

1 A conceptual framework for studying the strength of
2 plant–animal mutualistic interactions

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Abstract

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The strength of species interactions influences strongly the structure and dynamics of ecological systems. Thus, quantifying such strength is crucial to understand how species interactions shape communities and ecosystems. Although the concepts and measurement of interaction strength in food webs have received much attention, there has been comparatively little progress in the context of mutualism. We propose a conceptual scheme for studying the strength of plant–animal mutualistic interactions. We first review the interaction strength concepts developed for food webs, and explore how these concepts have been applied to mutualistic interactions. We then outline and explain a conceptual framework for defining ecological effects in plant–animal mutualisms. We give recommendations for measuring interaction strength from data collected in field studies based on a proposed approach for the assessment of interaction strength in plant–animal mutualisms. This approach is conceptually integrative and methodologically feasible, as it focuses on two key variables usually measured in field studies: the frequency of interactions and the fitness components influenced by the interactions.

43 **Introduction**

44 Organisms interact with other organisms in multiple ways. The consequences of
45 interactions for the participating species vary widely in their relative importance—from
46 weak to strong—and their sign—from negative to neutral to positive. These features of
47 species interactions influence strongly the structure and dynamics of ecological systems
48 (Yodzis, 1981; McCann *et al.*, 1998; Wootton & Emmerson, 2005; Bascompte *et al.*, 2006;
49 Okuyama & Holland, 2008). Thus, quantifying the strength of the ecological interactions
50 among species and revealing their underlying mechanisms is crucial to understand how
51 they contribute to shaping communities and ecosystems.

52 Historically, ecological theory has focused mostly on antagonistic interactions, particularly
53 predation and competition, and only in recent decades are mutualistic interactions being
54 incorporated into mainstream ecological theory (Bronstein, 1994; Stachowicz, 2001;
55 Bruno *et al.*, 2003). The theoretical concepts and empirical measurement of the
56 magnitude of antagonistic interactions have received much attention (see, e.g., Paine,
57 1992; Laska & Wootton, 1998; Abrams, 2001; Berlow *et al.*, 2004; Wootton & Emmerson,
58 2005; Novak & Wootton, 2008), with substantial effort put into combining data and
59 theory (Laska & Wootton, 1998; Wootton & Emmerson, 2005). In contrast, there has been
60 little discussion about the conceptual basis of interaction strength in plant–animal
61 mutualisms, in spite of the widespread occurrence of this type of mutualism in nature and
62 its importance for the maintenance of natural and agricultural ecosystems (Bronstein,
63 1994; Stachowicz, 2001; Begon *et al.*, 2006; Garibaldi *et al.*, 2013). Furthermore, although
64 several empirical studies have provided data on the relative importance of animal
65 mutualists for particular plant species (Schemske & Horvitz, 1984; Herrera, 1987;
66 Pettersson, 1991; Schupp, 1993; Olsen, 1997; Vázquez *et al.*, 2005; Ness *et al.*, 2006; Sahli
67 & Conner, 2006), little effort has been made to estimate the reciprocal effects of plants on
68 animals, and to link theoretical concepts with data. Thus, there is a serious vacuum in
69 the development and application of ecological theory to the study of mutualism.

70 Below we provide a synthesis of the concepts of interaction strength developed in the

71 context of antagonistic, consumer–resource interactions and apply them to the study of
72 mutualistic interactions.

73 **Interaction strength concepts in food webs**

74 There is a long history of conceptual and empirical work on interaction strength in the
75 context of predator–prey interactions and food webs (reviewed in Laska & Wootton, 1998;
76 Berlow *et al.*, 1999, 2004; Wootton & Emmerson, 2005). In this body of literature,
77 interaction strength has usually been defined as “an estimate of the magnitude of the
78 effect of one species on another” (Laska & Wootton, 1998). Although this verbal definition
79 is simple and intuitive, a more quantitative definition has been elusive, and has been
80 shaped by the multiple interests and goals of researchers and the type of data available
81 (Berlow *et al.*, 2004; Laska & Wootton, 1998; Wootton & Emmerson, 2005). Four common
82 concepts of interaction strength in food webs include (i) per-capita interaction strength,
83 the direct effect of an individual of one species on an average individual of another species,
84 represented by the elements j, i of the community matrix \mathbf{A} , $A_{ji} = \partial(dn_j/(n_j dt))/\partial n_i$,
85 which describe the response of the per capita growth rate of species j ($dn_j/(n_j dt)$) to a
86 small, pulsed perturbation in the abundance of species i (n_i), evaluated at the community
87 equilibrium (Levins, 1968; Laska & Wootton, 1998); (ii) the direct effects of an individual
88 of one species on the whole population of another species at equilibrium, represented by
89 the elements j, i of the Jacobian matrix \mathbf{J} , $J_{ji} = \partial(dn_j/dt)/\partial n_i$, which describe the
90 response of the population-level growth rate of species j to a change in the abundance of
91 species i , evaluated at the community equilibrium (May, 1973); (iii) the total effects (via
92 direct as well as indirect pathways) on the equilibrium abundances of one species to a
93 constant rate of removal or addition of individuals of another species at the neighborhood
94 of an equilibrium, represented by the elements of the inverted negative Jacobian matrix
95 (Yodzis, 1988, see below); and (iv) the differences in the abundances at equilibrium
96 between a community with all species present, and the same community with the focal
97 species removed, which define the removal matrix (MacArthur, 1972; Paine, 1980).

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98 The above four concepts of interaction strength have several important differences. First,
99 while the former three concepts require an explicit or implicit mathematical model
100 describing the population dynamics of the interacting species, the latter concept is
101 empirically based (Laska & Wootton, 1998). Second, concepts i–iii deal only with small
102 perturbations around a population equilibrium, concept iv concerns the removal of an
103 entire population. Third, the four concepts involve different properties of the species
104 recipient of the effect (Abrams, 1987): per-capita interaction strength applies to the
105 (average) individual response of the species receiving the effect, the elements of the
106 Jacobian matrix apply to population growth rates of the recipient species, and the
107 elements of both the inverted and removal matrices apply to equilibrium (or long-term
108 mean) population density of the species recipient of the effect. These three properties of
109 recipient species (i.e., per capita growth rate, population growth rate, and long-term
110 population densities) concern different temporal scales: whereas per capita and
111 instantaneous population growth rate may be measured over one or a few generations,
112 equilibrium population density should be measured after multiple generations (see
113 definitions of short-term and long-term ecological effects below).

114 Ecologists have also used multiple empirical approaches to obtain estimates of interaction
115 strength, including field and laboratory experiments, observational field studies,
116 allometric relationships, and the analysis of system dynamics (Wootton & Emmerson,
117 2005). Field experiments consist mostly in the removal of one or more species from a
118 study system and the measurement of a certain response variable (usually abundance) of
119 the focal species (Bender *et al.*, 1984; Paine, 1992; Berlow *et al.*, 1999), with interaction
120 strength usually defined as either per-capita effects or the elements of the removal matrix.
121 Laboratory experiments have been used to estimate component parameters of
122 mathematical models describing interacting species systems (Wootton & Emmerson,
123 2005). These mathematical models, once parameterized with the empirical estimates for
124 the particular system under study, are used to calculate interaction strength under any of
125 the above definitions (e.g., Levitan, 1987; Schmitz, 1997). When experimentation is not
126 possible, observational approaches allow estimating per-capita interaction strengths based

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127 on measurements of interaction parameters such as feeding rates, diet composition, and
128 abundances of predators and prey (e.g., Wootton, 1997; Novak & Wootton, 2008). When
129 direct estimation of interaction strength in the field is difficult, allometric relationships
130 and the analysis of system dynamics are good alternatives (e.g., Wootton, 1997; Sala &
131 Graham, 2002; Emmerson & Raffaelli, 2004). Allometric approaches are based on the
132 assumption that per-capita interaction strength scales with body sizes of prey and their
133 predators (large-bodied organisms interact more strongly than small-bodied organisms), a
134 reasonable assumption given that numerous biological processes also scale with body size
135 (Yodzis & Innes, 1992; Woodward *et al.*, 2005). Finally, analysis of system dynamics fits
136 models to population time series to estimate model parameters (Pascual & Kareiva, 1996;
137 Laska & Wootton, 1998).

138 The above approaches usually assume that interaction strength is an invariant property
139 of a pair of species within a community. Unfortunately, this assumption is usually
140 incorrect, as ecological communities vary greatly over time (Abrams, 2001). Because of
141 the nonlinearity that characterizes communities, it is usually not possible to predict if
142 two experiments that manipulated the same species in the same way will result in the
143 same ecological effects. Furthermore, the empirical studies aimed at parameterizing
144 dynamic food web models commonly assume linear functions to describe the interaction
145 among species, with interaction strength represented as a constant. This assumption is
146 unrealistic, as interaction strength is more likely to be a function of the densities of
147 interacting species, not a scalar (Abrams, 2001; Berlow *et al.*, 2004). Nonlinear functional
148 responses are usually a better alternative (Novak & Wootton, 2008; Novak, 2010; Berlow
149 *et al.*, 2004), but using them requires to explore new ways to estimate biologically
150 reasonable model coefficients from empirical data, such as foraging and metabolic rates,
151 body sizes, biomass distributions and other species traits. Systematic natural history
152 observations and a better communication between field ecologists and theoreticians are
153 needed to determine possible functional forms of interactions (Abrams, 2001; Berlow
154 *et al.*, 2004).

155 **Interaction strength concepts applied to plant–animal** 156 **mutualisms**

157 As with the development of general ecological theory, the development of interaction
158 strength concepts for mutualistic interactions has lagged behind conceptual development
159 for predator–prey interactions. Box 1 presents the main classes of models that have been
160 used to study the population dynamics of mutualistic interactions. As in food webs, the
161 simplest mathematical models of mutualistic interactions have defined interaction
162 strength as a single parameter α_{ij} representing the per capita effect of an individual of
163 species j on an individual of species i , assuming a linear (type I) functional response for
164 the mutualistic interaction (the third term of the equations for Model class 1 in Box 1).
165 However, a type I functional response is obviously unrealistic, as the benefit of a
166 mutualistic interaction cannot increase indefinitely with increasing abundance of the
167 interaction partner, unless we make the assumption of being at the close vicinity of an
168 equilibrium. Other models use instead a saturating function to represent the mutualistic
169 interaction (typically a type II functional response; the third term in equations for Model
170 class 2), thus assuming that the effect of an interaction saturates with increasing
171 abundance of all the interaction partners. In principle, this function could also have a
172 peak of the benefit at intermediate mutualist densities, beyond which the benefit of the
173 interaction would decrease (Holland *et al.*, 2002; Morris *et al.*, 2010), thus approaching a
174 type IV functional response (Andrews, 1968). This class of models has also been made
175 more complex by incorporating inter-specific competition among species of the same
176 guild, i.e. among pollinator species and among plant species (Bastolla *et al.*, 2009). A
177 third class of models is based on the logistic equation, assuming that the carrying
178 capacity of each mutualist species depends on the density of its interaction partners.
179 More mechanistically, consumer–resource models envision mutualistic interactions as a
180 special case of consumer–resource dynamics, which consider the transfer of energy and/or
181 nutrients between an organism (consumer) and a resource (Holland *et al.*, 2002; Holland
182 & DeAngelis, 2010). A fifth class of models incorporates adaptive behaviour of

183 pollinators and floral resources as a separate state variable in consumer–resource
184 mutualistic models (Valdovinos *et al.*, 2013). These mechanistic consumer–resource
185 models include several key processes involved in these mutualistic interactions, and are
186 thus a promising approach to combine theory and data, and to synthesize mutualistic and
187 food web theory. A final class of models considers a landscape of patches occupied by
188 plants and animals interacting mutualistically, in which the fraction of patches occupied
189 by plants and animals results from the balance between colonization and extinction. The
190 choice of the model of mutualistic interactions is crucial for our understanding of the
191 dynamics of mutualistic systems, because it may affect strongly the results and
192 conclusions of model-based assessments of interaction strength.

193 Ecologists have not always been consistent in their definition of interaction strength in
194 the above dynamic models of mutualistic interactions. In the first two classes of models
195 of Box 1, interaction strength has usually been defined explicitly as the per-capita effect
196 of one species on another (i.e., α_{ij} and α_{ji}). Some other studies (Ramos-Jiliberto *et al.*,
197 2009, 2012; Valdovinos *et al.*, 2009, 2013) have used species removal to study the
198 resulting community patterns and dynamics, which is similar to the removal matrix
199 approach described above for food webs. In many other studies of plant–animal
200 mutualistic networks, the underlying definition of interaction strength is still less clear.

201 Compared to predator–prey interactions, in the context of mutualistic interactions there
202 has been relatively little effort to quantify interaction strength empirically with measures
203 that are relevant at the level of demography and population dynamics. Many studies of
204 plant–animal mutualisms have defined related concepts such as “effectiveness” (Schupp,
205 1993; Olsen, 1997; Vázquez *et al.*, 2005; Sahli & Conner, 2006), “efficiency” (Schemske &
206 Horvitz, 1984; Pettersson, 1991) or “quality” (Herrera, 1987; Ness *et al.*, 2006). These
207 concepts are usually defined as the contribution of an animal mutualist to the
208 reproduction of a plant. For example, Schupp (1993, p. 16) defines the effectiveness of a
209 seed disperser species on a plant species as “the number of new adults resulting from the
210 dispersal activities of a disperser” (see also Schupp *et al.*, 2010). Similarly, Herrera (1987)
211 defines the “quality” of an ecological interaction as “the fitness consequences of the

212 interaction when it occurs”. In addition, some recent studies have also performed
213 manipulative removal experiments to assess the short-term effect of animal (Brosi &
214 Briggs, 2013) or plant (Lopezaraiza-Mikel *et al.*, 2007) species on other species of the
215 community. Brosi & Briggs (2013) conducted experimental removals of the most
216 abundant pollinator species from several study plots in sub-alpine meadows, recording
217 the change in the seed production of a focal plant species, which is close to estimating
218 some elements of the removal matrix. Similarly, Lopezaraiza-Mikel *et al.* (2007)
219 experimentally removed the flowers of the alien plant *Impatiens glandulifera* and explored
220 the response of the rest of the assemblage of co-flowering native plants in terms of flower
221 visitation and pollen transport by pollinators. Most of these studies have considered only
222 the plant’s perspective (i.e., the animal’s effect on the plant’s fitness), although recently
223 some studies have started to consider also the animal’s perspective (i.e., the plant’s effect
224 on the animal’s fitness; see, e.g., Roulston & Goodell, 2011; Vázquez *et al.*, 2012).

225 Because quantifying interaction strength in the field is difficult and time-consuming, it
226 may be unfeasible to obtain such estimates for all pairwise interactions in a network. To
227 circumvent this problem, interaction frequency (e.g., the number of visits of pollinators or
228 frugivores to plants) has been suggested as a good proxy for the magnitude of effects
229 between pairs of interacting species. Specifically, Vázquez *et al.* (2005) showed
230 mathematically that interaction frequency will be a good proxy for total (population
231 level) effects of animals on plants when the magnitude of variation of interaction
232 frequency is large compared to the magnitude of variation in the per-visit effect, and/or
233 when total effects and per-visit effects are positively correlated. Analysis of empirical
234 data of the effects of pollinators or frugivores on plants, and of plants on pollinators,
235 confirmed interaction frequency as a good surrogate of the magnitude of interactions in
236 several species (Vázquez *et al.*, 2005, 2012). We come back to this issue below (see
237 *Quantifying effect strength of plant–animal mutualistic interactions in nature*).

238 Another approach to the assessment of interaction strength in mutualistic interactions
239 considers phenology as a strong determinant of the outcome of interactions. Encinas-Viso
240 *et al.* (2012), in parallel and with similar arguments to Nakazawa & Doi (2012) for food

241 webs, assumed that the temporal overlap between interacting species, resulting from their
242 phenological dynamics, defines effect strengths. The rationale is that, as species do not
243 interact uninterruptedly through time in many ecosystems, their interactions are annulled
244 when their active stages (e.g. flowers and active pollinators) disappear temporarily from
245 the system. In addition, as the length of phenophases vary largely among species, it is
246 likely that the length of temporal overlap between phenophases of interacting species
247 explain a large part of the variance of effect strength. Under this view, instantaneous
248 effect strength is less important for defining annual average effect strength. Remarkably,
249 Encinas-Viso *et al.* (2012) found that phenology, without invoking other biological
250 constraints, can largely explain the main topological properties observed in real
251 plant–animal mutualistic webs, such as high nestedness and limited connectance. In
252 addition, they found that the length of the season affects strongly the stability and
253 diversity of mutualistic webs.

254 From the preceding paragraphs it is evident that the use of interaction strength concepts
255 in the context of mutualistic interactions has been conceptually and empirically limited,
256 thus providing a motivation for further synthesis. In the remainder of the article we
257 outline a conceptual scheme for defining effects in ecological interactions in general and in
258 plant–animal mutualistic interactions in particular. This conceptual framework
259 encompasses most previous concepts of interaction strength proposed in the literature.
260 We illustrate this framework by applying it to a model community of interacting plants
261 and pollinators, and give recommendations for its application to data collection in field
262 studies.

263 **A conceptual framework for ecological effects in** 264 **plant–animal mutualistic interactions**

265 Any interaction between two species can be defined as the reciprocal influence that the
266 species exert on each other. An *interaction* thus involves a bidirectional causal influence,

267 which can be decomposed into its constituent unidirectional *effects* of each species on the
268 other (Fig. 1). More precisely, an effect can be defined as the capacity to transmit
269 changes between variables (species' attributes in this case; Pearl, 2009; ArunKumar &
270 Venkatesan, 2011). As it is unlikely that the two effects of a pair of interacting species
271 have the same magnitude, the term “interaction strength” commonly used in the
272 ecological literature is ambiguous, and it is thus more meaningful to refer instead to
273 “effect strength”. Defining effects also requires specifying the relevant attributes whose
274 change is transmitted from the emitter to the receptor of the effect—usually abundance
275 (n) for the emitter and some property of the temporal trajectory of abundance (τ) for the
276 receptor. In addition, behavior could also be used as a meaningful variable for both
277 emitter and receptor. Thus, most commonly the ecological effect of species i on species j
278 represents how a change in the abundance of species i (n_i) triggers a deviation in the
279 abundance trajectory of species j (τ_j). While a change in abundance is an easily
280 measurable property of ecological populations, a change in the trajectory of abundance is
281 more elusive, and, as we will see below, depends on the temporal scale at which
282 interaction strength is defined.

283 When dealing with ecological effects, it is important to make a distinction between the
284 different time frames in which we measure the response of one species to another. In the
285 short term, a change in the receptor species follows as an immediate response to the
286 instantaneous change (usually in terms of abundance) in the species exerting the effect
287 (the emitter). In contrast, in the long term, a sustained change in the emitter will cause a
288 change in the focal (receptor) species, but also in other intermediate species acting as
289 secondary emitters. In addition, the altered focal receptor species will drive further
290 modifications in their neighbors that will be transmitted back to the focal receptor, and
291 so on, until the entire system reaches a new steady state. Long-term effects will thus
292 encompass the time needed to reach a new steady state, which will depend on the
293 dynamics of the system and thus on the generation times of the species involved (Yodzis,
294 1988). Therefore, as shown below, long-term effects can be reduced to a combination of
295 short-term effects determined by the structure of interactions in the community.

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296 The precise definitions of short-term and long-term effect strength will depend on how we
297 define the trajectory of the receptor species j , τ_j . For short-term effects, it is customary
298 to define τ_j as $dn_j/(n_j dt)$, the per capita rate of population change (Wootton &
299 Emmerson, 2005). Then,

$$D_{ji} = \frac{\partial}{\partial n_i} \left(\frac{dn_j}{n_j dt} \right) \quad (1)$$

300 where D_{ji} is the strength of the short-term, per capita effect that species i exerts on
301 species j , which is equal to the elements of the community matrix (Levins, 1968).

302 Long-term effects are a function of a specific set of direct and indirect effects, i.e., the
303 direct effects between the two focal species and the other direct effects between all pairs
304 of interacting species in their “sphere of influence” (the state and functioning of all species
305 directly or indirectly involved in the interaction; Brose *et al.*, 2005). Thus, for long-term
306 effects, per capita rate of change is not the best measure of τ_j , because in the long-term it
307 approaches zero whenever a new equilibrium is reached, and thus the effect strength will
308 be entirely determined by the growth rate of the receptor (which could also be zero) at
309 the instant of exerting a perturbation. Instead, long-term population density at
310 equilibrium, n_j^* , is a more appropriate measure of τ_j . Thus we can define long-term effect
311 strength as $L_{ji} = dn_j^*/dI_i$, where I_i is the rate of adding or removing individuals of
312 species i . As shown in detail by Dambacher *et al.* (2005), the calculation of long-term
313 effect strength can be done by means of the inverse of the negative Jacobian matrix, \mathbf{J}
314 (see definition for \mathbf{J} above, section *Interaction strength concepts in food webs*). Using the
315 property $\mathbf{M}^{-1} = \text{adj}(\mathbf{M})/\det(\mathbf{M})$, where \mathbf{M}^{-1} is the inverse, $\text{adj}(\mathbf{M})$ the adjugate, and
316 $\det(\mathbf{M})$ the determinant of a matrix \mathbf{M} (Dambacher *et al.*, 2005), we can express the
317 magnitude of long-term effects as

$$L_{ji} = \frac{dn_j^*}{dI_i} = \frac{1}{\det(-\mathbf{J})} \text{adj}(-\mathbf{J})_{ji} \quad (2)$$

318 As long as we are interested in the relative strength of effects within a community, the

319 first part of the rightmost expression can be disregarded and we can redefine the
 320 long-term (net) effect of species i on species j as

$$L_{ji} = \text{adj}(-\mathbf{J})_{ji} \quad (3)$$

321 A property of eq. 3 is that it includes terms of the growth equations of species other than
 322 i and j , which are not directly involved in the focal interaction. Thus, in general L_{ji} will
 323 be a function of its sphere of influence. The subset of species determining the effect
 324 strength in a focal interaction is defined by the functional relationships assumed for the
 325 population dynamics (“dynamic rules”) and by the pattern of interactions among the
 326 species within the community (“network topology”).

327 We illustrate the calculation of effect strength in a web of mutualistic interactions with
 328 the help of a model that includes what we believe are several key processes involved in
 329 these interactions. Consider the mutualistic web of Fig. 2, which represents the
 330 interactions between species that belong to two guilds, plants and pollinators, each one
 331 with a specialist and a generalist. The network is nested, as observed in many empirical
 332 mutualistic webs (Bascompte *et al.*, 2003), and is governed by dynamic rules, as
 333 described by the following model:

$$\frac{dp}{pdt} = r_p + B(p, q, a, y) - C(p, q, a, y) - s(p) - u(q) \quad (4a)$$

$$\frac{dq}{qdt} = r_q + E(p, q, a) - O(p, q, a) - e(q) - h(p) \quad (4b)$$

$$\frac{da}{adt} = r_a + G(p, q, a, y) - b(a) - l(y) \quad (4c)$$

$$\frac{dy}{ydt} = r_y + W(p, a, y) - m(y) - k(a) \quad (4d)$$

334 In this model, p and q represent the population size or biomass of the generalist and
 335 specialist plants, respectively, and a and y represent the population size or biomass of the
 336 generalist and specialist pollinators. Parameters r_p , r_q , r_a and r_y are intrinsic rates of

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337 population growth of each species. Functions B , E , G and W represent the per capita
338 benefits obtained from direct interactions and depend on the population size of the
339 directly interacting species and that of the other species of the guild which could interfere
340 with visitation. For plants, benefits represent enhanced reproduction, survival or growth;
341 for animals, resource (reward) uptake or other fitness gains. For plants, there is a per
342 capita cost (C and O) derived from producing and offering rewards, which, like benefits,
343 are functions of the species involved in the visitation rate of each plant species. Functions
344 s , e , b and m are density-dependence terms, while functions u , h , l and k represent
345 inhibition to population growth derived from direct interspecific competition within a
346 given guild (e.g., space-limitation of plant recruitment and animal nesting). This model
347 includes several fundamental dynamic features of plant–animal mutualistic interactions
348 (see Box 1). First, the population growth rate of each species results from an intrinsic
349 growth rate, the positive effect of the mutualism and negative density dependence (Gause
350 & Witt, 1935; Bascompte *et al.*, 2006). Second, the positive effects among mutualists are
351 not restricted to a linear relationship respect to the abundance of the partner (Holland
352 *et al.*, 2006). Third, there is interspecific competition among plant and among animal
353 species (Bastolla *et al.*, 2009). Finally, there is a cost function related to mutualism in
354 the equation of plant species, which leads to explicit consumer–resource dynamics (Box 1,
355 model class 4; Holland & DeAngelis, 2010). Of course, the model can be made more
356 sophisticated if multiple state variables are defined for each species (Valdovinos *et al.*,
357 2013).

358 As discussed in the previous section, effect strength can be measured at two contrasting
359 temporal scales. Short-term effects are expressed commonly as the partials of the per
360 capita population growth rate of the receptor species respect to changes in the abundance
361 of the emitter (eq. 1). Long-term effects, in contrast, are often represented by the total
362 derivative of equilibrium abundance of the receptor respect to changes in the abundance
363 of the emitter, which can be calculated from the adjugate of the negative community
364 matrix (eq. 3). Given that for models of even minimal complexity the adjugate can be
365 quite large, which can make calculation of effect strength difficult, it may be more

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analytically convenient to start with short-term effect strengths, and then use them as the building blocks of long-term effects. For example, for the general model (eq. 4), short-term effect strength of other species on the generalist plant p are

$$\frac{\partial}{\partial q} \frac{dp}{p dt} = \frac{\partial B(p, q, a, y)}{\partial q} - \frac{\partial u(q)}{\partial q} \quad (5a)$$

$$\frac{\partial}{\partial a} \frac{dp}{p dt} = \frac{\partial B(p, q, a, y)}{\partial a} - \frac{\partial C(p, q, a, y)}{\partial a} \quad (5b)$$

$$\frac{\partial}{\partial y} \frac{dp}{p dt} = \frac{\partial B(p, q, a, y)}{\partial y} - \frac{\partial C(p, q, a, y)}{\partial y} \quad (5c)$$

It should be noted that effect strength between species that belong to the same guild is given by the difference between the gain in benefit as a consequence of the interaction and the fitness loss produced by the direct competition between the interacting species. On the other hand, the effect strength between species of different guilds is given by the difference between the gain in benefit as a consequence of the interaction and the fitness loss produced by the cost of the interaction. For simplicity, such cost is assumed to be null in the case of animals, although it may be included if needed.

Long-term effect strength, measured through the elements of the adjugate of the negative Jacobian matrix, gives the change in equilibrium density of the receiver as a consequence of a constant influx of individuals of the emitter species. Long-term effects are usually composed of many terms and thus they are difficult to measure in real communities. Below we present the effect strength between species of different guilds and between species of the same guild in our study system (eq. 4). Specifically, we will consider the effects of an animal on a plant, and between plants, by applying eq. 3 to the Jacobian matrix associated to the system represented by eq. 4. Thus, the the long-term effect strength of the generalist animal on the generalist plant is

$$L_{pa} = D_{yy}(D_{pa}D_{qq} - D_{qa}D_{pq}) - D_{qq}D_{ya}D_{py} \quad (6)$$

385 where D_{ji} refers to the short-term, direct effects of species i on species j , as given in eq.
 386 1. Making certain reasonable assumptions, it is often possible to know the sign of each
 387 direct effect and that of each term in the right hand of eq. 6. For example, we assume
 388 that the direct benefit of a mutualistic interaction exceeds the cost associated to it, and
 389 that the direct interactions between species of the same guild are negative due to
 390 interference and competition. Notice that the specific functional form of each D_{ji} term in
 391 eq. 6 as well as the general structure of L_{pa} will depend on the particular model
 392 considered (see, e.g., Box 1), and the network structure of the system. It should also be
 393 noted that the net, long-term effect of a on p is composed of three feedback cycles, in this
 394 case three paths (Fig. 2). The first path is the direct effect and contributes positively to
 395 the long-term effect. The second path contributes negatively to the total effect, and
 396 represents the beneficial effect of animal a on p 's competitor q . This translates into a
 397 negative indirect path from a to p . The last component of the long-term effect constitutes
 398 also a negative contribution, and represents the suppression of animal y 's growth rate by
 399 its competitor, which leads to a reduced mutualistic effect of y on p .

400 The long-term effect strength of the specialist plant on the generalist plant is given by

$$L_{pq} = D_{pq}(D_{aa}D_{yy} - D_{ay}D_{ya}) - D_{pa}D_{aq}D_{yy} + D_{aq}D_{ya}D_{py} \quad (7)$$

401 Four feedback cycles compose this net effect (Fig. 2, bottom panel). The first cycle is
 402 governed by the direct, short-term negative effect of q on p driven by direct competition.
 403 The second cycle is a positive contribution to this long term effect, which results from the
 404 negative of the product between two subcomponents: a positive feedback cycle (two
 405 mutually detrimental short term effects due to competition) between the two animals,
 406 and a negative short term effect of q on p . The third cycle is a positive contribution to
 407 the net effect, given by indirect mutualism from q to p through a . The last component is
 408 a negative contribution (which reinforces the negative effect), governed by the
 409 enhancement by q of the growth rate of a , which suppresses its competitor y , finally
 410 suppressing the growth rate of p .

411 The above mathematical framework is consistent with the interaction strength concepts
412 most widely used in the ecological literature (Brose *et al.*, 2004; Wootton & Emmerson,
413 2005). Thus, given a proper model of community dynamics, this framework allows us to
414 define short-term and long-term effect strength by eqs. 1 and 3, respectively.

415 **Quantifying effect strength of plant–animal mutualistic** 416 **interactions in nature**

417 Measuring effect strength in the field usually involves a great experimental effort,
418 especially for assessing the magnitude of long-term effects, L_{ji} . There are two main ways
419 of measuring L_{ji} : directly, or indirectly by combining a series of short-term effects (Fig.
420 3). We can assess L_{ji} directly through press perturbation experiments, in which the
421 perturbation is sustained through an extended period of time (Bender *et al.*, 1984). A
422 direct assessment of L_{ji} through press experiments requires manipulating the population
423 density (adding or, more simply, removing individuals) of the emitter in a sustained way,
424 and recording the change in equilibrium abundance in the receptor species by comparing
425 the manipulated plots with appropriate controls. The time span needed for this kind of
426 experiments is usually long.

427 Alternatively, we can measure long-term effects indirectly by measuring a series of
428 short-term effects, which can be done through at least three alternative routes (Fig. 3).
429 First, as mentioned above for food webs (see section *Interaction strength concepts in food*
430 *webs*), we can conduct field experiments and observations to parameterize a dynamic
431 model such as that presented in eq. 4, calculate the short-term as shown in eq. 5, and
432 then use them to construct the Jacobian matrix to calculate long-term effects (eq. 3), as
433 illustrated in eqs. 6–7. Although this approach may be feasible for simple systems with
434 few interacting species as in the above example (eq. 4), it may become logistically
435 unfeasible for larger systems.

436 A second route for calculating long-term effects indirectly by combining a series of

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437 short-term effects is to conduct pulse experiments, in which the perturbation occurs once
438 at a specific point in time (Bender *et al.*, 1984; Paine, 1992). As we have seen above (eqs.
439 6, 7), each element of L_{ji} is computed as a function of a specific set of elements D_{kl} . For
440 brevity, we define the per capita population growth rate as $F_k = dn_k/(n_k dt)$, which can
441 be inserted into eq. 1 to obtain $D_{kl} = \partial F_k / \partial n_l$. The D_{kl} elements represent direct
442 interactions between species that belong to the sphere of influence of L_{ji} . For simplicity,
443 we define this set as $S_{ji} = \{D_{kl} \text{ for all species } k \text{ and } l \text{ that belong to the sphere of}$
444 $\text{influence of } L_{ji}\}$. For computing a given L_{ji} from its D_{kl} components it is necessary to
445 know the species composition and topology of the community. Then, from this
446 information we obtain the community structure represented by the structure of the
447 Jacobian matrix \mathbf{J} (see details in Box 2). Nevertheless, note that even so a dynamic
448 model is not necessary at this step, as the procedures outlined in Box 2 rest on a specific
449 set of assumptions that lead to the basic structure of effects among the species (i.e.,
450 which elements of the Jacobian matrix are zero and which are not). This set of
451 assumptions represent in fact a model. By applying eq. 3 to the \mathbf{J} matrix we obtain the
452 symbolic expressions for calculating long-term effects, including the set S_{ij} . We can
453 concentrate our experimental effort on measuring each element D_{kl} . Thus, we can
454 perform a pulse experiment for each D_{kl} , after which the change in the per capita
455 population growth rate of the receptor, relative to the control, is recorded.

456 Unfortunately, the use of pulse experiments, although standard in ecology for measuring
457 short-term effects, is not a panacea. Short-term effects should be measured with this
458 method by introducing a constant flux of emitter individuals in the population, which is
459 impossible because organisms come in integers, and then estimating the derivative of
460 abundance with respect to time at the moment of the introduction, which is also often
461 violated because some time after the pulsed introduction is needed for detecting changes
462 in population sizes. To minimize these problems, experimenters should avoid conducting
463 pulse experiments on small populations, and should record the response of the receiver
464 species shortly after the manipulation. Even more important, experimenters should bear
465 in mind that the errors of these calculations will accumulate when combining several D_{kl}

466 estimates to calculate L_{ji} . That said, Schmitz (1997) has shown that calculating
 467 long-term effects through the inverse Jacobian matrix (as shown in eqs. 2, 3, 6 and 7) is a
 468 useful tool for assessing the qualitative outcome of long-term experiments, even under a
 469 considerable amount of variation in the values of the responses. Furthermore, although
 470 conducting pulse experiments is certainly possible (see, for example, Lopezaraiza-Mikel
 471 *et al.*, 2007; Brosi & Briggs, 2013), they still require substantial experimental effort, and
 472 in many situations they may be unfeasible, especially for community-wide studies
 473 involving many pairs of interacting plant and animal species.

474 A third route to calculate long-term effects indirectly by combining a series of short-term
 475 effects, which allows a further reduction in experimental effort, is to decompose each
 476 short-term effect D_{kl} into quantities that are easier to measure in the field (Fig. 3). For
 477 simplicity, we start by assuming that the per capita rate of change of the receptor is
 478 determined entirely (or is extremely sensitive to) a given fitness component, such as seed
 479 production, fecundity or survival. To this end, it is possible to use the chain rule of
 480 differential calculus to decompose D_{kl} in terms of fitness components and the frequency
 481 of interaction events,

$$D_{kl} = \frac{\partial F_k}{\partial n_l} = \frac{\partial F_k}{\partial Z_k} \frac{\partial Z_k}{\partial V_{kl}} \frac{\partial V_{kl}}{\partial n_l} \quad (8)$$

482 where F_k is the per capita population growth rate of the receptor species k (as defined in
 483 eq. 1), Z_k is a fitness component of the receptor likely to respond to the interaction with
 484 the emitter species l , V_{kl} is the frequency of interaction events between species k and l ,
 485 and n_l is the abundance of the emitter species l (see Box 2 for the use of short-term
 486 effects to calculate long-term effects, and Box 3 for the derivation and rationale behind
 487 eq. 8). Note that eq. 8 assumes for simplicity that the influence that the abundance of
 488 the emitter species n_l exerts on the interaction frequency between the receptor k and its
 489 other neighbors (different from l) is negligible (see Box 3). Given that these derivatives
 490 are functions that can hardly be assumed to be linear, in practice they must be evaluated
 491 at a specific point within the variable's space. This point could be, for example, the set of

492 abundances and traits present at the instant of the investigation, or at a future time,
493 when the community reaches equilibrium. Thus, the first (left) term of the rightmost
494 expression of eq. 8 represents the effect that the change in a fitness component of species
495 k exerts on its own per capita growth rate, the second term is the effect that the change
496 in the frequency of interaction events between species k and l exerts on the fitness
497 component Z_k , which captures the positive and negative terms of eq. 5, and the third
498 term is the effect that the change in the abundance of species l exerts on the frequency of
499 interaction events between species k and l . Incorporating frequency of interaction in the
500 estimation of D_{kl} makes sense given that in plant–animal mutualisms individuals are
501 involved in multiple interaction events throughout their lifespan (i.e., a bee visits many
502 flowers), a property of plant–animal mutualistic interactions that sets them apart from
503 food webs. Note that, in the context of benefit–cost model discussed in the previous
504 section (eqs. 4 and 5), the benefit–cost relationship is implicit in the short-term effects
505 described by eq. 8, as it represents the net benefits that can normally be observed in field
506 studies (i.e., gross benefits minus costs). As a whole, the three types of observations
507 involved in the decomposition of eq. 8 should be substantially simpler to obtain than
508 manipulating the abundances of each emitter species and measuring the response in the
509 receiver species in terms of its overall population growth rate.

510 The choice of the fitness component Z_k considered as surrogate of F_k is crucial for the
511 assessment of effect strength. Two main criteria should be born in mind: the per capita
512 rate of change of the receptor should be sensitive to the variation of the fitness
513 component, and the fitness component should in turn be sensitive to the variation in
514 interaction frequency. The greater the product of these two sensitivities, the better the
515 chosen fitness component as a surrogate of F_k for the assessment of effect strength. For
516 example, for plant–pollinator interactions an obvious choice of a fitness component is seed
517 production for plants, and either fecundity or survival for animals.

518 In cases in which per capita population growth rate is not uniquely determined by one
519 fitness component involved in the plant–animal interaction under study, several
520 components of F_k should be considered instead (Reed & Bryant, 2004; Crone, 2001). In

521 this case, it is also necessary to know the effect of changing the value of each chosen
 522 fitness component of the receptor species on its own per capita growth rate. Thus, each
 523 component D_{kl} of the set S_{ji} can be computed as

$$D_{kl} = \frac{\partial F_k}{\partial n_l} = \sum_{r=1}^h \frac{\partial F_k}{\partial Z_{kr}} \frac{\partial Z_{kr}}{\partial V_{kl}} \frac{\partial V_{kl}}{\partial n_l} \quad (9)$$

524 for any given set of h fitness components with values $Z_{k1}, Z_{k2}, \dots, Z_{kh}$.

525 Once we have identified the appropriate fitness components to be measured, we need to
 526 quantify the three partial derivatives in the rightmost expression of eq. 8 or 9. The first
 527 derivative involves estimating the response of F_k to a particular fitness component Z_k
 528 involved in the interaction (e.g., seed production), which is often done by constructing a
 529 matrix population model and calculating sensitivities of the fitness components of
 530 interest (Caswell, 2001). There are many good examples of this estimation
 531 (Bierzychudek, 1982; Ehrlén & Eriksson, 1995; Parker, 1997; Knight, 2004; Ashman
 532 *et al.*, 2004; Bruna *et al.*, 2009; Law *et al.*, 2010). Evaluating this first part of eq. 8 is
 533 important, as the fitness component affected by the mutualistic interaction does not
 534 necessarily contribute significantly to population growth rate. For example, fecundity
 535 usually contributes poorly to growth rates of perennial plants (Bierzychudek, 1982;
 536 Ehrlén & Eriksson, 1995; Parker, 1997; Knight, 2004; Feldman & Morris, 2011).

537 The next step in the decomposition of short-term effects is to calculate the response of
 538 the fitness component Z_k to changes in the frequency of interaction events (the second
 539 partial derivative in the rightmost expression of eqs. 8 and 9; Fig. 3). For example, for
 540 plants we can study the contribution of particular pollinator species to the seed
 541 production of a particular plant species, which can be done for plants with pollinator
 542 exclusion experiments in which flowers are experimentally exposed to one visit of a
 543 particular pollinator species and the resulting seed production is measured afterwards
 544 (e.g., Herrera, 1987; Olsen, 1997; Vázquez *et al.*, 2005; Sahli & Conner, 2006); equivalent
 545 observations can be done for plant-seed disperser interactions (e.g., Fleming & Williams,
 546 1990; Wheelwright, 1991; Jordano & Schupp, 2000). For animals, we can study the

547 contribution of particular plant species to the reproduction of a particular animal species
548 (Vázquez *et al.*, 2012).

549 Finally, we must estimate the response of visitation frequency to changes in the
550 abundance of the emitter species (the rightmost partial derivative in eq. 8; Fig. 3). This
551 can be done easily in the field by counting the number of animal visits to plants (see, e.g.,
552 Herrera, 1989; Fleming & Williams, 1990; Olsen, 1997; Jordano & Schupp, 2000; Vázquez
553 *et al.*, 2005; Sahli & Conner, 2006; Vázquez *et al.*, 2012), weighing them by the degree of
554 daily, seasonal and inter-annual temporal overlap between the interacting organisms,
555 obtained from direct phenological observations (e.g., flowering, fruiting or nesting
556 phenology). Thus, this term will be greater for species with longer daily, seasonal and
557 inter-annual overlap of their activity periods. In addition, if among-species variation in
558 the frequency of interaction per emitter individual (third derivative) is substantially
559 greater than variation in the fitness response to increments in visitation (the product of
560 the first two derivatives), then the short-term effect strength could be approximated
561 using only information on the frequency of interaction events (Vázquez *et al.*, 2005,
562 2012). Note that the short term effect D_{ij} as defined here is different from both
563 interaction strength (per visit) and species impact (per population) as defined in Vázquez
564 *et al.* (2012), but that it may be approximated by species impact divided by abundances.

565 **Concluding remarks**

566 We have outlined a conceptual framework that applies interaction strength concepts to
567 mutualistic interactions. This framework encompasses most definitions used in the food
568 web literature, and thus provides a conceptually solid basis for future discussions on the
569 strength of plant–animal mutualistic interactions.

570 As is clear from our review, most past studies of plant–animal mutualistic interactions,
571 included our own, have considered interaction strength concepts implicitly and
572 imprecisely. Furthermore, antagonistic (e.g., trophic) and mutualistic interactions differ

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573 in some obvious ways, which implies that interaction strength concepts developed in the
574 context of antagonistic interactions cannot be automatically applied to mutualistic
575 interactions. For example, whereas in predator–prey interactions prey are assumed to
576 experience only detrimental—either lethal or nonlethal—direct effects from the
577 interactions with their predator, in plant–animal mutualisms the effects of interactions
578 always have potential benefits and costs. Another distinctive attribute of plant–animal
579 mutualisms is that all participant individuals are involved in multiple interaction events
580 throughout their lifespan, which again sets them apart from food webs; visitation
581 frequency is also of paramount practical relevance, as it is this attribute of interactions
582 what is usually recorded in field studies. For these reasons, improving the conceptual
583 framework for defining and measuring interaction strength in plant–animal mutualisms is
584 clearly necessary for further progress.

585 Our framework emphasizes the concept of unidirectional effect as the basic component of
586 ecological interactions. Although this concept is not new, we believe that applying it to
587 the study of the strength of ecological interactions will help clarify its meaning, its
588 quantitative definition and its measurement. We have also emphasized the temporal scale
589 at which effect strength is defined, considering short-term effects as the building blocks of
590 long-term effects. Clearly, quantifying short-term effects will be considerably simpler and
591 less prone to error than quantifying long-term effects. As we have proposed, such
592 short-term effects can be estimated by considering key attributes of plant–animal
593 mutualistic interactions, namely the ability of plant and animal individuals to interact
594 multiple times throughout their lifespan, the influence of biological rhythms of interacting
595 species that determine frequency of interaction, and fitness components relevant at the
596 level of demography and population dynamics. The relative importance of these
597 components as determinants of effect strength in plant–animal mutualistic interactions in
598 ecological communities stands out as a key avenue for future research. Furthermore, our
599 framework could also be extended to incorporate the spatial and temporal variation in
600 the strength of ecological effects as an inherent feature of ecological interactions, which
601 would help deal with the problem of variability in interaction strengths pointed out by

602 Abrams (2001) for food-webs.

603 Ecological interactions are the threads that weave together the fabric of life. The
604 structure of this fabric is shaped by the relative strength of the effects among interacting
605 species. Quantifying the importance of these effects and understanding how they
606 contribute to shaping communities and ecosystems is thus at the heart of our quest to
607 grasp how nature works, how our activities influence it and what we can do to curb these
608 effects. Our review was motivated by the need of clarifying the conceptual framework for
609 defining, analyzing and assessing effect strength in the context of plant–animal
610 mutualisms. Although, as we argued above, this type of ecological interactions have
611 several unique features that justify developing their own conceptual framework, a more
612 ambitious goal would be the development of a comprehensive and inclusive framework for
613 effect strength in all classes of ecological interactions. Developing such a framework
614 represents a challenging next step for the advancement of ecological theory.

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928 **Figure legends**

929 **Figure 1.** Ecological interactions and effects. For a given ecological interaction between
930 two species x_1 and x_2 , there are two unidirectional effects, one exerted by x_1 on x_2 , and
931 the reciprocal effect of x_2 on x_1 .

932 **Figure 2.** Representation of four-species model community of plants (white circles) and
933 animals (black circles) used to demonstrate the conceptual framework proposed in this
934 paper. Top panel: An idealized mutualistic web composed of a generalist plant (p), a
935 specialist plant (q), a generalist pollinator (a) and a specialist pollinator (y). Links
936 represent mutualistic interactions. Middle panels: Decomposition of the paths that
937 contribute to the net, long-term effect strength of animal a on plant p . Bottom panels:
938 Decomposition of the paths that contribute to the net, long-term effect strength of plant
939 q on plant p . In the middle and bottom panels, continuous and dashed arrows show paths
940 that result in a positive and negative contribution to the net effect, respectively;
941 mutualistic links that do not take part of this effect are shown in light tones; self-effects
942 not shown.

943 **Figure 3.** Multiple approaches for estimating short- and long-term effects (filled boxes)
944 in plant–animal mutualistic interactions. Boxes at the base of the diagram indicate the
945 basic empirical measures needed for the assessments. Long-term effects can be assessed
946 directly through press experiments (sustained alteration of the emitter’s abundance).
947 Alternatively, long-term effects can be assessed indirectly from short-term effects through
948 the experimental assessment of parameters of dynamic population models, pulse
949 experiments, or the field assessment of components of short-term effects (see text for
950 details).

951 **Figure 4** Representation of intra-guild interference effects (competition for mutualists)
952 on mutualistic interactions discussed in Box 2. Left: Graph with only raw mutualistic

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953 interactions, equivalent to the adjacency matrix. Middle left: Each of the interference
954 effects, depicted as dashed links from species to each focal interaction (dark grey).
955 Middle right: The resulting species-to-species intra-guild effect. Right: resulting graph of
956 mutualistic and interference interactions, equivalent to the Jacobian matrix.

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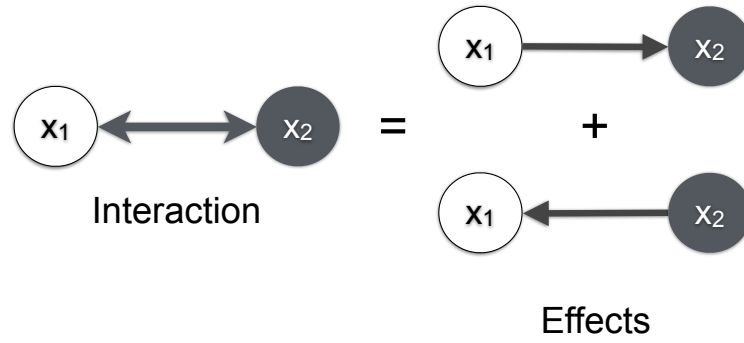


Figure 1

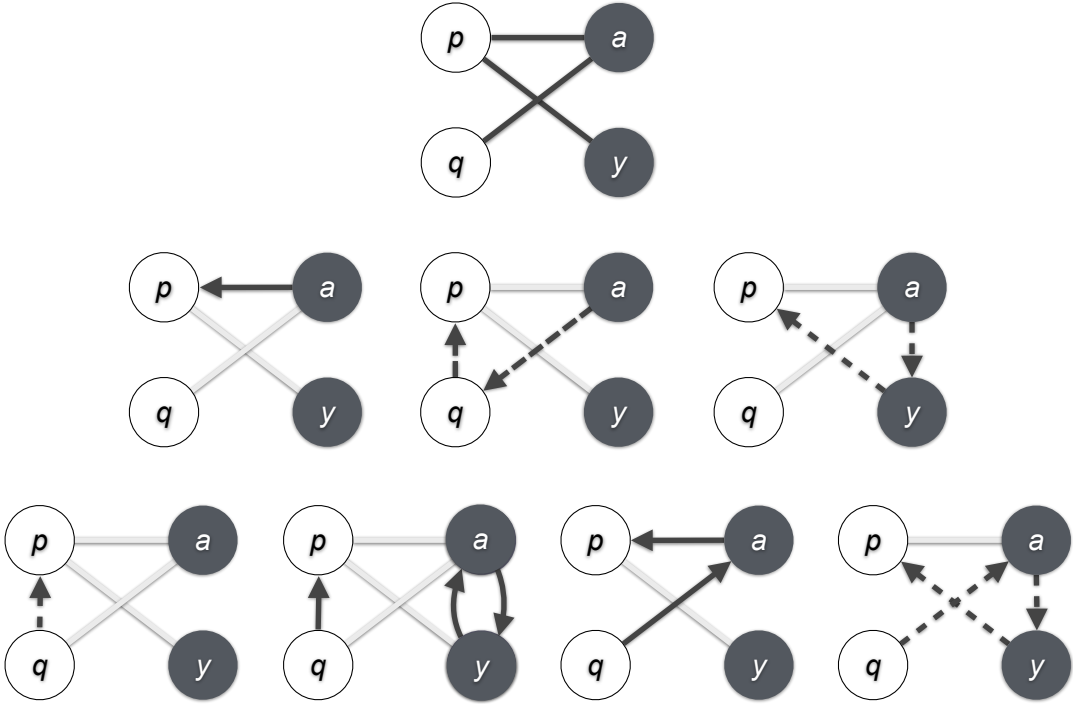


Figure 2

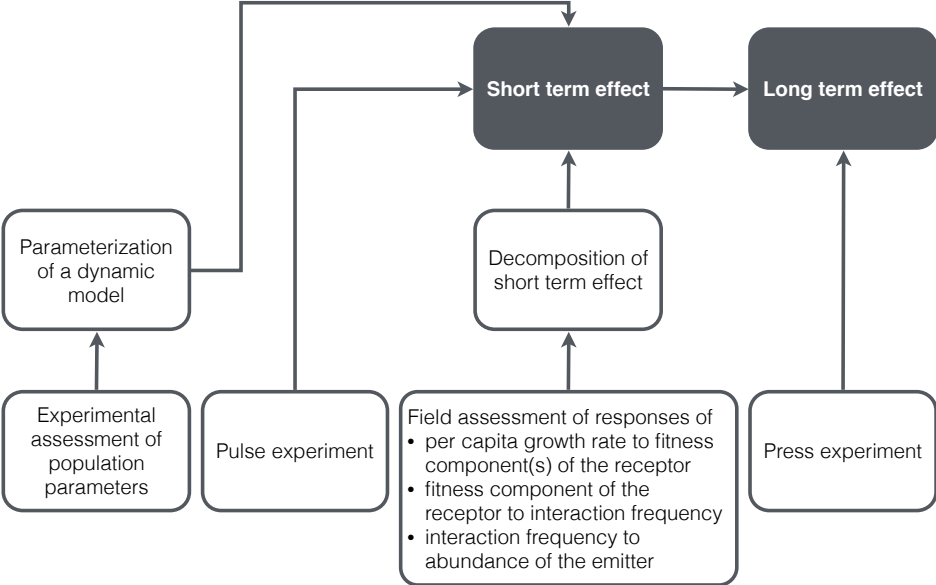


Figure 3

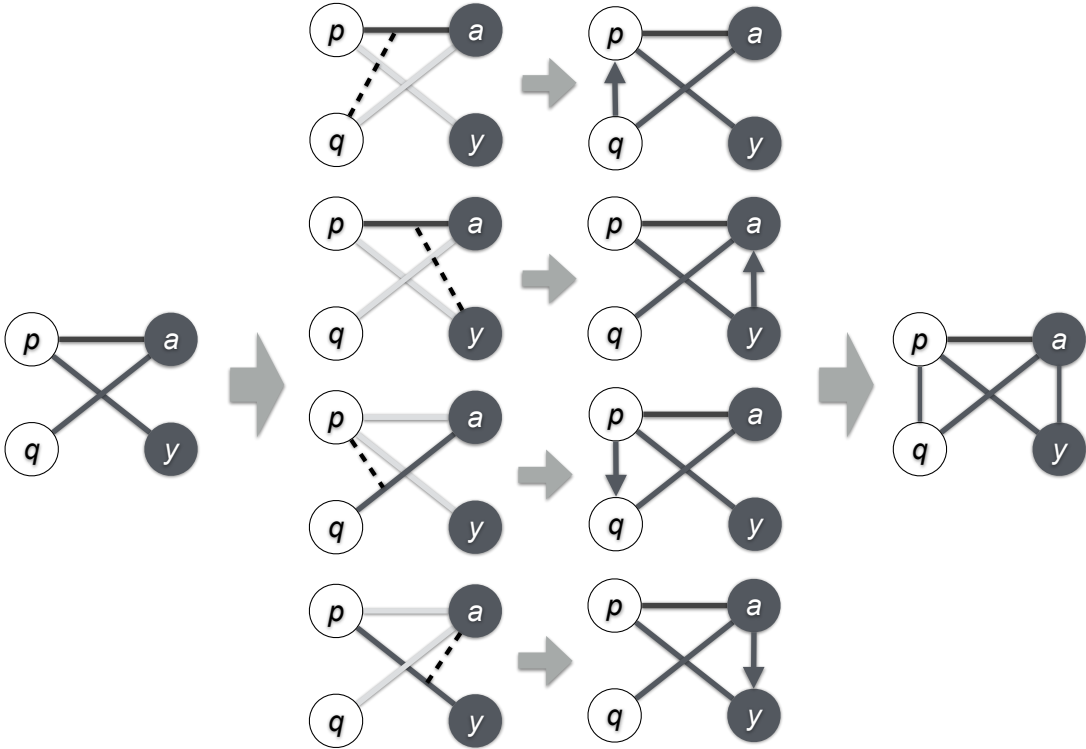


Figure 4

957 **Box 1. Representative classes of population dynamic**
 958 **models of mutualistic interactions**

959 We have identified six major classes of population dynamic models of mutualistic
 960 interactions. In model classes 1–5 below, P_i and A_j are the abundances of plant and
 961 animal species.

962 **1. Classic Lotka–Volterra model with linear functional response for**
 963 **mutualistic interaction** (Gause & Witt, 1935; Vandermeer & Boucher, 1978; Travis &
 964 Post, 1979; Heithaus *et al.*, 1980; Addicott, 1981; Wolin & Lawlor, 1984; Ringel *et al.*,
 965 1996; Bascompte *et al.*, 2006):

$$\begin{aligned}\frac{dP_i}{dt} &= r_i P_i - \gamma_i P_i^2 + \sum_{j=1}^m \alpha_{ij} P_i A_j \\ \frac{dA_j}{dt} &= r_j A_j - \gamma_j A_j^2 + \sum_{i=1}^n \alpha_{ji} P_i A_j\end{aligned}$$

966 Here, the first term of both equations represents exponential growth governed by the
 967 intrinsic growth rates of plants (r_i) and animals (r_j), the second term intraspecific
 968 competition governed by coefficients γ_i and γ_j , and the third term the mutualistic
 969 interaction with a linear functional response, summed for all mutualist species interacting
 970 with a focal species, governed by per-capita interaction strength coefficients α_{ij} and α_{ji} .
 971 In the sums, m and n are the total number of plant and animal species in the community,
 972 respectively.

973 **2. Lotka–Volterra model with saturating functional response for mutualistic**
 974 **interaction** (Holland *et al.*, 2002, 2006; Okuyama & Holland, 2008; Bastolla *et al.*, 2009):

$$\begin{aligned}\frac{dP_i}{dt} &= r_i P_i - \sum_{k=1}^m \gamma_{ik} P_k P_i + \sum_{j=1}^n \frac{\alpha_{ij} P_i A_j}{1 + \alpha_{ij} h_{ij} A_j} \\ \frac{dA_j}{dt} &= r_j A_j - \sum_{l=1}^n \gamma_{jl} A_l A_j + \sum_{i=1}^m \frac{\alpha_{ji} P_i A_j}{1 + \alpha_{ji} h_{ji} P_i}\end{aligned}$$

975 A key difference between this model class and the previous one is the form of the third
 976 term, which in this case is a saturating functional response, governed by per-capita
 977 interaction strengths α_{ij} and α_{ji} and by handling times h_{ij} and h_{ji} . In some versions of
 978 this class of models (e.g., Holland *et al.*, 2002, 2006; Okuyama & Holland, 2008) the
 979 second term includes only intra-specific competition, as in model class 1 (i.e., $\gamma_i P_i^2$ and
 980 $\gamma_j A_j^2$), whereas more recent versions (e.g., Bastolla *et al.*, 2009) include both intra- and
 981 inter-specific competition (i.e., $\sum_{k=1}^m \gamma_{ik} P_k P_i$ and $\sum_{l=1}^n \gamma_{jl} A_l A_j$).

982 **3. Logistic model modified with carrying capacity as a function of density of**
 983 **interaction partners** (Whittaker, 1975; May, 1976, 1981; Addicott, 1981; Wolin &
 984 Lawlor, 1984):

$$\begin{aligned}\frac{dP_i}{dt} &= r_i P_i \left(1 - \frac{P_i}{\sum_{j=1}^m f(A_j)} \right) \\ \frac{dA_j}{dt} &= r_j A_j \left(1 - \frac{A_j}{\sum_{i=1}^n f(P_i)} \right)\end{aligned}$$

985 This third class of models is based on the logistic equation, in which exponential growth
 986 ($r_i P_i$ and $r_j A_j$) is limited by density-dependent regulation, with the carrying capacity of
 987 each population defined as a function of the abundances of its interaction partners
 988 (functions $f(A_j)$ and $f(P_i)$).

989 **4. Consumer–resource** (Holland *et al.*, 2002; Holland & DeAngelis, 2010):

$$\begin{aligned}\frac{dP}{dt} &= r_p P + c_p \left(\frac{\alpha_{pa} P A}{h_{pa} + A} \right) - q_p \left(\frac{\beta_p P A}{e_{pa} + P} \right) - d_p P^2 \\ \frac{dA}{dt} &= r_a A + c_a \left(\frac{\alpha_{ap} P A}{h_{ap} + P} \right) - q_a \left(\frac{\beta_a P A}{e_{ap} + A} \right) - d_a A^2\end{aligned}$$

990 In consumer–resource models, exponential growth (first term) is regulated by the benefits
 991 (second term) and costs (third term) of the interaction, resulting from the production of
 992 the resources by each interacting species, with constants c_p , c_a , q_p and q_a representing
 993 conversion rates, α_{pa} , α_{ap} , β_{pa} and β_{ap} representing the saturation levels and h_{pa} , h_{ap} , e_{pa}
 994 and e_{ap} representing the half saturation constants; the fourth term represents
 995 density-dependent mortality, governed by death rates d_p and d_a . Note that this model
 996 has been proposed by Holland *et al.* (2002) and Holland & DeAngelis (2010) for two
 997 species P and A , and to our knowledge it has not been extended to multispecies systems.

998 **5. Consumer–resource with adaptive foraging and floral resources as state**
 999 **variables** (Valdovinos *et al.*, 2013):

$$\begin{aligned}\frac{dP_i}{dt} &= r_i \left(1 - \sum_l \gamma_l P_l \right) \sum_j e_{ij} \sigma_{ij} V_{ij}(P_i, A_j, \alpha_{ij}) - d_i P_i \\ \frac{dA_j}{dt} &= \sum_i c_{ij} f_{ij}(R_i, P_i) V_{ij}(P_i, A_j, \alpha_{ij}) - d_j A_j \\ \frac{dR_i}{dt} &= \beta_i P_i - \phi_i R_i - \sum_j f_{ij}(R_i, P_i) V_{ij}(P_i, A_j, \alpha_{ij}) \\ \frac{d\alpha_{ij}}{dt} &= \frac{G_i}{a_j} \left(c_{ij} f_{ij}(R_i, P_i) V_{ij}(P_i, A_j, \alpha_{ij}) - \alpha_{ij} \sum_{k=1}^m c_{kj} f_{kj}(R_k, P_k) V_{ij}(P_i, A_j, \alpha_{ij}) \right)\end{aligned}$$

1000 Here, plants exhibit intra and inter-specific density-dependence of magnitude γ in their
 1001 recruitment rate, which is governed by the rate $V_{ij} = P_i A_j \alpha_{ij} \tau_{ij}$ at which pollinators of
 1002 each species visit the plant. The function α_{ij} is the foraging effort displayed by pollinator
 1003 j on plant i , which takes values between 0 and 1; the sum of α_{ij} over all plants visited by
 1004 pollinator j is equal to one. The parameter τ_{ij} is the visitation efficiency of animal j to

1005 plant i . The parameter G_j is the basal adaptation rate of foraging α_{ij} of animal j on its
 1006 plant resources, i.e. the speed of change in α_{ij} when the term within parenthesis in the
 1007 equation for $d\alpha_{ij}/dt$ is nonzero. The parameter τ_{ij} is the visitation efficiency of animal j
 1008 to plant i . Animals grow by consumption rate f_{ij} of floral resources R in their visits to
 1009 host plants. Floral resources R are produced at a rate β , self-limited at a rate ϕ and
 1010 consumed by animal visitors. Parameters e_{ij} , σ_{ij} and c_{ij} are conversion terms, while r_i
 1011 and d_i have the same meaning as in other model classes.

1012 **6. Patch dynamics** (Armstrong, 1987; Amarasekare, 2004; Fortuna & Bascompte, 2006;
 1013 Ramos-Jiliberto *et al.*, 2009, 2012; Valdovinos *et al.*, 2009):

$$\frac{dP_i}{dt} = \sum_{j=1}^n \left(c_{ij} \frac{P_i A_j}{\Omega} \right) (1 - d - P_i) - e_i P_i$$

$$\frac{dA_j}{dt} = c_j A_j (\Omega - A_j) - e_j A_j$$

1014 In this last class of models, P_i and A_j represent the fraction of patches occupied by plant
 1015 and animal species i and j , modeled as functions of colonization and extinction rates for
 1016 plants (c_{ij} and e_i) and animals (c_j and e_j), the fraction of patches lost by habitat
 1017 destruction, and the total number of available patches for animals (Ω).

1018 **Box 2. Obtaining the symbolic Jacobian matrix from**
 1019 **the adjacency matrix of plant–animal mutualistic**
 1020 **networks**

1021 For calculating long term effects by means of eq. 3, we need to have the Jacobian matrix
 1022 \mathbf{J} of the network, which can be obtained from the adjacency matrix Δ by making some
 1023 assumptions, as outlined below.

1024 From field records of interactions among plants and animal visitors, we can obtain the
 1025 mutualistic structure represented by the adjacency matrix Δ , a square matrix of size
 1026 equal to the species richness, filled with a symbol in cells i, j and j, i for all pairs of
 1027 species ij that have been recorded interacting in the field, and zeros elsewhere.

1028 Then we need to compute a symbolic Jacobian matrix \mathbf{J} , which depends on, but is not
 1029 equal to, Δ . More precisely, \mathbf{J} has in general more nonzero elements than Δ . These
 1030 elements not contained in Δ are, nevertheless, reachable from the topology of mutualistic
 1031 interactions. We need to follow three basic assumptions. First, the plant-animal
 1032 mutualistic interactions rest on interaction frequency (visitation) between plants and
 1033 animals. Second, interaction frequency between plant i and animal j depends on the
 1034 abundances of the interacting species i and j . Third, the interaction frequency between
 1035 plant i and animal j depends also on the abundances of the immediate neighbors of i and
 1036 j . This last assumption is explained by the interference effect of other animal species
 1037 visiting plant i on the visit to i performed by j , and by the interference of other plants
 1038 visited by j exerted on j 's visits to i . This rationale is illustrated in Fig. 4. Thus, given
 1039 the bipartite nature of mutualistic networks, for obtaining matrix \mathbf{J} from Δ we need to
 1040 uncover the connections of length-two between pair of species of the same guild (i.e.,
 1041 among plants and among animals). This is easily done by calculating the square of Δ .
 1042 Thus, the symbolic matrix \mathbf{J} is obtained by labeling all nonzero elements of $\Delta + \Delta^2$.
 1043 These steps also ensure incorporating self-limitation in every population. To this symbolic
 1044 \mathbf{J} we could apply eq. 3 for obtaining the set S_{ij} and the combination of its elements

1045 needed for calculating long term effects. We provide an example of these steps below.

1046 **1. The adjacency matrix.** From field observations we can describe the topology of
 1047 mutualistic interactions between plants and animals (i.e., who visits who). This
 1048 information can be depicted as a graph (e.g., Fig. 2, top panel) or, alternatively, in an
 1049 adjacency matrix Δ , where a “1” in cell i, j indicates that species i visits species j or
 1050 viceversa. As an example, consider the following adjacency matrix corresponding to the
 1051 graph of Fig. 2:

$$\Delta = \begin{bmatrix} 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 0 \\ 1 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \end{bmatrix}$$

1052 **2. Identifying interference effects.** For bipartite networks, we can use the square of
 1053 Δ for obtaining those effects (see main text) that depend on the topology of mutualistic
 1054 interactions:

$$\Delta^2 = \begin{bmatrix} 2 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 \\ 0 & 0 & 2 & 1 \\ 0 & 0 & 1 & 1 \end{bmatrix}$$

1055 The elements i, j of Δ^2 indicate the number of paths of length two occurring from species
 1056 i to species j in the network. In bipartite networks, the paths of length two connect
 1057 species of the same guild that have in common a direct neighbor. Thus, an integer in cell
 1058 i, j of Δ^2 indicates that species i and j interfere to each other. Values in the diagonal i, i
 1059 indicate the number of indirect self effects, equivalent to the number of direct neighbors
 1060 of species i . A graphical illustration of this concept is given in Fig. 4.

1061 **3. Identifying all short term effects.** Integrating direct mutualistic effects (i.e.,
 1062 visitation) and interference effects (which could be considered interaction modifications;
 1063 see Dambacher & Ramos-Jiliberto, 2007), we obtain

$$\Delta + \Delta^2 = \begin{bmatrix} 2 & 1 & 1 & 1 \\ 1 & 1 & 1 & 0 \\ 1 & 1 & 2 & 1 \\ 1 & 0 & 1 & 1 \end{bmatrix}$$

1064 **4. Symbolic Jacobian matrix.** All nonzero elements of the latter matrix are given a
 1065 label, which renders the matrix \mathbf{J} to be used in eq. 3 for calculating long term effects.

$$\mathbf{J} = \begin{bmatrix} D_{pp} & D_{pq} & D_{pa} & D_{py} \\ D_{qp} & D_{qq} & D_{qa} & 0 \\ D_{ap} & D_{aq} & D_{aa} & D_{ay} \\ D_{yp} & 0 & D_{ya} & D_{yy} \end{bmatrix}$$

1066 **Box 3. Decomposition of short-term effects**

1067 In this box we show the rationale and assumptions behind eqs. 8–9 and their connection
 1068 to the model proposed in eq. 4 and its derivatives in eq. 5. The discussion below applies
 1069 to the effect strength of a generalist animal on a generalist plant (with population sizes a
 1070 and p respectively), as presented in our example in eq. 4 and Fig. 2. In this example,
 1071 populations q and y represent, respectively, the population sizes of specialist plants and
 1072 animals. Recall from eq. 4a the dynamics of the generalist plant:

$$\frac{dp}{pdt} = r_p + B(p, q, a, y) - C(p, q, a, y) - sp - u(q) \quad (10)$$

1073 where the focal effect strength is defined in eq. 5b:

$$\frac{\partial}{\partial a} \frac{dp}{pdt} = \frac{\partial B(p, q, a, y)}{\partial a} - \frac{\partial C(p, q, a, y)}{\partial a}, \quad (11)$$

1074 where, as defined in the main text, B and C are benefits and costs for the plant derived
 1075 from the interaction with the animal. Here it is assumed that the animal, through
 1076 visiting the plant, modifies a plant's fitness component (e.g., fertility) that increases its
 1077 per capita growth rate. At the same time, another plant's fitness component (e.g., energy
 1078 allocation to rewards) is promoted by the same animal that decreases the plant's per
 1079 capita rate of change.

1080 Assuming that the mutualist's effects are mediated mainly by visitation rate V_{pa} of
 1081 animals to plants and fitness component Z_p of the receptor species considered as a proper
 1082 fitness proxy, we redefine the functions B and C (see also Box 2) as

$$B(p, q, a, y) = B(Z_{p1}(V_{pa}(p, q, a, y), V_{py}(p, a, y))) \quad (12)$$

$$C(p, q, a, y) = C(Z_{p2}(V_{pa}(p, q, a, y), V_{py}(p, a, y))), \quad (13)$$

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1083 where Z_{p1} and Z_{p2} are two fitness components of the plant that determine benefits and
 1084 costs for the plant, respectively, of its mutualistic interactions, and that depend on
 1085 visitation rates from the animal mutualists. Then, substituting 12 and 13 into 11 renders

$$\frac{\partial}{\partial a} \frac{dp}{pdt} = \frac{\partial}{\partial a} B(Z_{p1}(V_{pa}(p, q, a, y), V_{py}(p, a, y))) - \frac{\partial}{\partial a} C(Z_{p2}(V_{pa}(p, q, a, y), V_{py}(p, a, y))). \quad (14)$$

1086 Applying the chain rule and rearranging terms, the above expression expands to

$$\begin{aligned} \frac{\partial}{\partial a} \frac{dp}{pdt} = & \frac{\partial}{\partial Z_{p1}} B(Z_{p1}(V_{pa}(p, q, a, y), V_{py}(p, a, y))) \frac{\partial Z_{p1}}{\partial V_{pa}} \frac{\partial V_{pa}}{\partial a} \\ & - \frac{\partial}{\partial Z_{p1}} C(Z_{p2}(V_{pa}(p, q, a, y), V_{py}(p, a, y))) \frac{\partial Z_{p1}}{\partial V_{pa}} \frac{\partial V_{pa}}{\partial a} \\ & + \frac{\partial}{\partial Z_{p2}} B(Z_{p1}(V_{pa}(p, q, a, y), V_{py}(p, a, y))) \frac{\partial Z_{p2}}{\partial V_{pa}} \frac{\partial V_{pa}}{\partial a} \\ & - \frac{\partial}{\partial Z_{p2}} C(Z_{p2}(V_{pa}(p, q, a, y), V_{py}(p, a, y))) \frac{\partial Z_{p2}}{\partial V_{pa}} \frac{\partial V_{pa}}{\partial a} \\ & + \frac{\partial}{\partial Z_{p1}} B(Z_{p1}(V_{pa}(p, q, a, y), V_{py}(p, a, y))) \frac{\partial Z_{p1}}{\partial V_{py}} \frac{\partial V_{py}}{\partial a} \\ & - \frac{\partial}{\partial Z_{p1}} C(Z_{p2}(V_{pa}(p, q, a, y), V_{py}(p, a, y))) \frac{\partial Z_{p1}}{\partial V_{py}} \frac{\partial V_{py}}{\partial a} \\ & + \frac{\partial}{\partial Z_{p2}} B(Z_{p1}(V_{pa}(p, q, a, y), V_{py}(p, a, y))) \frac{\partial Z_{p2}}{\partial V_{py}} \frac{\partial V_{py}}{\partial a} \\ & - \frac{\partial}{\partial Z_{p2}} C(Z_{p2}(V_{pa}(p, q, a, y), V_{py}(p, a, y))) \frac{\partial Z_{p2}}{\partial V_{py}} \frac{\partial V_{py}}{\partial a}. \end{aligned} \quad (15)$$

1087 For simplicity, we assume $\frac{\partial V_{pa}}{\partial a} \gg \frac{\partial V_{py}}{\partial a}$ and neglect the last four lines of equation 15.

1088 Then, grouping terms and dropping the arguments of B y C for readability,

$$\frac{\partial}{\partial a} \frac{dp}{pdt} = \frac{\partial(B-C)}{\partial Z_{p1}} \frac{\partial Z_{p1}}{\partial V_{pa}} \frac{\partial V_{pa}}{\partial a} + \frac{\partial(B-C)}{\partial Z_{p2}} \frac{\partial Z_{p2}}{\partial V_{pa}} \frac{\partial V_{pa}}{\partial a}. \quad (16)$$

1089 Given that all terms other than B and C in 10 are independent from Z_{p1} and Z_{p2} , we

1090 have that $\frac{\partial(B-C)}{\partial Z_{p1}} = \frac{\partial}{\partial Z_{p1}} \frac{dp}{pdt} = \frac{\partial F_p}{\partial Z_{p1}}$, and an analogous expression for the fitness component

1091 Z_{p2} . Then, eq. 16 becomes

$$\frac{\partial F_p}{\partial a} = \frac{\partial F_p}{\partial Z_{p1}} \frac{\partial Z_{p1}}{\partial V_{pa}} \frac{\partial V_{pa}}{\partial a} + \frac{\partial F_p}{\partial Z_{p2}} \frac{\partial Z_{p2}}{\partial V_{pa}} \frac{\partial V_{pa}}{\partial a}, \quad (17)$$

1092 which is equivalent to eq. 9 in the main text for the above two plant fitness components.

1093 Finally, by assuming that only a single fitness component Z_{p1} is relevant for determining

1094 capita growth rate of species p (as assumed in eq. 8), then eq. 17 reduces to

$$\frac{\partial F_p}{\partial a} = \frac{\partial F_p}{\partial Z_{p1}} \frac{\partial Z_{p1}}{\partial V_{pa}} \frac{\partial V_{pa}}{\partial a}, \quad (18)$$

1095 thus recovering eq. 8 of the main text. In the case that a fitness component under

1096 consideration could participate in determining both cost and benefit functions B and C ,

1097 this development also holds without significant changes.