

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

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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.

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27

## 28 Abstract

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

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## 45 Keywords

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

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## 56 1. Introduction

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

81  
82 Understanding stable coexistence within plant-pollinator-herbivore communities  
83 requires explicitly accounting for both the mutualistic (i.e. plant-pollinator) and the antagonistic  
84 (i.e. plant-herbivore) interaction. A large body of empirical evidence indeed documents non-  
85 additive effects of pollination and herbivory on plant densities, in both uncultivated (Gómez,  
86 2005; Herrera, 2000; Herrera et al., 2002; Pohl et al., 2006) and cultivated (Lundin et al., 2013;  
87 Strauss and Murch, 2004; Sutter and Albrecht, 2016) plant species. The strength of the  
88 mutualistic interaction is affected by the antagonistic interaction and vice versa, explaining such

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

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

103  
104 In plant-pollinator-herbivore communities, the typical module consists of two animal  
105 species - a pollinator and a herbivore - sharing a common resource plant species (Fig. 1A.a).  
106 The resulting indirect interaction between pollinators and herbivores is an antagonism (Fig.  
107 1A.a, Holland *et al.* 2013). Pollinators allow the community to sustain a higher herbivore  
108 density by increasing plant productivity while herbivores, on the other hand, decrease pollinator  
109 density by reducing resource availability. Theoretical works indicate that the presence of  
110 pollinators can even make the herbivore population viable (Georgelin and Loeuille, 2014;  
111 Mougi and Kondoh, 2014a). As illustrated by Georgelin & Loeuille (2014), direct vs. indirect  
112 ecological effects can be of similar magnitude. Their study indeed reports a constant herbivore  
113 density despite increasing herbivore mortality. In their model, over a wide range of herbivore  
114 mortalities, the direct mortality-induced losses on herbivores are totally offset by the indirect  
115 gain resulting from a higher pollinator density consecutive to the herbivorous predation release  
116 on plants. Further increasing mortality, however, leads to the abrupt collapse of the herbivore  
117 population, which illustrates that combining different interactions also has important  
118 implications in terms of community stability (Mougi and Kondoh, 2014b).

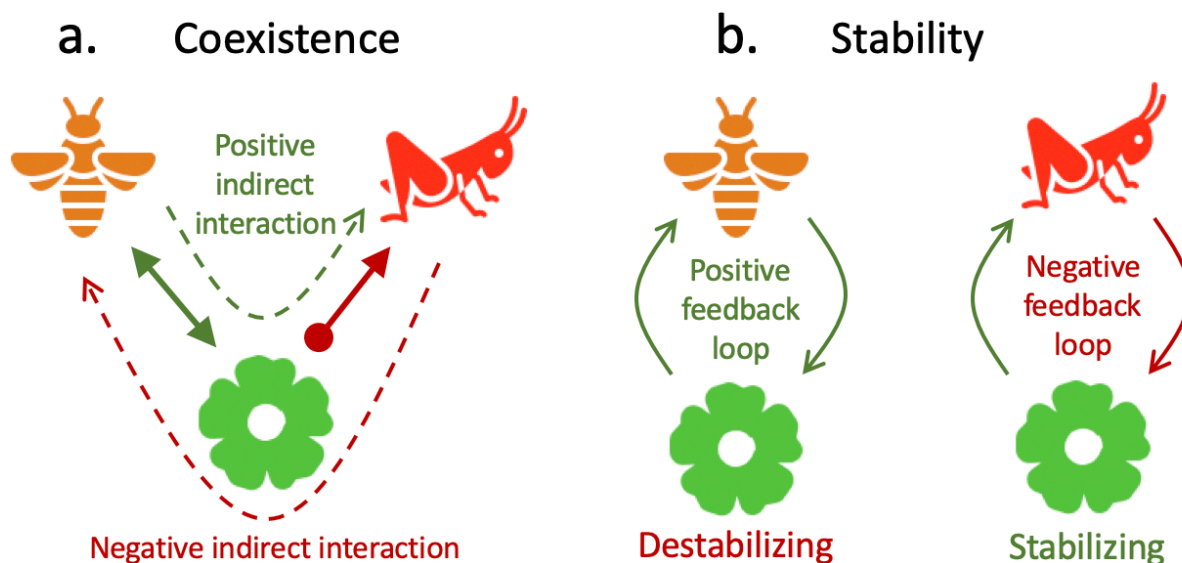
119 Mutualisms, such as pollination, intrinsically entail positive feedback loops (Fig. 1A.b).  
120 Positive feedbacks are destabilizing (Levins, 1974; Neutel and Thorne, 2014) as they tend to  
121 amplify the direct effect of a perturbation. As a result, unstable behaviors have been identified  
122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

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

132  
133 The goal of the present paper is to understand how stable coexistence within plant-  
134 pollinator-herbivore communities constrains the relative strengths of pollination and herbivory,  
135 i.e. the relative per capita effects of each interacting animal species on plant population growth.  
136 In contrast with most previous theoretical works on mutualistic-antagonistic modules, the  
137 relationships governing stable coexistence we obtain are analytical. Such relationships between  
138 pollination and herbivory are derived from the population dynamics of the characteristic three-  
139 species module (Fig. 1A.a), in which both animal intake rates (i.e. functional responses) are  
140 assumed linear to achieve analytical tractability. We discuss such an assumption at the end of  
141 the present work (section 4). Finally, the per-capita effect of plant-animal interactions on  
142 community dynamics is mediated by animal densities, which in turn depend on other ecological  
143 parameters such as animal mortalities or intraspecific competition rates. We therefore extend  
144 our analysis by studying their influence, which confirms the robustness of our results. In what  
145 follows, we show that stable coexistence within plant-pollinator-herbivore communities  
146 requires a balance between the strengths of pollination and herbivory. Such a pattern ensues  
147 from the opposite effect each interaction has on coexistence and stability (Fig. 1A). Coexistence  
148 is favored by pollination and disfavored by herbivory, as a result of both direct and indirect  
149 ecological interactions (Fig. 1A.a). Stability is enhanced by herbivory and reduced by  
150 pollination, as a result of the respective feedback loops (Fig. 1A.b). It is interesting to note that  
151 a large body of empirical literature (e.g. Irwin *et al.* 2003) reports shared preferences for plant  
152 phenotypes between pollinators and herbivores that would favor balanced interactions, which  
153 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. $\frac{\partial H^*}{\partial a_{ph}} < 0$

157  
158 **Figure 1: A. Predicted effects of interactions on stable coexistence.** a. Predicted effects on densities.  
159 Solid (resp. dashed) arrows for direct (resp. indirect) interactions. b. Predicted effects on stability. **B.**  
160 **Variation of biomass densities at stable coexistence with the strength of interactions.** These first  
161 analytical results are in line with predictions (see A.a). Analytical proofs in appendix B.IV.

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164

## 165 2. Model presentation

### 166 2.1 Ecological dynamics

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

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

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

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

169  
 170 Plants have a positive intrinsic growth rate ( $r_p > 0$ , autotrophs), while both pollinators ( $r_m <$   
 171  $0$ ) and herbivores ( $r_h < 0$ ) have a negative one (heterotrophs). As in previous models (e.g.  
 172 Sauve *et al.* 2014), we thus assume the plant-animal interaction to be obligate for animals and  
 173 facultative for the plant. Intraspecific competition is accounted for. The animal competition  
 174 rates ( $c_m, c_h$ ) correspond to interference while, for the plant species ( $c_p$ ), this rate essentially  
 175 captures the competition for resources such as light, water, and nutrients (Craine and Dybzinski,  
 176 2013). Interspecific interactions, whose strength is  $a_{pm}$  for pollination and  $a_{ph}$  for herbivory,  
 177 affect population growths proportionally to biomass densities. The use of a linear functional  
 178 response for mutualism exposes the model to unbounded population growths (May, 1981). It,  
 179 however, enables testing whether this behavior could be top-down controlled by herbivory,  
 180 placing our work in the line of research tackling how the community context could explain the  
 181 stability of mutualisms in nature (e.g. Ringel *et al.* 1996). Finally,  $e_m$  and  $e_h$  are the conversion  
 182 efficiencies from plants to animals. Parameter details are given in table 1.

183  
 184 **Table 1:** List of all model parameters and variables with their biological significance, value,  
 185 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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187

## 188 2.2 Ecological equilibria

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

196

## 197 2.3 Two-population subcommunities

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



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

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

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

216

### 217 3. Results

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

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

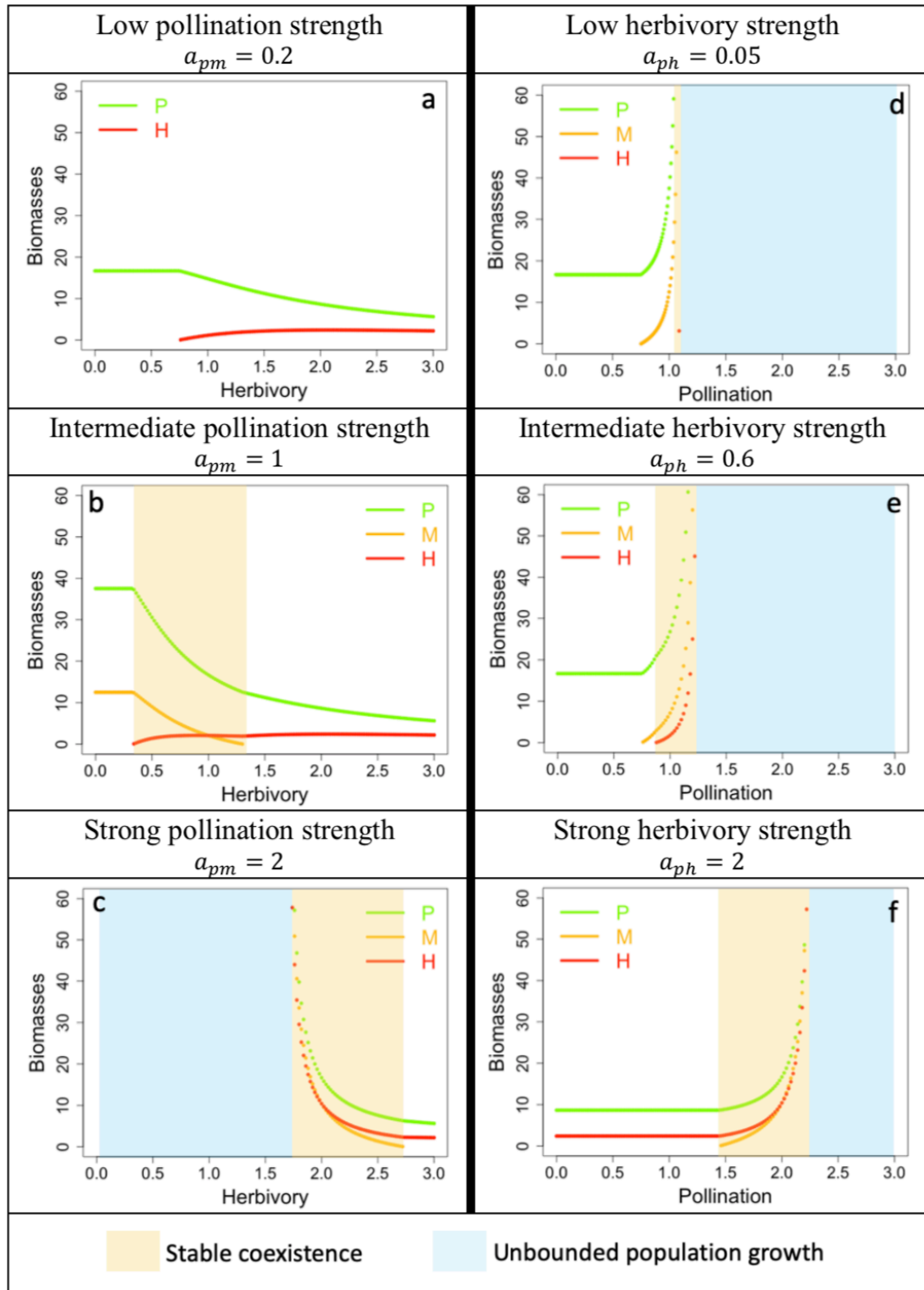
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234 In line with our predictions (Fig. 1A.b), stability displays opposite patterns: it is favored  
235 by herbivory and disfavored by pollination. For a given level of herbivory, populations display  
236 unstable dynamics for high pollination strengths (Fig. 2 d-e-f, blue background). This instability  
237 captures the unbounded growth of biomass densities driven by the mutualism. As herbivory  
238 gets stronger, higher pollination levels are needed for unbounded growth to happen (Fig. 2d vs  
239 2e vs 2f). Herbivory can indeed restore stability (Fig. 2c): starting from an initially unbounded  
240 situation, increasing herbivory restores finite densities.

241

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

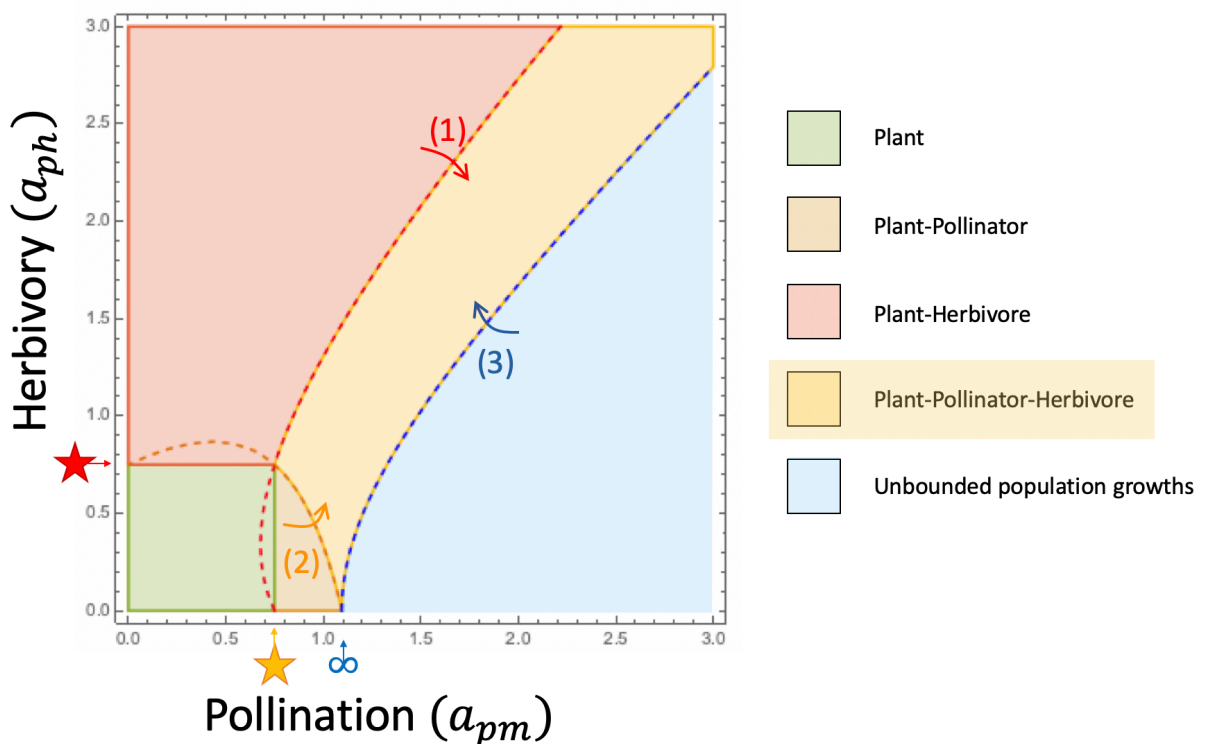
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251  
 252 **Figure 2: Biomass densities at equilibrium depend interactively on pollination and**  
 253 **herbivory strengths.** The curves are determined analytically (see appendix B.III). **a-b-c**  
 254 Dependence of densities on herbivory for three pollination levels. In **a**, pollination intensity is  
 255 too low for pollinators to persist. **d-e-f** Dependence of densities on pollination for three  
 256 herbivory levels. Parameter set:  $r_p = 10, r_m = r_h = -2.5, c_p = 0.6, c_m = c_h = 0.4, e_m =$   
 257  $e_h = 0.2$ .  
 258

### 259 3.1 Relationships governing stable coexistence

260 Positive animal densities necessarily imply a positive plant density because animals are  
 261 obligate plant-interactors (Appendix C.I.1). In other words, the coexistence equilibrium is  
 262 feasible if, and only if, both animal species have positive densities, which leads to two  
 263 inequalities. It is stable if, and only if, all three eigenvalues of the Jacobian matrix (Appendix  
 264 B.III.1) calculated at the coexistence equilibrium have a negative real part, which is equivalent  
 265 to the three Routh-Hurwitz inequalities (Appendix B.III.3). One of these inequalities is satisfied  
 266 if feasibility is assumed. Therefore, there are four relationships (i.e. inequalities) that are  
 267 necessary and sufficient for the stable coexistence of plants, pollinators and herbivores  
 268 (Appendix C.II). These relationships, as well as their biological interpretations, are presented  
 269 in Table 2. We illustrate the biological implications underlying them using Fig. 3, which  
 270 indicates the community composition depending on the strengths of pollination and herbivory.  
 271



272  
 273 **Fig. 3: Stable coexistence requires balanced pollination vs. herbivory strengths.** Given the strength  
 274 of pollination ( $a_{pm}$ ) and herbivory ( $a_{ph}$ ), the stable equilibria are determined and the point of the graph  
 275 is colored accordingly. In blue, no equilibrium is stable so densities grow unboundedly. Arrows (1), (2),  
 276 and (3) indicate the transitions enabling the satisfaction of relationships (1), (2), and (3) (**Table 2**),  
 277 indicated by the dashed red, orange, and blue curve, respectively. These three relationships are sufficient  
 278 to achieve stable coexistence given the parameter set (as in **Fig. 2**), indicating that relationship (4) is

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

284

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

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

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

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

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

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

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

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

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

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

320

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

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

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

330

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

333 (1974): the negative feedback with long time lags (level 3) is weaker than the shorter-loop  
 334 negative feedback (level 1 & 2) (details in Appendix C.II.4). Also, the constraints imposed by  
 335 this relationship on interaction strengths are not analytically tractable, due to the effect of  
 336 interactions on equilibrium densities.

337

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

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

<p>(4)</p> $(c_p P^* + c_m M^* + c_h H^*)(P^* M^* (c_p c_m - e_m a_{pm}^2) + P^* H^* (c_p c_h + e_h a_{ph}^2) + M^* H^* c_m c_h) - P^* M^* H^* (c_h c_m c_p - c_h e_m a_{pm}^2 + c_m e_h a_{ph}^2) > 0$	<p>Stability</p>	<p>Negative feedback at level 3 is weaker than the product of negative feedback at lower levels (1 &amp; 2)</p>	<p>Undetermined</p>
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348

349 By combining relationships (1') and (3'), we obtain a necessary condition for stable  
 350 coexistence (relationship (5)) which implies a positive correlation between pollination and  
 351 herbivory. Stable coexistence within plant-pollinator-herbivore communities requires a balance  
 352 between the strengths of pollination and herbivory. Stable coexistence in Fig. 3 (yellow)  
 353 therefore happens around the first diagonal, where pollination and herbivory are of similar  
 354 magnitudes.

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

355

### 356 3.2 Other ecological parameters also affect stable coexistence

357

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

365

366



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

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

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

398  
399 To summarize, the results obtained from studying the effect of these other parameters  
400 support our main results, i.e. pollination favors feasibility at the expense of stability while it is

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

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Pollinators are favored

Pollinators are favored

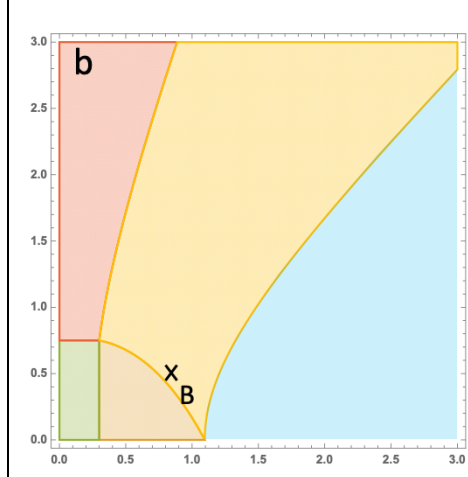
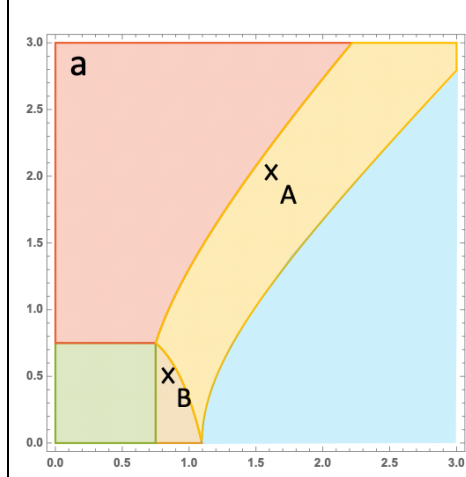
A

Intrinsic growth rates

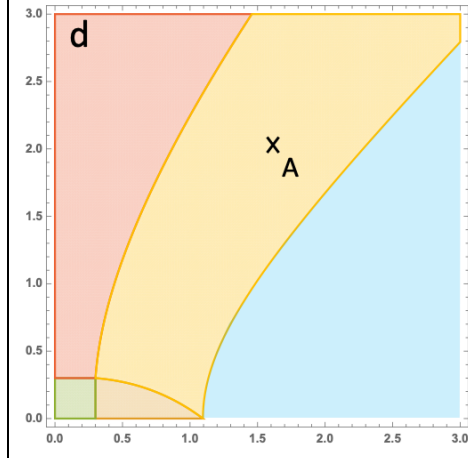
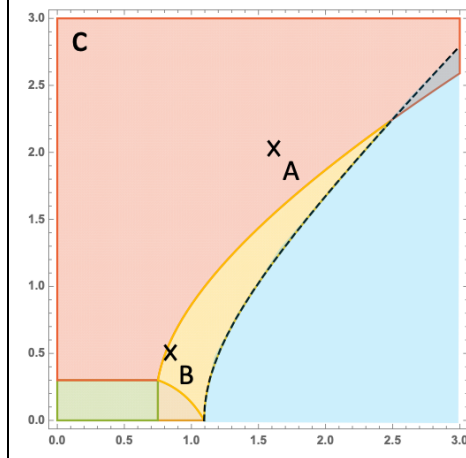
$$\frac{r_m}{r_p} = -0.25$$

$$\frac{r_m}{r_p} = -0.1$$

$$\frac{r_h}{r_p} = -0.25$$



$$\frac{r_h}{r_p} = -0.1$$



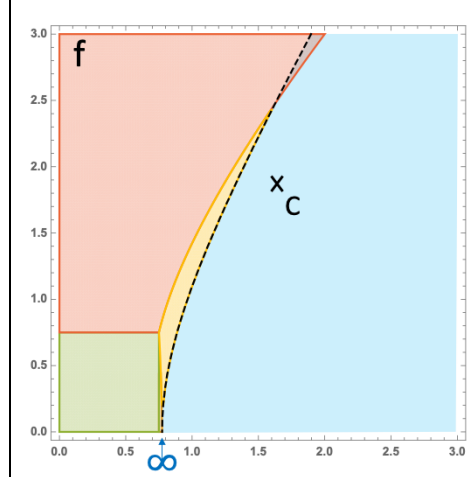
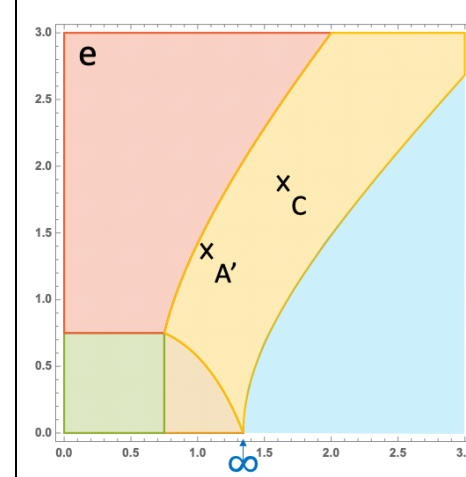
B

Competition rates

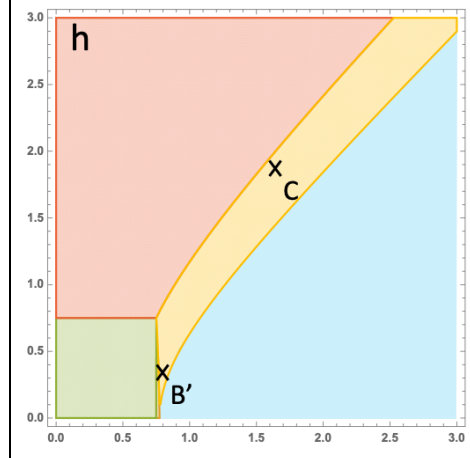
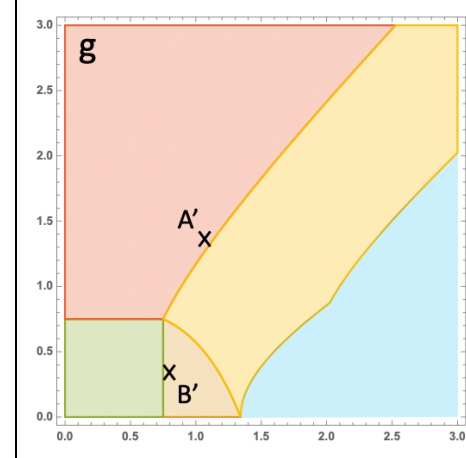
$$c_m = 0.6$$

$$c_m = 0.2$$

$$c_h = 0.6$$



$$c_h = 0.2$$



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

## 426 4. Discussion

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

438  
439           The balance between pollination and herbivory is driven by the opposite effects each  
440 type of interaction has on coexistence (i.e. feasibility) and stability.

441           In line with theoretical findings (Georgelin and Loeuille, 2014; Mougi and Kondoh,  
442 2014b; Sauve et al., 2016a), we show that pollination increases herbivore density by enhancing  
443 plant density, while the effect of herbivory on pollinators is utterly opposite. This remains true  
444 when mutualism is modeled as a modified consumer-resource interaction, thus accounting for  
445 exploitative competition between animal species (Holland *et al.* 2013). Congruent direct effects  
446 on plant densities have been confirmed by several field experiments (Herrera, 2000; Herrera et  
447 al., 2002; Sutter and Albrecht, 2016), but empirical documentation of the consecutive indirect  
448 ecological effects between herbivore and pollinator species remains weak (e.g. Gómez 2005).

449  
450           In contrast with feasibility, we find stability to be favored by herbivory and disfavored  
451 by pollination, in line with the theory on feedback loops (relationship (3), Levins 1974). Several  
452 studies have indeed shown that pollination networks are prone to display unstable dynamics,  
453 such as sudden collapses consecutive to the crossing of tipping points (Dakos and Bascompte,  
454 2014; Kaiser-Bunbury et al., 2010; Lever et al., 2014), as positive feedbacks amplify and  
455 propagate disturbances. The important role of predation (herbivorous here) in stabilizing  
456 population dynamics, on the other hand, has early been identified (Menge and Sutherland, 1976;  
457 Nicholson, 1954; Oksanen et al., 1981). Our results confirm that the consecutive negative  
458 feedback can stabilize the dynamics of mutualistic-antagonistic communities. It is important to

459 note, however, that the effects of each interaction type on the stability of such communities are  
460 inconsistent across models (Georgelin and Loeuille, 2014; Holland et al., 2013; Sauve et al.,  
461 2016a). The different assumptions on the variation of the animal intake rates with plant density  
462 (i.e. functional responses) largely explain such contrasting results. It is nonetheless frequent to  
463 observe that the stability of the whole community is driven by the subcommunity displaying  
464 stable dynamics when considered in isolation. Yet, unstable dynamics are possible when  
465 merging two stable subcommunities as shown by Mougi & Kondoh (2014b). In their work,  
466 cycling densities are reported, driven by a delayed plant recovery after its exploitation by  
467 herbivores. The delay ensues from the fact that most of the productivity gain from pollination  
468 is captured by herbivores, which might be particularly problematic in an agricultural context,  
469 especially given that it has been reported in empirical studies several times (Gómez, 2005;  
470 Herrera et al., 2002). An integrative management of pollination and biological control can,  
471 fortunately, enable synergetic interactions between ecosystem services (Sutter and Albrecht,  
472 2016).

473  
474 It is important to highlight that instability, in our model, encompasses two behaviors  
475 whose biological implications are utterly different: (1) the loss of one or several species (Fig.  
476 3, red-brown-green areas) vs. (2) the unbounded growth of population densities (Fig. 3, blue  
477 area) driven by an “orgy of mutual benefaction” (May, 1981). While coexistence is not  
478 maintained in the first case, it is in the second case. Another notion of stability – permanence  
479 (Hutson and Schmitt, 1992) - enables to distinguish between these two cases: a biological  
480 community is said to be permanent if the densities of all species are always above a minimal  
481 threshold. Unbounded population growth is thus a case of “permanent coexistence” (Hutson  
482 and Law, 1985), a concept that captures the diversity of population dynamics that permit the  
483 coexistence of species in real biological communities. The orgy of mutual benefaction is,  
484 however, seldom observed in nature in spite of mutualisms being widespread (Bronstein, 1994).  
485 This indicates that the assumptions of simple models of mutualism are likely violated in real  
486 biological systems. The functional response, which we assume linear for both interactions in  
487 order to gain analytical tractability, could saturate at high pollination levels when the handling  
488 time becomes limiting (e.g. Soberon & Martinez Del Rio 1981). The community context can  
489 also impede unrealistic population growth (Freedman et al., 1987; Heithaus et al., 1980; Ringel  
490 et al., 1996). While intraspecific competitions prevent this behavior up to a given level of  
491 pollination (Holland et al., 2002), we show here that the presence of a third species – the  
492 herbivore – allows for even stronger pollination levels to be compatible with biologically

493 relevant finite population densities (relationship (3)). It is thus not surprising that orgies of  
494 mutual benefaction are not observed in nature as any two-species mutualism displaying such  
495 dynamics would accumulate enemies until restoring the balance required for stable coexistence.  
496 Several mechanisms could underlie this community assembly process. Firstly, as the plant  
497 biomass is booming, more and more herbivore species are becoming viable in the focal patch  
498 (e.g. relationship (2'a)). Because the plant population defines the threshold beyond which  
499 herbivore species can invade, as the plant density grows, the filter existing on the possible  
500 herbivore community weakens, and more herbivores species are susceptible to come and  
501 control the dynamics. Secondly, existing trophic links would likely strengthen as a result of  
502 adaptive foraging on the booming plant species in response to its abundance increase relative  
503 to other available resources. Adaptive foraging has notably been proposed as an important  
504 stabilizing process within complex trophic networks (Kondoh, 2003). In particular, Mougi &  
505 Kondoh (2014a) show how the interplay between adaptive foraging, pollination, and herbivory  
506 can support the maintenance of stable coexistence in plant-pollinator-herbivore communities.  
507

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

520  
521         Empirical evidence linked to species traits also supports the idea of a balanced  
522 interaction pattern. Indeed, a large number of studies documents shared preferences for plant  
523 phenotypes between pollinators and herbivores. Favoring balanced pollination vs. herbivory,  
524 shared preferences have been reported for a large number of plant traits, including flower color  
525 (Irwin et al., 2003), floral display (Cariveau et al., 2004; Gómez, 2003), chemical volatiles  
526 (Andrews et al., 2007; Theis et al., 2014), nectar quantity (Adler and Bronstein, 2004) or

527 reproductive system (Asikainen and Mutikainen, 2005). Such a pattern implies that plant  
528 species are subject to an ecological trade-off between attracting pollinators and deterring  
529 herbivores (Strauss et al., 2002, 1999). Our work indicates that this trade-off might be  
530 ubiquitous as it fosters the stable coexistence of plant-pollinator-herbivore communities,  
531 explaining why it has been reported across a broad diversity of plant taxa. Traits of plant species  
532 might be subject to conflicting selection arising from such a trade-off (Strauss and Whittall,  
533 2006), with potentially important implications in terms of diversity maintenance. In the case of  
534 the wild radish *Raphanus sativus*, for instance, it has been shown that the maintenance of a  
535 flower color dimorphism (white vs. pink) was due to both the pollinators and the herbivores  
536 interacting preferentially with white morphs (Irwin et al., 2003; McCall et al., 2013; Stanton,  
537 1987). The question of whether such dimorphism emerged, in the first place, because of the  
538 interplay between pollination and herbivory, remains open. The study of mutualistic-  
539 antagonistic communities, plant-pollinator-herbivore in particular (Strauss and Irwin, 2004),  
540 thus offers opportunities to significantly improve our understanding of the ecological processes  
541 supporting the coexistence of species in natural systems, but also of the complex eco-  
542 evolutionary dynamics driving the maintenance of biodiversity.

543

544

## 545 Acknowledgments

546 The authors would like to thank Prof. Sharon Y. Strauss, and Dr. François Duchenne, for their  
547 helpful feedback on the manuscript.

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