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Stable Coexistence in Plant-Pollinator-Herbivore Communities Requires Balanced Mutualistic vs Antagonistic Interactions

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1 Stable coexistence in plant-pollinator-herbivore communities 2 requires balanced mutualistic vs antagonistic interactions

3

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14

15 Running headline

16 Stable coexistence: pollination vs. herbivory

17

18 Statement of authorship

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

23

24 Data accessibility statement

25 No data were used in the present work.

26

27 The manuscript is submitted as a Research Paper and contains an abstract of 148 words, the
28 main text of 5081 words, 69 references, 4 figures, and 2 tables.

29 Abstract

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

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46 Keywords

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

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57 1. Introduction

58 Multiple species interacting closely together form an ecological community. A topic of
59 long-standing interest in community ecology is to understand what mechanisms drive the
60 coexistence of species and its maintenance over time. It is now well established that the way
61 ecological interactions connect species - the type of interactions, the network topology as well
62 as the distribution of interaction strengths - plays a decisive role. Combining modelling
63 approaches with empirical data, several works indicate for instance that weak trophic
64 interactions are crucial to maintain the stability of complex food webs (McCann et al., 1998;
65 Neutel et al., 2002). Deriving general laws is, however, difficult. The network properties and
66 topologies favoring the maintenance of coexistence indeed vary with the type of interaction
67 characterizing the community, mutualism or antagonism in particular (Thébaud and Fontaine,
68 2010). The ecological processes and structural patterns supporting the maintenance of
69 coexistence within single-interaction-type communities can, moreover, considerably differ
70 from the ones at play within communities with several interaction kinds (e.g. Mougi and
71 Kondoh, 2012; Sauve et al., 2014). Studies of such communities should therefore significantly
72 improve our understanding of ecological communities, especially given that most species get
73 simultaneously involved in a diversity of interaction networks (Fontaine et al., 2011; Kéfi et
74 al., 2012). Most terrestrial plant species ($\approx 90\%$ of flowering plants, Ollerton et al., 2011), for
75 instance, are involved in a mutualistic interaction with their animal pollinators, while suffering
76 from herbivorous predation (antagonism). Plant-pollinator-herbivore communities are, in
77 addition, of particular interest due to their critical role in agricultural production (Klein et al.,
78 2007; Oerke, 2006), as well as the serious threats global change poses to them (Atwood et al.,
79 2020; Potts et al., 2010). The study of stable coexistence within these communities is thus of
80 high applied relevance while offering the opportunity to gain new conceptual insights into the
81 functioning of mutualistic-antagonistic communities.

82

83 Understanding stable coexistence within plant-pollinator-herbivore communities
84 requires explicitly accounting for both the mutualistic (i.e. plant-pollinator) and the antagonistic
85 (i.e. plant-herbivore) interaction. A large body of empirical evidence indeed documents non-
86 additive effects of pollination and herbivory on plant densities, in both uncultivated (Gómez,
87 2005; Herrera, 2000; Herrera et al., 2002; Pohl et al., 2006) and cultivated (Lundin et al., 2013;
88 Strauss and Murch, 2004; Sutter and Albrecht, 2016) plant species. The strength of the
89 mutualistic interaction is affected by the antagonistic interaction and vice versa, explaining such

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

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

104

105 In plant-pollinator-herbivore communities, the typical module consists of two animal
106 species - a pollinator and a herbivore - sharing a common resource plant species (Fig. 1A.a).
107 The resulting indirect interaction between pollinators and herbivores is an antagonism (Fig.
108 1A.a, Holland *et al.* 2013). Pollinators allow the community to sustain a higher herbivore
109 density by increasing plant productivity while herbivores, on the other hand, decrease pollinator
110 density by reducing resource availability. Theoretical works indicate that the presence of
111 pollinators can even make the herbivore population viable (Georgelin and Loeuille, 2014;
112 Mougi and Kondoh, 2014a). As illustrated by Georgelin & Loeuille (2014), direct vs. indirect
113 ecological effects can be of similar magnitude. Their study indeed reports a constant herbivore
114 density despite increasing herbivore mortality. In their model, over a wide range of herbivore
115 mortalities, the direct mortality-induced losses on herbivores are totally offset by the indirect
116 gain resulting from a higher pollinator density consecutive to the herbivorous predation release
117 on plants. Further increasing mortality, however, leads to the abrupt collapse of the herbivore
118 population, which illustrates that combining different interactions also has important
119 implications in terms of community stability (Mougi and Kondoh, 2014b).

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

124 population growths driven by an “orgy of mutual benefaction” (May, 1981). The latter is,
125 however, seldom observed in nature. One possible explanation is that antagonistic interactions,
126 such as predation, could prevent this behavior in real systems. Negative feedback loops born
127 from antagonistic interactions (Neutel and Thorne, 2014) could restore stability by
128 counterbalancing the positive loops arising from mutualisms (Fig. 1A.b). This hypothesis
129 implies that the relative magnitude of pollination vs. herbivory plays a critical role, which is in
130 line with the findings of several theoretical investigations on mutualistic-antagonistic modules
131 (Georgelin and Loeuille, 2014; Holland et al., 2013; Mougi and Kondoh, 2014b; Sauve et al.,
132 2016a).

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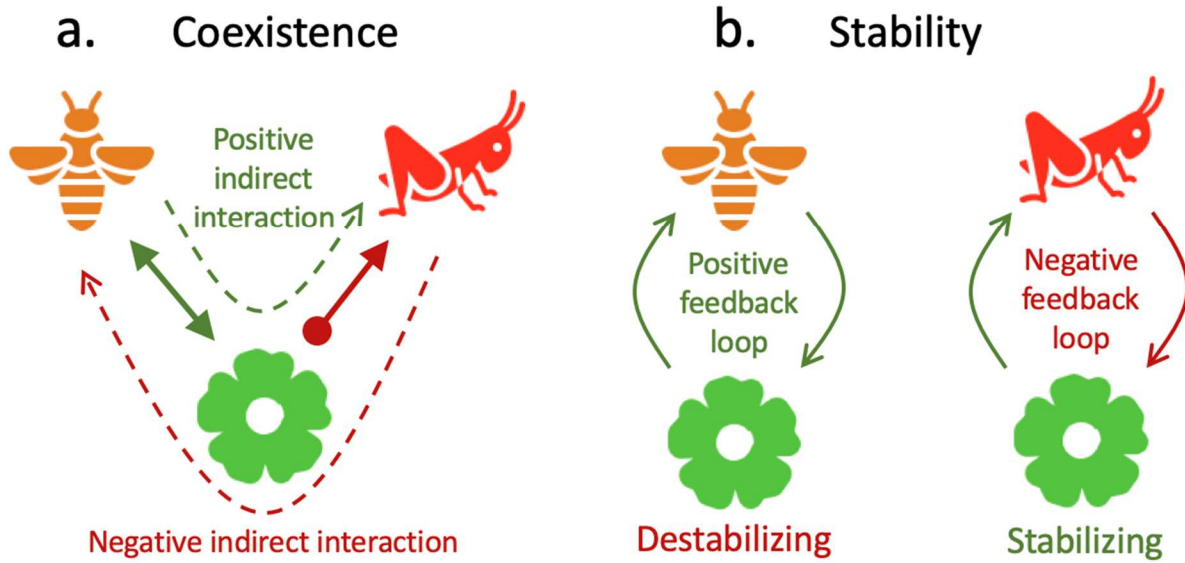
134 The goal of the present paper is to understand how stable coexistence within plant-
135 pollinator-herbivore communities constrains the relative strengths of pollination and herbivory,
136 i.e. the relative per capita effects of each interacting animal species on plant population growth.
137 In contrast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

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A Predicted effects of interactions on



B First analytical results are in line with predictions

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

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Figure 1: A. Predicted effects of interactions on stable coexistence. **a.** Predicted effects on densities. Solid (resp. dashed) arrows for direct (resp. indirect) interactions. **b.** Predicted effects on stability. **B. Variation of biomass densities at stable coexistence with the strength of interactions.** Biomass densities at equilibrium are denoted P^*, M^*, H^* for plants, pollinators and herbivores. The strengths of pollination and herbivory are respectively a_{pm} and a_{ph} . Other model parameters introduced here: intraspecific competition for plants and pollinators (c_p, c_m), conversion efficiency from plants to pollinators e_m . See table 1 for a detailed presentation of all model parameters. These first analytical results are in line with predictions (see A.a). Analytical proofs in appendix B.IV.

169 **2. Model presentation**

170 **2.1 Ecological dynamics**

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

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

173
 174 Plants have a positive intrinsic growth rate ($r_p > 0$, autotrophs), while both pollinators ($r_m <$
 175 0) and herbivores ($r_h < 0$) have a negative one (heterotrophs). As in previous models (e.g.
 176 Sauve *et al.* 2014), we thus assume the plant-animal interaction to be obligate for animals and
 177 facultative for the plant. Intraspecific competition is accounted for. The animal competition
 178 rates (c_m, c_h) correspond to interference while, for the plant species (c_p), this rate essentially
 179 captures the competition for resources such as light, water, and nutrients (Craine and Dybzinski,
 180 2013). Interspecific interactions, whose strength is a_{pm} for pollination and a_{ph} for herbivory,
 181 affect population growths proportionally to biomass densities. The use of a linear functional
 182 response for mutualism exposes the model to unbounded population growths (May, 1981). It,
 183 however, enables testing whether this behavior could be top-down controlled by herbivory,
 184 placing our work in the line of research tackling how the community context could explain the
 185 stability of mutualisms in nature (e.g. Ringel *et al.* 1996). Finally, e_m and e_h are the conversion
 186 efficiencies from plants to animals. Parameter details are given in table 1.

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

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

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

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192 2.2 Ecological equilibria

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When the three population growth rates vanish (equations (1) are null), we reach an ecological equilibrium (P^*, M^*, H^*) . At equilibrium, each population can either be present or absent, leading to 8 potential equilibria whose expressions are given in table 2. The present work focuses on the “coexistence equilibrium”, i.e. the equilibrium in which the three species are present. We study under which conditions of interaction strengths - (a_{pm}, a_{ph}) - the coexistence equilibrium corresponds to positive biomass densities (i.e. is feasible), and is stable (i.e. is resilient to small perturbations, i.e. local stability as in May, 1972). Detailed definitions are provided in Appendix B.I.

203 **Table 2: Expressions of the eight potential ecological equilibria within our plant-**
 204 **pollinator-herbivore community.** Reminder of our assumptions: $r_p > 0, r_m < 0, r_h < 0$. For
 205 two-species equilibria, an index indicates which two species coexist at equilibrium (e.g. P_{PM}^*).

Equilibrium	Expression
All extinct	$P^* = 0; M^* = 0; H^* = 0$
Plants	$P^* = r_p/c_p; M^* = 0; H^* = 0$
Pollinators	$P^* = 0; M^* = r_m/c_m; H^* = 0$
Herbivores	$P^* = 0; M^* = 0; H^* = r_h/c_h$
Plants & pollinators	$P_{PM}^* = \frac{c_m r_p + a_{pm} r_m}{c_p c_m - e_m a_{pm}^2}; M_{PM}^* = \frac{e_m a_{pm} r_p + c_p r_m}{c_p c_m - e_m a_{pm}^2}; H_{PM}^* = 0$
Plants & herbivores	$P_{PH}^* = \frac{c_h r_p - a_{ph} r_h}{c_p c_h + e_h a_{ph}^2}; M_{PH}^* = 0; H_{PH}^* = \frac{e_h a_{ph} r_p + c_p r_h}{c_p c_h + e_h a_{ph}^2}$
Pollinators & herbivores	$P_{MH}^* = 0; M_{MH}^* = r_m/c_m; H_{MH}^* = r_h/c_h$
Three-species coexistence	$P^* = \frac{c_h c_m r_p + c_h a_{pm} r_m - c_m a_{ph} r_h}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2}$ $M^* = \frac{c_h e_m a_{pm} r_p + (c_p c_h + e_h a_{ph}^2) r_m - e_m a_{pm} a_{ph} r_h}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2}$ $H^* = \frac{c_m e_h a_{ph} r_p + e_h a_{pm} a_{ph} r_m + (c_p c_m - e_m a_{pm}^2) r_h}{c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2}$

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214 2.3 Two-population subcommunities

215 The plant-pollinator-herbivore community is constituted of two subcommunities –
216 plant-pollinator and plant-herbivore – sharing the same plant species. Such subcommunities
217 have extensively been studied in the literature (e.g. Goh 1976; Vandermeer & Boucher 1978).
218 We briefly report here their dynamics (see Appendix B.II for details).

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

222 Two distinct regimes are possible for the plant-pollinator subcommunity, depending on
223 the comparison between pollination strength and self-limiting competitions (Appendix B.II.2).

224 (1) If the pollination positive feedback loop (destabilizing, Fig. 1A.b) is smaller than that from
225 competition, there is one feasible and globally stable equilibrium. This equilibrium corresponds
226 to plant-pollinator coexistence when the carrying capacity of plants is large enough to support
227 the pollinator population. Otherwise, plants persist while pollinators go extinct. (2) If the
228 pollination positive feedback loop is stronger than that from competition, unbounded
229 population densities are possible. In this case, when the carrying capacity of plants is sufficient
230 to make pollinators viable, populations unboundedly grow irrespective of initial densities.
231 Otherwise, unbounded growth is observed if initial densities are large enough while only plants
232 persist if it is not the case.

233

234 3. Results

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

246 community. As pollination increases, the minimal level of herbivory allowing herbivores to
247 persist gets lower (Fig. 2a vs 2b). Pollination favors the feasibility of coexistence. On the
248 contrary, herbivory disfavors the feasibility of coexistence. As herbivory gets stronger, the
249 minimal level of pollination allowing pollinators to persist gets higher (Fig. 2d&e vs 2f).

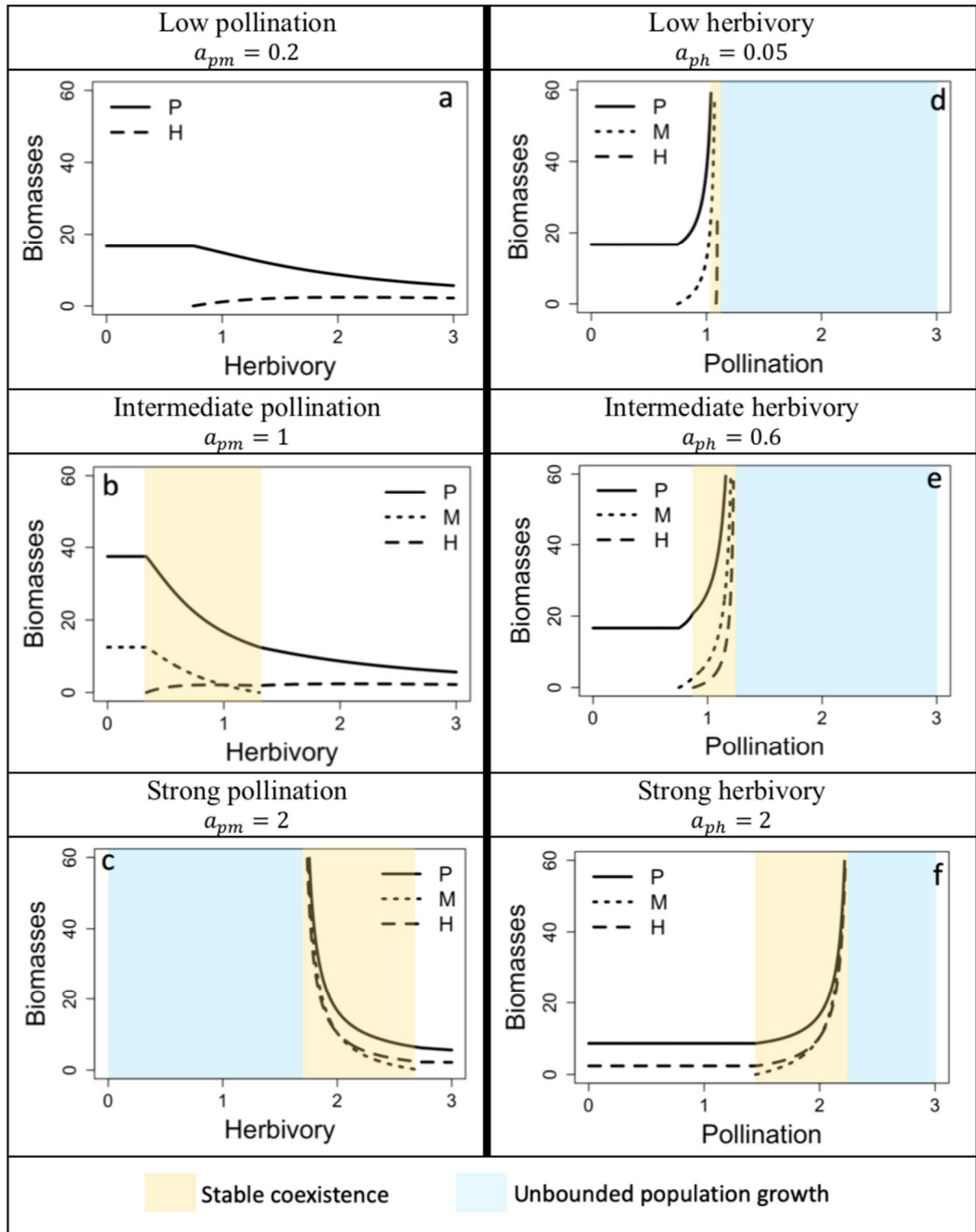
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251 In line with our predictions (Fig. 1A.b), stability displays opposite patterns: it is favored
252 by herbivory and disfavored by pollination. For a given level of herbivory, populations display
253 unstable dynamics for high pollination strengths (Fig. 2 d-e-f, blue background). This instability
254 captures the unbounded growth of biomass densities driven by the mutualism. As herbivory
255 gets stronger, higher pollination levels are needed for unbounded growth to happen (Fig. 2d vs
256 2e vs 2f). Herbivory can indeed restore stability (Fig. 2c): starting from an initially unbounded
257 situation, increasing herbivory restores finite densities.

258

259 The strength of pollination contributes positively to the feasibility of coexistence and
260 negatively to its stability. It is the opposite for herbivory. Although presented for a given
261 parameter set (Fig. 2), these two main results are general as they derive from the analytical
262 relationships governing stable coexistence (table 3). They imply that stable coexistence requires
263 a balance between the strengths of pollination and herbivory to achieve both feasibility and
264 stability. Such a balance can be observed in Fig. 2: as one interaction gets stronger, the range
265 of the other interaction intensities allowing stable coexistence shifts toward larger values
266 (yellow background, Fig. 2b vs 2c, Fig. 2e vs 2f).

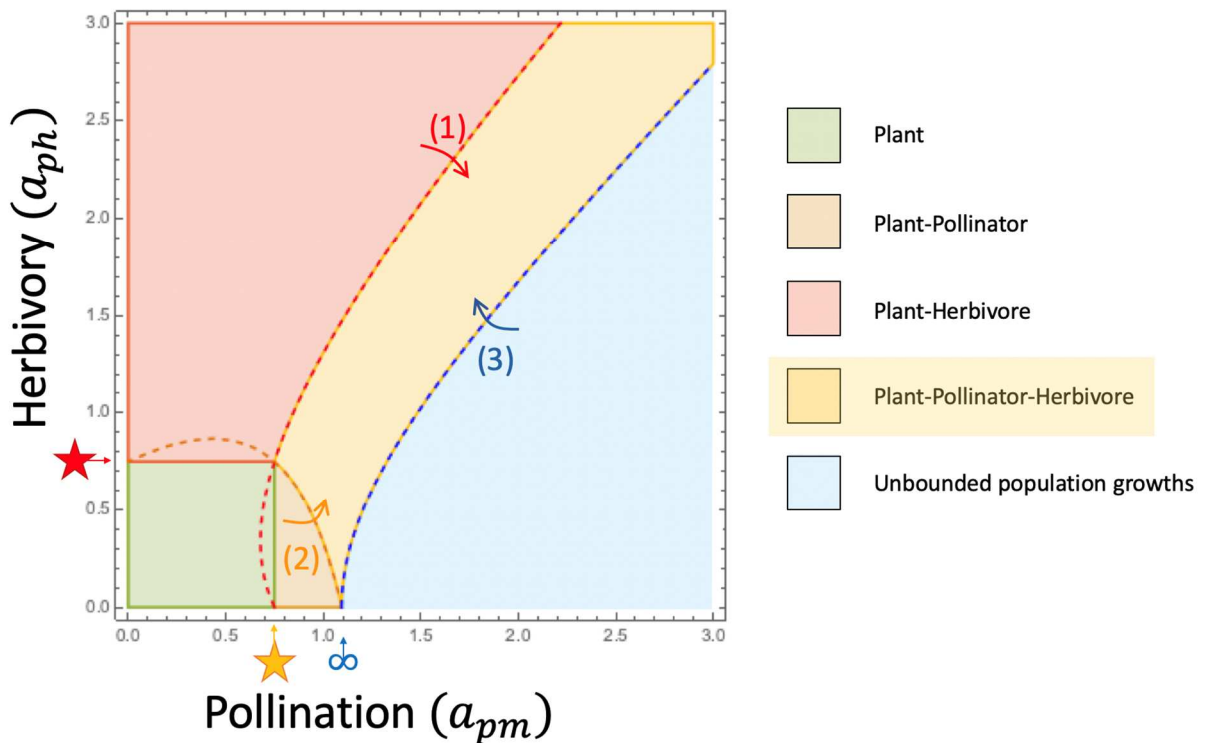
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268
 269 **Fig. 2: Biomass densities at equilibrium depend interactively on pollination and herbivory**
 270 **strengths.** The curves are determined analytically (see appendix B.III). **a-b-c** Dependence of densities
 271 on herbivory for three pollination levels. In **a**, pollination intensity is too low for pollinators to persist.
 272 **d-e-f** Dependence of densities on pollination for three herbivory levels. Parameter set: $r_p = 10, r_m =$
 273 $r_h = -2.5, c_p = 0.6, c_m = c_h = 0.4, e_m = e_h = 0.2$.
 274

275 3.1 Relationships governing stable coexistence

276 Positive animal densities necessarily imply a positive plant density because animals are
 277 obligate plant-interactors (Appendix C.I.1). In other words, the coexistence equilibrium is
 278 feasible if, and only if, both animal species have positive densities, which leads to two
 279 inequalities. It is stable if, and only if, all three eigenvalues of the Jacobian matrix (Appendix
 280 B.III.1) calculated at the coexistence equilibrium have a negative real part, which is equivalent
 281 to the three Routh-Hurwitz inequalities (Appendix B.III.3). One of these inequalities is satisfied
 282 if feasibility is assumed. Therefore, there are four relationships (i.e. $(R1, R2, R3, R4)$ in table 3)
 283 that are necessary and sufficient for the stable coexistence of plants, pollinators and herbivores
 284 (Appendix C.II). These relationships, as well as their biological interpretations, are presented
 285 in Table 3. We illustrate the biological implications underlying them using Fig. 3, which
 286 indicates the community composition depending on the strengths of pollination and herbivory.
 287



288
 289 **Fig. 3: Stable coexistence requires balanced pollination vs. herbivory strengths.** Given the strength
 290 of pollination (a_{pm}) and herbivory (a_{ph}), the stable equilibria are determined and the point of the graph
 291 is colored accordingly. In blue, no equilibrium is stable so densities grow unboundedly. Arrows (1), (2),
 292 and (3) indicate the transitions enabling the satisfaction of relationships $(R1)$, $(R2)$, and $(R3)$ (**Table**
 293 **3**), indicated by the dotted red, orange, and blue curve, respectively. These three relationships are
 294 sufficient to achieve stable coexistence given the parameter set (as in **Fig. 2**), indicating that relationship

295 (R4) is less constraining here. The orange (resp. red) star indicates the level of pollination (resp.
 296 herbivory) that makes pollinators (resp. herbivores) viable when only plants are present (hence at
 297 carrying capacity). Unbounded growth is possible in the plant-pollinator subcommunity when the
 298 strength of pollination is higher than the level figured by an infinity symbol. Note that stable coexistence
 299 (yellow area) requires the two interactions to be of similar magnitude. Parameter set: $r_p = 10, r_m = r_h =$
 300 $-2.5, c_p = 0.6, c_m = c_h = 0.4, e_m = e_h = 0.2$

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302 Assuming stability (relationship (R3) actually), coexistence is feasible if and only if
 303 relationships (R1) and (R2) are satisfied.

304 Relationship (R1) indicates that the per capita growth rate of pollinators, when low in
 305 density and within a plant-herbivore community at ecological equilibrium, is positive
 306 (Appendix C.II.1). Pollinators are thus able to invade the plant-herbivore community so that
 307 this relationship governs the transition (red dotted curve, arrow (1)) between the plant-herbivore
 308 equilibrium (red) and the coexistence equilibrium (yellow) in Fig. 3. Besides, the plant density
 309 within the plant-herbivore community (P_{PH}^* , expression in table 2) decreases when herbivory
 310 (a_{ph}) intensifies (Appendix C.II.1). In such a situation, pollination (a_{pm}) has to get stronger as
 311 well in order for pollinators to invade the plant-herbivore community (inequality (R1')), the
 312 prime sign indicates that this inequality is obtained by rewriting relationship (R1)).

$$\underbrace{\frac{-r_m}{e_m P_{PH}^*}}_{\substack{\text{increasing} \\ \text{with } a_{ph}}} \leq a_{pm} \quad (R1')$$

313 The interpretation of the second relationship (R2) depends on whether unbounded
 314 population growth is possible or not within the plant-pollinator community, i.e. on the
 315 competition loop ($c_p c_m$) being weaker or stronger than the pollination feedback loop
 316 ($e_m a_{pm}^2$).

317 If unbounded growth is not possible, relationship (R2) indicates that the per capita
 318 growth rate of herbivores, when low in density and within a plant-pollinator community at
 319 ecological equilibrium, is positive. In this case, the relationship governs the transition (orange
 320 dotted curve, arrow (2)) between the plant-pollinator equilibrium (orange) and the coexistence
 321 equilibrium (yellow) in Fig. 3. We mathematically demonstrate that in such a case, the
 322 feasibility of coexistence implies its global stability (Appendix B.IV). Relationships (R1) and
 323 (R2) are thus necessary and sufficient for stable coexistence (Fig. 3, left side of ∞).
 324 Furthermore, stronger pollination (a_{pm}) makes herbivores viable at lower predation intensities

325 (a_{ph}) (inequality (R2'. 1)) due to a higher plant density within the plant-pollinator community
 326 (P_{PM}^* , expression in table 2) (Appendix C.II.2).

327 If unbounded growth is possible, relationship (R2) sets an upper limit to the strength of
 328 herbivory (inequality (R2'. 2)), which we interpret as a condition for herbivores to not exclude
 329 pollinators by reducing plant biomass too strongly. In fact, inequality (R2'. 2) (feasibility of
 330 H^* , see equations (2)) is critical for a parameter configuration over which the persistence of
 331 herbivores is due to the presence of pollinators (Appendix C.II.2, Fig. S3). In such parameter
 332 instances, P_{PM}^* loses its biological meaning (as the plant-pollinator equilibrium is unstable) and
 333 decreases with pollination (a_{pm}), and alternative stable states are possible (Fig. S3). Note that
 334 no transition corresponds to inequality (R2'. 2) in Fig. 3 as relationship (R2) is only
 335 constraining at the left of the infinity symbol (∞) for the given parameter set.

$$\left\{ \begin{array}{l} e_m a_{pm}^2 \leq c_p c_m \\ \frac{-r_h}{e_h P_{PM}^*} \leq a_{ph} \\ \text{decreasing} \\ \text{with } a_{pm} \end{array} \right. \quad (R2'. 1)$$

$$\left\{ \begin{array}{l} c_p c_m \leq e_m a_{pm}^2 \\ a_{ph} \leq \frac{-r_h}{e_h P_{PM}^*} \\ \text{increasing} \\ \text{with } a_{pm} \end{array} \right. \quad (R2'. 2)$$

336 Inequalities (R1') and (R2') (derived from relationships (R1) & (R2) respectively)
 337 clearly show that pollination favors the feasibility of coexistence while herbivory disfavors it.
 338 These inequalities indeed tend to be satisfied when pollination strengthens or herbivory
 339 weakens.

340

341 Assuming feasibility, coexistence is stable if and only if relationships (R3) and (R4)
 342 are satisfied.

343 Relationship (R3) corresponds to the total feedback at level 3 (i.e. summation of the
 344 strengths of all three-element combinations of non-overlapping feedback loops, details in
 345 Appendix C.II.3) being negative. Pollination disfavors stability by contributing positively to
 346 this feedback, while it is the opposite for herbivory. Stability requires the competitive and the
 347 herbivory feedback loops to overcome the pollination feedback loop. Rewriting relationship
 348 (R3) into inequality (R3') emphasizes the consecutive constraint limiting pollination. It
 349 governs the transition (blue dotted curve, arrow (3)) from unbounded growth (blue) to stable
 350 coexistence (yellow) in Fig. 3.

$$a_{pm} < \underbrace{\sqrt{\frac{c_h c_m c_p + c_m e_h a_{ph}^2}{e_m}}}_{\text{increasing with } a_{ph}} \quad (R3')$$

351

352 Relationship (R4) is harder to interpret. Given that relationships (R3) and (R4) imply
 353 that the feedback at each level is negative, relationship (R4) could be interpreted as proposed
 354 by Levins (1974): the negative feedback with long time lags (level 3) is weaker than the shorter-
 355 loop negative feedback (level 1 & 2) (details in Appendix C.II.4). Also, the constraints imposed
 356 by this relationship on interaction strengths are not analytically tractable, due to the effect of
 357 interactions on equilibrium densities.

358

359 **Table 3: Analytical relationships governing stable coexistence.** The fourth column indicates how
 360 each relationship is affected by the strength of interactions (favored +, disfavored -). Note that the third and fourth
 361 columns present a simplified summary of our analysis (see subsequent text and Appendix C, especially tables S3
 362 & S4). Notations: P_{PM}^* plant density at plant-pollinator equilibrium; P_{PH}^* plant density at plant-herbivore
 363 equilibrium; “num” numerator; “den” denominator (see table 2 for expressions). Finally, the interplay between
 364 pollination and herbivory is difficult to disentangle in relationship (R2), which led us to distinguish two cases
 365 (inequality (R2'.1) for (1) and (R2'.2) for (2) below). An increase in pollination (a_{pm}) makes the relationship
 366 shift from (1) to (2). In (2), P_{PM}^* loses its biological significance as the plant-pollinator subcommunity grows
 367 unboundedly. P_{PM}^* is, in this case, a mathematical function (expression in table 2), which explains its
 368 counterintuitive behavior with the variation of pollination strength*.

Relationship	Mathematical meaning	Biological interpretation	Effect of interaction strengths
(R1) $r_m + e_m a_{pm} P_{PH}^* \geq 0$	Feasibility ($num(M^*) \geq 0$)	Pollinators can invade the plant-herbivore community	$a_{pm} +$ (direct) $a_{ph} - (P_{PH}^* \searrow)$

<p style="text-align: center;">(R2)</p> $(c_p c_m - e_m a_{pm}^2)(r_h + e_h a_{ph} P_{PM}^*) \geq 0$	<p style="text-align: center;">Feasibility ($num(H^*) \geq 0$)</p>	<p style="text-align: center;">(1) Stable plant-pollinator dynamics with herbivores able to invade the plant-pollinator community <u>or</u> (2) Plant-pollinator orgy with bounded herbivory</p>	<p>(1) $a_{pm} + (P_{PM}^* \nearrow)$ $a_{ph} +$ (direct) (2) $a_{pm} + (P_{PM}^* \searrow)^*$ $a_{ph} -$ (direct)</p>
<p style="text-align: center;">(R3)</p> $c_h e_m a_{pm}^2 - c_p c_m c_h - c_m e_h a_{ph}^2 < 0$	<p style="text-align: center;">Feasibility ($den(M^*, H^*) \geq 0$) Stability</p>	<p style="text-align: center;">Total feedback at level 3 is negative</p>	<p style="text-align: center;">$a_{pm} -$ $a_{ph} +$ (feedback loops, Fig. 1b)</p>
<p style="text-align: center;">(R4)</p> $(c_p P^* + c_m M^* + c_h H^*)(P^* M^* (c_p c_m - e_m a_{pm}^2) + P^* H^* (c_p c_h + e_h a_{ph}^2) + M^* H^* c_m c_h) - P^* M^* H^* (c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) > 0$	<p style="text-align: center;">Stability</p>	<p style="text-align: center;">Negative feedback at level 3 is weaker than the product of negative feedback at lower levels (1 & 2)</p>	<p style="text-align: center;">Undetermined</p>

369

370 By combining inequalities (R1') and (R3'), we obtain a necessary condition for stable
371 coexistence (inequality (2)) which implies a positive correlation between pollination and
372 herbivory. Stable coexistence within plant-pollinator-herbivore communities requires a balance
373 between the strengths of pollination and herbivory. Stable coexistence in Fig. 3 (yellow)
374 therefore happens around the first diagonal, where pollination and herbivory are of similar
375 magnitudes.

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

376

377 3.2 Other ecological parameters also affect stable coexistence

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

385

386

387 First of all, when stable coexistence is possible, it happens when the strengths of
388 pollination and herbivory are approximately of the same magnitude (yellow area, Fig. 4 and S4
389 & S5 & S6 in Appendix D), as analyzed above (inequality (2)).

390 Stable coexistence is facilitated when the pollinator intrinsic growth rate is higher than
391 the herbivore one. The range of pollination and herbivory strengths allowing stable coexistence
392 indeed gets wider on the upper right of Fig. 4A. The explanation relies on two points: the
393 feasibility of coexistence is favored by pollination and disfavored by herbivory; intrinsic growth
394 rates play a major part in the feasibility of coexistence (relationships (R1) & (R2)), but only a
395 minor part in its stability (no effect on relationship (R3)). Analytical details are available in
396 Appendix D. I. An increase in the pollinator growth rate makes it easier for pollinators to invade
397 the plant-herbivore community (Fig. 4c vs 4d, point A). Due to a higher plant density,
398 herbivores can also invade the plant-pollinator community more easily (Fig. 4a vs 4b, point B).
399 Likewise, a higher herbivore growth rate enables an easier invasion of the plant-pollinator
400 community by herbivores (Fig. 4a vs 4c, point B). It, however, makes the invasion of the plant-
401 herbivore community by pollinators harder due to the reduction of plant density (Fig. 4a vs 4c,
402 point A). Note finally that despite similar growth rates, the community is endangered when
403 these growth rates are too low (Fig. S4, Appendix D).

404 Stable coexistence is facilitated when competition is stronger among pollinators than
405 among herbivores. The range of pollination and herbivory strengths allowing stable
406 coexistence indeed gets wider in the lower-left of Fig. 4B. Such a pattern is due to the effect of
407 competition rates on stability (relationship (R3)), which is much stronger than their effect on
408 feasibility (relationships (R1) & (R2)). Analytical details are available in Appendix D.II. As

409 competition among herbivores gets stronger, the plant density within the plant-herbivore
410 community increases as a result of predation release. It becomes easier for pollinators to invade
411 (Fig. 4g vs 4e, point A'). Unbounded dynamics are, however, facilitated (Fig. 4h vs 4f, point
412 C) because the positive destabilizing loop increases more than the negative stabilizing loops
413 (relationship ($R3$)). In the plant-pollinator community, a lower pollinator density ensuing from
414 a stronger competition rate is responsible for a lower plant density. It thus becomes harder for
415 herbivores to invade (Fig. 4h vs 4g, point B'). Stability is, however, enhanced due to the
416 stronger control of the pollination positive feedback in both the plant-pollinator subcommunity
417 (Fig. 4f vs 4e, infinity symbol) and the three-species community (Fig. 4f vs 4e, point C).

418

419 To summarize, the results obtained from studying the effect of these other parameters
420 support our main results, i.e. pollination favors feasibility at the expense of stability while it is
421 the opposite for herbivory. Indeed, any parameter variation that benefits pollinators (higher
422 growth rate r_m , weaker competition c_m or higher conversion efficiency e_m (Appendix D.III))
423 favors feasibility, disfavors stability or both. Likewise, any parameter variation that benefits
424 herbivores (higher growth rate r_h , weaker competition c_h or higher conversion efficiency e_h
425 (Appendix D.III)) disfavors feasibility, favors stability or both.

426

427

428 4. Discussion

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

440

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

443 In line with theoretical findings (Georgelin and Loeuille, 2014; Mougi and Kondoh,
444 2014b; Sauve et al., 2016a), we show that pollination increases herbivore density by enhancing
445 plant density, while the effect of herbivory on pollinators is utterly opposite. This remains true
446 when mutualism is modeled as a modified consumer-resource interaction, thus accounting for
447 exploitative competition between animal species (Holland *et al.* 2013). Congruent direct effects
448 on plant densities have been confirmed by several field experiments (Herrera, 2000; Herrera et
449 al., 2002; Sutter and Albrecht, 2016), but empirical documentation of the consecutive indirect
450 ecological effects between herbivore and pollinator species remains weak (e.g. Gómez 2005).

451
452 In contrast with feasibility, we find stability to be favored by herbivory and disfavored
453 by pollination, in line with the theory on feedback loops (relationship (R3), Levins 1974).
454 Several studies have indeed shown that pollination networks are prone to display unstable
455 dynamics, such as sudden collapses consecutive to the crossing of tipping points (Dakos and
456 Bascompte, 2014; Kaiser-Bunbury et al., 2010; Lever et al., 2014), as positive feedbacks
457 amplify and propagate disturbances. The important role of predation (herbivorous here) in
458 stabilizing population dynamics, on the other hand, has early been identified (Menge and
459 Sutherland, 1976; Nicholson, 1954; Oksanen et al., 1981). Our results confirm that the
460 consecutive negative feedback can stabilize the dynamics of mutualistic-antagonistic
461 communities. It is important to note, however, that the effects of each interaction type on the
462 stability of such communities are inconsistent across models (Georgelin and Loeuille, 2014;
463 Holland et al., 2013; Sauve et al., 2016a). The different assumptions on the variation of the
464 animal intake rates with plant density (i.e. functional responses) largely explain such
465 contrasting results. It is nonetheless frequent to observe that the stability of the whole
466 community is driven by the subcommunity displaying stable dynamics when considered in
467 isolation. Yet, unstable dynamics are possible when merging two stable subcommunities as
468 shown by Mougi & Kondoh (2014b). In their work, cycling densities are reported, driven by a
469 delayed plant recovery after its exploitation by herbivores. The delay ensues from the fact that
470 most of the productivity gain from pollination is captured by herbivores, which might be
471 particularly problematic in an agricultural context, especially given that it has been reported in
472 empirical studies several times (Gómez, 2005; Herrera et al., 2002). An integrative management
473 of pollination and biological control can, fortunately, enable synergetic interactions between
474 ecosystem services (Sutter and Albrecht, 2016).

475

476 It is important to highlight that instability, in our model, encompasses two behaviors
477 whose biological implications are utterly different: (1) the loss of one or several species (Fig.
478 3, red-brown-green areas) vs. (2) the unbounded growth of population densities (Fig. 3, blue
479 area) driven by an “orgy of mutual benefaction” (May, 1981). While coexistence is not
480 maintained in the first case, it is in the second case. Another notion of stability – permanence
481 (Hutson and Schmitt, 1992) - enables to distinguish between these two cases: a biological
482 community is said to be permanent if the densities of all species are always above a minimal
483 threshold. Unbounded population growth is thus a case of “permanent coexistence” (Hutson
484 and Law, 1985), a concept that captures the diversity of population dynamics that permit the
485 coexistence of species in real biological communities. The orgy of mutual benefaction is,
486 however, seldom observed in nature in spite of mutualisms being widespread (Bronstein, 1994).
487 This indicates that the assumptions of simple models of mutualism are likely violated in real
488 biological systems. The functional response, which we assume linear for both interactions in
489 order to gain analytical tractability, could saturate at high pollination levels when the handling
490 time becomes limiting (e.g. Soberon & Martinez Del Rio 1981). The community context can
491 also impede unrealistic population growth (Freedman et al., 1987; Heithaus et al., 1980; Ringel
492 et al., 1996). While intraspecific competitions prevent this behavior up to a given level of
493 pollination (Holland et al., 2002), we show here that the presence of a third species – the
494 herbivore – allows for even stronger pollination levels to be compatible with biologically
495 relevant finite population densities (relationship ($R3$)). It is thus not surprising that orgies of
496 mutual benefaction are not observed in nature as any two-species mutualism displaying such
497 dynamics would accumulate enemies until restoring the balance required for stable coexistence.
498 Several mechanisms could underlie this community assembly process. Firstly, as the plant
499 biomass is booming, more and more herbivore species are becoming viable in the focal patch
500 (e.g. inequality ($R2'.1$)). Because the plant population defines the threshold beyond which
501 herbivore species can invade, as the plant density grows, the filter existing on the possible
502 herbivore community weakens, and more herbivores species are susceptible to come and
503 control the dynamics. Secondly, existing trophic links would likely strengthen as a result of
504 adaptive foraging on the booming plant species in response to its abundance increase relative
505 to other available resources. Adaptive foraging has notably been proposed as an important
506 stabilizing process within complex trophic networks (Kondoh, 2003). In particular, Mougi &
507 Kondoh (2014a) show how the interplay between adaptive foraging, pollination, and herbivory
508 can support the maintenance of stable coexistence in plant-pollinator-herbivore communities.

509

510 Empirical evidence suggesting a balance between pollination and herbivory in natural
511 communities does exist. At the module scale, several experimental studies manipulating the
512 presence of animal species find the effects of pollination and herbivory on plant fecundity to be
513 roughly of the same magnitude, approximately canceling each other (Gómez, 2005; Herrera,
514 2000; Herrera et al., 2002; Sutter and Albrecht, 2016). At the network scale, Melián *et al.* (2009)
515 show that most strong interactions, mutualistic and antagonistic, are concentrated in the same
516 few plant species of the Doñana Biological Reserve (Spain). Sauve *et al.* (2016b) exhibit a
517 positive correlation between the number of pollinators and herbivores that interact with a given
518 plant of the Norwood farm (UK). In line with our results, this correlation contributes positively
519 to the stability of the community. Our results also imply that cascades of extinctions may be
520 expected within plant-pollinator-herbivore networks as a result of the current global pollinator
521 decline (Potts et al., 2010), given the weakening of pollination relative to herbivory.

522

523 Empirical evidence linked to species traits also supports the idea of a balanced
524 interaction pattern. Indeed, a substantial amount of studies documents shared preferences for
525 plant phenotypes between pollinators and herbivores. Favoring balanced pollination vs.
526 herbivory, shared preferences have been reported for a large number of plant traits, including
527 flower color (Irwin et al., 2003), floral display (Cariveau et al., 2004; Gómez, 2003), chemical
528 volatiles (Andrews et al., 2007; Theis et al., 2014), nectar quantity (Adler and Bronstein, 2004)
529 or reproductive system (Asikainen and Mutikainen, 2005). This preference pattern implies that
530 plants are subject to an ecological trade-off between attracting pollinators and deterring
531 herbivores (Strauss et al., 1999). Such a trade-off has been reported across a wide diversity of
532 plant taxa (Strauss et al., 2002). Our work indicates that it might be ubiquitous as it fosters a
533 balance between the strengths of pollination and herbivory, and hence stable plant-pollinator-
534 herbivore coexistence. When sampling natural ecosystems, at any given time, stable
535 communities should indeed be more frequently encountered than unstable ones owing to a
536 longer ‘lifespan’. Communities displaying such an ecological trade-off should accordingly be
537 more frequently encountered. This trade-off might thus be construed as an emergent property
538 of plant-pollinator-herbivore communities, i.e. a property that emerges when considering a
539 large number of such communities rather than one that apply for each considered community.

540

541 Traits of plant species might be subject to conflicting selection arising from such a trade-
542 off (Strauss and Whittall, 2006), with potentially important implications in terms of diversity

543 maintenance. In the case of the wild radish *Raphanus sativus*, for instance, it has been shown
544 that the maintenance of a flower color dimorphism (white vs. pink) was due to both the
545 pollinators and the herbivores interacting preferentially with white morphs (Irwin et al., 2003;
546 McCall et al., 2013; Stanton, 1987). The question of whether such dimorphism emerged, in the
547 first place, because of the interplay between pollination and herbivory, remains open. The study
548 of mutualistic-antagonistic communities, plant-pollinator-herbivore in particular (Strauss and
549 Irwin, 2004), thus offers opportunities to significantly improve our understanding of the
550 ecological processes supporting the coexistence of species in natural systems, but also of the
551 complex eco-evolutionary dynamics driving the maintenance of biodiversity.

552
553

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557
558

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Stable coexistence ?

