths (Fig. S2)
413 mainly affects the composition and stability of the ecological communities, i.e. background
414 colors in Fig. 5 & S2. The selective landscape, characterized by stabilizing vs. runaway
415 selection close the pollinator vs. herbivore phenotype (as in Fig. 2A), remains essentially
416 unaltered. In particular, increasing the basal rate of pollination eventually selects for phenotypes
417 leading to unstable community dynamics (e.g. Fig. 5a vs. 5b). Increasing the rate of herbivory
418 restores stability (e.g. Fig. 5b vs. 5d). Note also the narrower set of plant phenotypes allowing
419 coexistence when herbivory becomes more specialized (e.g. Fig. S2a vs. S2c). Close to the
420 herbivore phenotype, the resulting increase in herbivory strength (equation 2) reduces plant
421 density so that pollinators no longer survive. Close to the pollinator phenotype, the resulting
422 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).

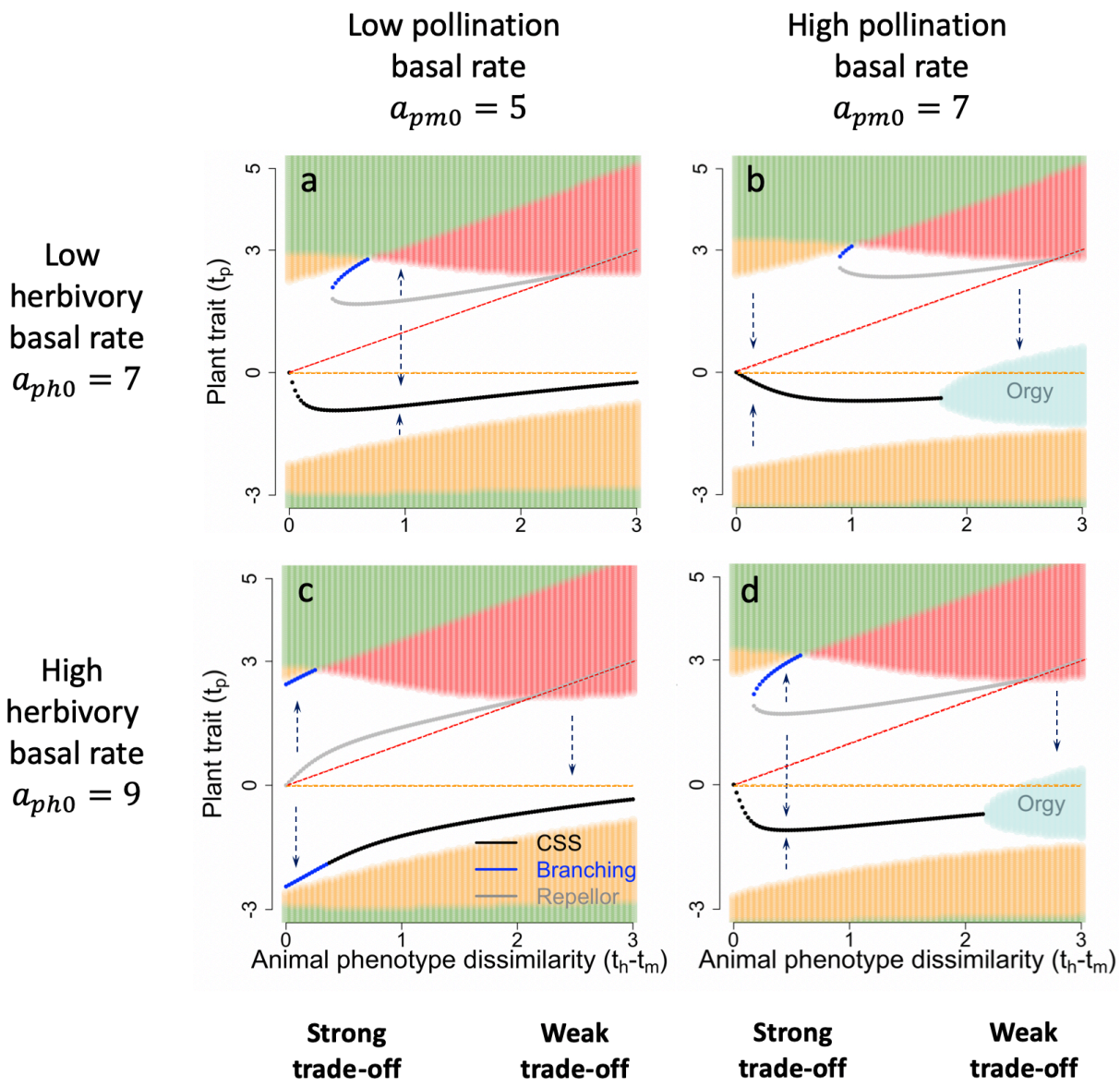


Fig. 5: Effect of the basal rates of plant-animal interactions on community eco-evolutionary dynamics. At strong trade-offs, eco-evolutionary dynamics are primarily altered by changes affecting evolutionary singularities. At weak trade-offs, the alteration is mainly mediated by changes in the composition 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. 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: $\sigma_{Pol} = 1.7,\ \sigma_{Her} = 2$.

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 the case of strong trade-offs. Simulating the eco-evolutionary dynamics following the 676 branching points encountered during our second Monte Carlo experiment when constraining

451 the sampling of trade-off intensity, we indeed find that dimorphism is maintained in only 6%
452 of the cases, all occurring at very strong trade-offs ($t_h - t_m \leq 0.5$). At such trade-offs,
453 however, the maintenance of dimorphism is relatively frequent, representing around 27% of the
454 cases (details in appendix D). Interestingly, we find that the ratio of pollination to herbivory at
455 branching $\left(i.e.\ \frac{a_{pm}M^*}{a_{ph}H^*}\right]_{t_p^*}\Bigg)$ again largely explains the maintenance of dimorphism at these
456 strongest trade-offs (Wilcoxon test, $p_{value} < 10^{-10}$ & $effect_{size} \approx 50\%$, see Fig. 6A).
457 Dimorphism maintenance is associated with stronger herbivory than pollination, which
458 suggests a decisive role of herbivory in the process. We finally show that even a slight amount
459 of similarity-dependent competition suffices to maintain dimorphism in the cases where it is
460 lost (Fig. 6B). Competition between two plant phenotypes (t_{p1}, t_{p2}) then declines as their niche-
461 overlap (i.e. $t_{p1} - t_{p2}$) decreases (equation (5)), α and σ_c being the parameters controlling the
462 proportion and shape of similarity-dependent competition, respectively.

$$c_{Sim-Dep}(t_{p1}, t_{p2}) = (1-\alpha)c_p + \alpha e^{\frac{-(t_{p1}-t_{p2})^2}{2\sigma_c{}^2}} c_p \tag{5}$$

463

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

469

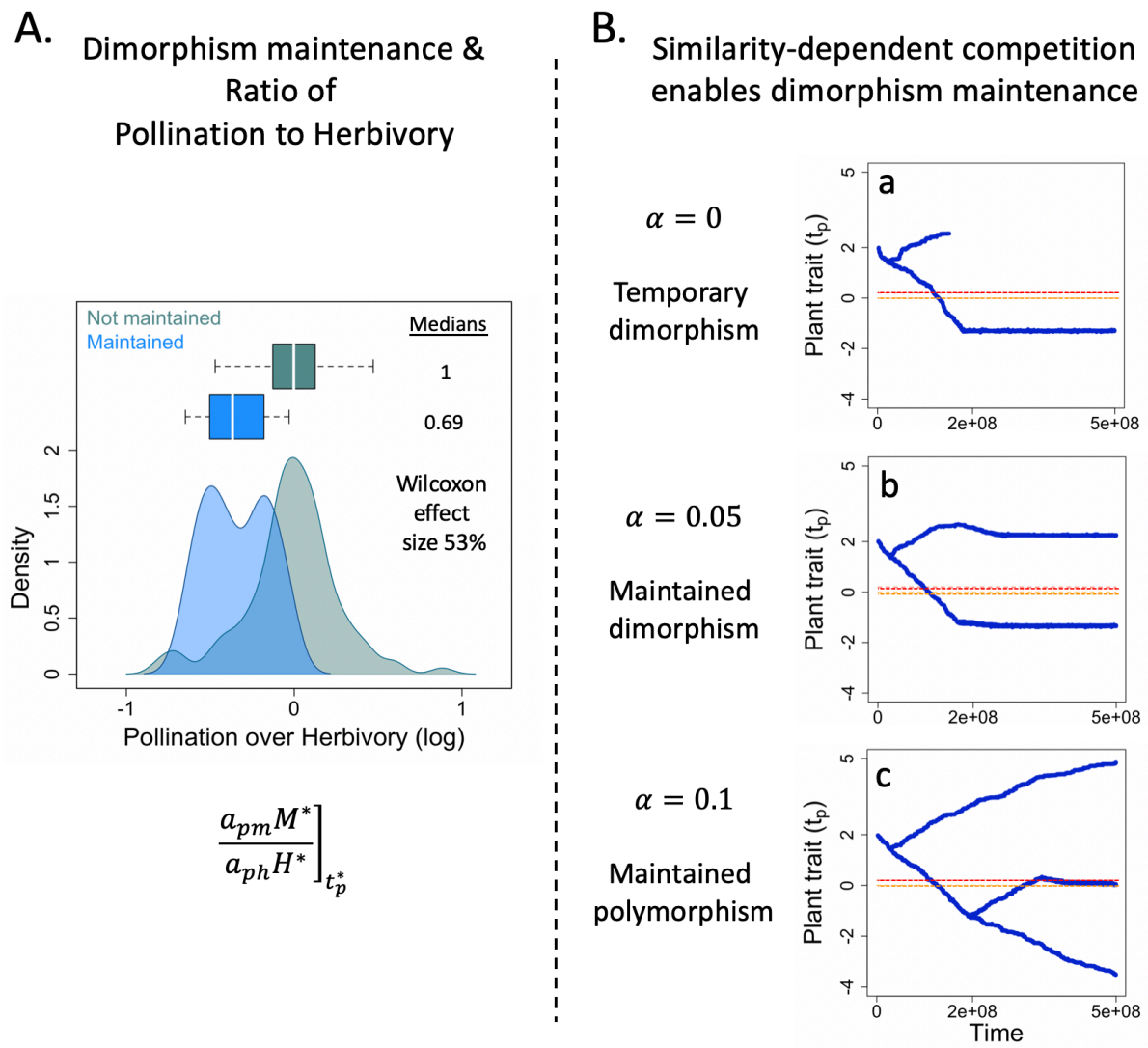


Fig. 6: The maintenance of plant dimorphism. A. Ratio of pollination and herbivory at branching explains the maintenance of plant dimorphism. The branchings considered here are those occurring at very strong trade-offs ($t_h - t_m \leq 0.5, 154/676$), given that dimorphism maintenance is only possible 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: ($t_m = 0, t_h = 0.2$).

Discussion

In this article, we investigate how the evolution of plant traits subject to an ecological trade-off between attracting pollinators and escaping herbivores (i.e. conflicting selection) drives the eco-evolutionary dynamics of plant-pollinator-herbivore communities. Stronger pollination makes stabilizing selection more prevalent and facilitates coexistence. Stronger herbivory increases the prevalence of runaway selection and threatens coexistence. Importantly, joint selection may be disruptive, leading to plant diversification. Such a diversification requires strong trade-offs, with the strongest trade-offs allowing its long-term maintenance. At weak trade-offs, coexistence is threatened as runaway dynamics are more frequent. Stabilizing selection can still maintain coexistence, but the intrinsic unbalance of plant-animal interactions makes it vulnerable to perturbations. The strength of the ecological trade-off appears as a structuring determinant of community eco-evolutionary dynamics.

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

509 presence of both pollinators and herbivores were less attractive to pollinators than those that
510 evolved with only pollinators, but still more attractive than plants that evolved with hand-
511 pollination, with or without herbivores. The presence of pollinators thus selected toward plant-
512 pollinator trait matching, but the presence of herbivores reduced such matching by adding a
513 runaway component to selection (equation (3)).
514
515 Recent data have highlighted the occurrence of vast insect declines (Hallmann et al.
516 2017; Outhwaite et al. 2022). Such declines may be accompanied by changes in the relative
517 frequency of antagonistic vs mutualistic interactions (e.g. herbivores vs pollinators). Given
518 massive pollinator declines (Potts et al. 2010) for instance, plant-animal interactions could
519 become increasingly biased towards antagonism. Given our results, this should favor runaway
520 selection thereby leading to plant phenotypes maladapted to pollinators, further accelerating
521 their declines (see also Weinbach et al. 2022). Herbivore extinctions are also expected as a
522 result of more frequent runaway dynamics. In natural communities, however, animal
523 morphologies, preferences, detection abilities or phenologies (i.e. t_m, t_h) also evolve to match
524 their resource phenotype (i.e. t_p, Thompson, 2009). The eco-evolutionary consequences of
525 diversity losses will therefore ultimately depend on the ability to coevolve fast enough (e.g.
526 evolutionary rescue, Gomulkiewicz and Holt 1995).
527
528 In line with the empirical evidence so far (Strauss et al. 2002; Strauss and Irwin 2004),
529 our study identifies the strength of ecological trade-off as a key driver of plant-animal eco-
530 evolutionary dynamics. We underline that trade-off intensity affects the maintenance of
531 coexistence, as well as the nature of joint selection, in particular the potential for disruptive
532 selection and plant diversification.
533

534 We find that coexistence is fragile or destroyed at weak trade-offs. Runaway dynamics
535 are more frequent (Fig. 4A). Evolutionary-induced unstable dynamics become possible (Fig.
536 5b&d). In the vicinity of the pollinator phenotype, the plant phenotype is more likely to stabilize
537 after the extinction of herbivores (i.e. Fig. 1B.1b), as indicated by the CSSs leaving the
538 coexistence area (Fig. 2A). When stabilizing selection occurs before herbivore extinction, their
539 low density makes them vulnerable to demographic stochasticity, Allee effects or external
540 disturbances. Because weak ecological trade-offs are associated with fragile plant-pollinator-
541 herbivore coexistence, they should be seldom encountered in natural communities.
542 Accordingly, shared animal preferences for plant phenotype are most often reported in the
543 empirical literature (Adler and Bronstein 2004; Strauss and Whittall 2006).
544
545 Selection can turn disruptive under stronger ecological trade-offs. We stress that
546 disruptive selection here arises from the joint selection of pollination and herbivory. In the
547 absence of either one interaction, branching is not possible here, as evolutionary dynamics
548 would run away from the herbivore phenotype in the absence of pollination, and would stabilize
549 at the pollinator phenotype in the absence of herbivory. Diversification we uncover here is thus
550 fundamentally different from the one uncovered in previous trait-matching models that consider
551 the two interactions separately (e.g. (Yoder and Nuismer 2010; Maliet et al. 2020). While
552 dimorphism can only be maintained when the trade-off is sufficiently strong, long-term
553 maintenance is frequent in such instances. Polymorphism then yields two contrasted
554 phenotypes: one that has many allies and enemies, while the other one has few interactions.
555 Interestingly, such a pattern has been frequently reported in the empirical literature. In *Primula*
556 *farinosa,* the fitness advantage of long-scaped phenotypes resulting from higher pollinator
557 visitation rates is balanced by higher levels of fruit predation, allowing the maintenance of
558 dimorphism in scape length (Ehrlén et al. 2002). The maintenance of color dimorphism in

559 *Raphanus sativus* (Irwin et al. 2003) and *Claytonia virginica* (Frey 2004) is similarly supported
560 by animal species preferentially interacting with the same plant phenotype. Several field studies
561 of tripartite networks also report a positive correlation between the number of pollinators and
562 herbivores of any given plant species (Melián et al. 2009; Sauve et al. 2016*b*), indicating a
563 rather widespread pattern. This mechanism of diversification under balanced interactions may
564 also apply on longer evolutionary timescales. Using a phylogenetic analysis on 32 *Nicotinia*
565 species, Adler *et al.* (2012) show that variations in nicotine defenses among species are largely
566 negatively correlated to pollinator reliance. These tobacco species are therefore either well-
567 defended with few pollinators, or lowly defended and relying on pollination.

568 We find that disruptive selection requires a local balance between pollination and
569 herbivory (Fig 2), while its prevalence within the selective landscape increases with the strength
570 of herbivory (Fig. 4B). This is not contradictory as those aspects describe selection at two
571 different scales. To put it simply, disruptive selection can be expected in any three-species
572 community when plant-animal interactions are well-balanced, but communities in which
573 herbivores are more ravenous (a_{ph0} ↗) will more likely exhibit such evolutionary dynamics.
574 Dimorphism is also more likely to be permanent with stronger herbivory (Fig. 6A), further
575 emphasizing its decisive role in diversification processes. Previous theoretical works that
576 contrast interaction types but one at a time have also highlighted the crucial role of antagonisms
577 for diversification (Kopp and Gavrilets 2006; Yoder and Nuismer 2010; Maliet et al. 2020).
578 Given these results, we note that observed declines in the diversity and abundances of herbivore
579 species (Sánchez-Bayo and Wyckhuys 2019; Atwood et al. 2020) may have far-reaching
580 consequences if they lead to future reductions in diversification rates.

581

582 Overall, dimorphism is often temporary within our framework. While we assume
583 constant competition rates in order to focus on how trophic vs mutualistic interactions shape

eco-evolutionary dynamics, similarity-dependent competition is likely to occur in natural communities (Macarthur and Levins 1967). Here, similar plants would share pollinators, which could lead to strong pollination niche-overlap competition for instance due to the dilution of pollen between plant species (Morales and Traveset 2008; Mitchell et al. 2009). Similarly, shared herbivores would increase apparent competition. Plant traits can also be simultaneously involved in both competitive and plant-animal interactions, either directly (e.g. phenological traits, Schwinning & Kelly 2013) or due to genetic correlations (e.g. plant size, Carmona *et al.* 2011). Accounting for a small amount of niche-overlap competition suffice to maintain dimorphism in our model, and enhances the potential for further diversification (Fig. 6B). 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 and Kelly 2011). Disruptive selection from the interplay of pollination, herbivory and niche-overlap competition can therefore be construed as a first step toward modeling the evolutionary emergence of plant-pollinator-herbivore networks, which would allow new insights into the eco-evolutionary processes supporting the diversity of natural communities.

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