REVIEW AND SYNTHESIS

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

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Abstract

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.

Keywords

Ecological networks, interaction strength, long-term effects, mutualism, plant–animal interactions, short-term effects.

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INTRODUCTION

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

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

Below we provide a synthesis of the concepts of interaction strength developed in the context of antagonistic, consumer–resource interactions and apply them to the study of mutualistic interactions.

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INTERACTION STRENGTH CONCEPTS IN FOOD WEBS

There is a long history of conceptual and empirical work on interaction strength in the context of predator–prey interactions and food webs (reviewed in Laska & Wooton 1998; Berlow *et al.* 1999, 2004; Wootton & Emmerson 2005). In this body of literature, interaction strength has usually been defined as 'an estimate of the magnitude of the effect of one species on another' (Laska & Wooton 1998). Although this verbal definition is simple and intuitive, a more quantitative definition has been ellusive, and has been shaped by the multiple interests and goals of researchers and the type of data available (Berlow *et al.* 2004; Laska & Wooton 1998; Wootton & Emmerson 2005). Four common concepts of interaction strength in food webs include (1) *per capita* interaction strength, the direct effect of an individual of one species on an average individual of another species, represented by the elements *j,i* of the community matrix **A**, $A_{ji} = \partial(dn_j/(n_j dt))/\partial n_i$, which describe the response of the *per capita* growth rate of species *j* ($dn_j/(n_j dt)$) to a small, pulsed perturbation in the abundance of species *i* (n_i), evaluated at the community equilibrium (Levins 1968; Laska & Wooton 1998); (2) the direct effects of an individual of one species on the whole population of another species at equilibrium, represented by the elements *j,i* of the Jacobian matrix **J**, $J_{ji} = \partial(dn_j/dt)/\partial n_i$, which describe the response of the population-level growth rate of species *j* to a change in the abundance of species *i*, evaluated at the community equilibrium (May 1973); (3) the total effects (via direct as well as indirect pathways) on the equilibrium abundances of one species to a constant rate of removal or addition of individuals of another species at the neighbourhood of an equilibrium, represented by the elements of the inverted negative Jacobian matrix (Yodzis 1988, see below); and (4) the differences in the abundances at equilibrium between a community with all species present, and the same community with the focal species removed, which define the removal matrix (MacArthur 1972; Paine 1980).

The above four concepts of interaction strength have several important differences. First, while the former three concepts require an explicit or implicit mathematical model describing the population dynamics of the interacting species, the latter concept is empirically based (Laska & Wooton 1998). Second, concepts 1–3 deal only with small perturbations around a population equilibrium, while concept 4 concerns the removal of an entire population. Third, the four concepts involve different properties of the species recipient of the effect (Abrams 1987): *per capita* interaction strength applies to the (average) individual response of the species receiving the effect, the elements of the Jacobian matrix apply to population growth rates of the recipient species, and the elements of both the inverted and removal matrices apply to equilibrium (or long-term mean) population density of the species recipient of the effect. These three properties of recipient species (i.e. *per capita* growth rate, population growth rate and long-term population densities) concern different temporal scales: whereas *per capita* and instantaneous population growth rate may be measured over one or a few generations, equilibrium population density should be measured after multiple generations (see definitions of short-term and long-term ecological effects below).

Ecologists have also used multiple empirical approaches to obtain estimates of interaction strength, including field and laboratory experiments, observational field studies, allometric relationships and the analysis of system dynamics (Wootton & Emmerson 2005). Field experiments consist mostly in the removal of one or more species from a study system and the measurement of a certain response variable (usually abundance) of the focal species (Bender *et al.* 1984; Paine 1992; Berlow *et al.* 1999), with interaction strength usually defined as either *per capita* effects or the elements of the removal matrix. Laboratory experiments have been used to estimate component parameters of mathematical models describing interacting species systems (Wootton & Emmerson 2005). These mathematical models, once parameterised with the empirical estimates for the particular system under study, are used to calculate interaction strength under any of the above definitions (e.g. Levitan 1987; Schmitz 1997). When experimentation is not possible, observational approaches allow estimating *per capita* interaction strengths based on measurements of interaction parameters such as feeding rates, diet composition and abundances of predators and prey (e.g. Wootton 1997; Novak & Wootton 2008). When direct estimation of interaction strength in the field is difficult, allometric relationships and the analysis of system dynamics are good alternatives (e.g. Wootton 1997; Sala & Graham 2002; Emmerson & Raffaelli 2004). Allometric approaches are based on the assumption that *per capita* interaction strength scales with body sizes of prey and their predators (large-bodied predators interact more strongly than small-bodied ones), a reasonable assumption, given that numerous biological processes also scale with body size (Yodzis & Innes 1992; Woodward *et al.* 2005). Finally, analysis of system dynamics fits models to population time series to estimate model parameters (Pascual & Kareiva 1996; Laska & Wooton 1998).

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

INTERACTION STRENGTH CONCEPTS APPLIED TO PLANT–ANIMAL MUTUALISMS

As with the development of general ecological theory, the development of interaction strength concepts for mutualistic interactions has lagged behind conceptual development for predator–prey interactions. Box 1 presents the main classes of models that have been used to study the population dynamics of mutualistic interactions. As in food webs, the simplest mathematical models of mutualistic interactions have defined interaction strength as a single parameter α_{ij} representing the *per capita* effect of an individual of species j on an individual of species i, assuming a linear (type I) functional response for the mutualistic interaction (the third term of the equations for Model class 1 in Box 1). However, a type I functional response is obviously unrealistic, as the benefit of a mutualistic interaction cannot increase indefinitely with increasing abundance of the interaction partner, unless we make the assumption of being at the close vicinity of an equilibrium. Other models use instead a saturating function to represent the mutualistic interaction (typically a type II functional response; the third term in equations for Model class 2), thus assuming that the effect of an interaction saturates with increasing abundance of all the interaction partners. In principle, this function could also have a peak of the benefit at intermediate mutualist densities, beyond which the benefit of the interaction would decrease (Holland *et al*. 2002; Morris *et al*. 2010), thus approaching a type IV functional response (Andrews 1968). This class of models has also been made more complex by incorporating interspecific competition among species of the same guild, i.e. among pollinator species and among plant species (Bastolla *et al*. 2009). A third class of models is based on the logistic equation, assuming that the carrying capacity of each mutualist species depends on the density of its interaction partners. More mechanistically, consumer–resource models envision mutualistic interactions as a special case of consumer–resource dynamics, which consider the transfer of energy and/or nutrients between an organism (consumer) and a resource (Holland *et al*. 2002; Holland & DeAngelis 2010). A fifth class of models incorporates adaptive behaviour of pollinators and floral resources as a separate state variable in consumer–resource mutualistic models (Valdovinos *et al*. 2013). These mechanistic consumer–resource models include several key processes involved in these mutualistic interactions, and are thus a promising approach to combine theory and data, and to synthesise mutualistic and food web theory. A final class of models considers a landscape of patches occupied by plants and animals interacting mutualistically, in which the fraction of patches occupied by plants and animals results from the balance between colonisation and extinction. The choice of the model of mutualistic interactions is crucial for our understanding of the dynamics of mutualistic systems, because it may affect strongly the results and conclusions of model-based assessments of interaction strength.

Ecologists have not always been consistent in their definition of interaction strength in the above dynamic models of mutualistic interactions. In the first two classes of models of Box 1, interaction strength has usually been defined explicitly as the *per capita* effect of one species on another (i.e. α_{ij} and

α_{ji}). Some other studies (Ramos-Jiliberto *et al*. 2009, 2012; Valdovinos *et al*. 2009, 2013) have used species removal to study the resulting community patterns and dynamics, which is similar to the removal matrix approach described above for food webs. In many other studies of plant–animal mutualistic networks, the underlying definition of interaction strength is still less clear.

Compared to predator–prey interactions, in the context of mutualistic interactions there has been relatively little effort to quantify interaction strength empirically with measures that are relevant at the level of demography and population dynamics. Many studies of plant–animal mutualisms have defined related concepts such as 'effectiveness' (Schupp 1993; Olsen 1997; Vázquez *et al*. 2005; Sahli & Conner 2006), 'efficiency' (Schemske & Horvitz 1984; Pettersson 1991) or 'quality' (Herrera 1987; Ness *et al*. 2006). These concepts are usually defined as the contribution of an animal mutualist to the reproduction of a plant. For example, Schupp (1993, p. 16) defines the effectiveness of a seed disperser species on a plant species as 'the number of new adults resulting from the dispersal activities of a disperser' (see also Schupp *et al*. 2010). Similarly, Herrera (1987) defines the 'quality' of an ecological interaction as 'the fitness consequences of the interaction when it occurs'. In addition, some recent studies have also performed manipulative removal experiments to assess the short-term effect of animal (Brosi & Briggs 2013) or plant (Lopezaraiza-Mikel *et al*. 2007) species on other species of the community. Brosi & Briggs (2013) conducted experimental removals of the most abundant pollinator species from several study plots in sub-alpine meadows, recording the change in the seed production of a focal plant species, which is close to estimating some elements of the removal matrix. Similarly, Lopezaraiza-Mikel *et al*. (2007) experimentally removed the flowers of the alien plant *Impatiens glandulifera* and explored the response of the rest of the assemblage of co-flowering native plants in terms of flower visitation and pollen transport by pollinators. Most of these studies have considered only the plant's perspective (i.e. the animal's effect on the plant's fitness), although recently some studies have started to consider also the animal's perspective (i.e. the plant's effect on the animal's fitness; see, e.g. Roulston & Goodell 2011; Vázquez *et al*. 2012).

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

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Box 1 Representative classes of population dynamic models of mutualistic interactions

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

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

$$\frac{dP_i}{d_t} = r_i P_i - \gamma_i P_i^2 + \sum_{j=1}^{m} \alpha_{ij} P_i A_j$$

$$\frac{dA_j}{d_t} = r_j A_j - \gamma_j A_j^2 + \sum_{i=1}^{n} \alpha_{ji} P_i A_j$$

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

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

$$\frac{dP_i}{d_t} = r_i P_i - \sum_{k=1}^{m} \gamma_{ik} P_k P_i + \sum_{j=1}^{n} \frac{\alpha_{ij} P_i A_j}{1 + \alpha_{ij} h_{ij} A_j}$$

$$\frac{dA_j}{d_t} = r_j A_j - \sum_{l=1}^{n} \gamma_{il} A_l A_j + \sum_{i=1}^{m} \frac{\alpha_{ji} P_i A_j}{1 + \alpha_{ji} h_{ji} P_i}$$

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

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

$$\frac{dP_i}{dt} = r_i P_i \left(1 - \frac{P_i}{\sum_{j=1}^{m} f(A_j)}\right)$$

$$\frac{dA_j}{dt} = r_j A_j \left(1 - \frac{A_j}{\sum_{i=1}^{n} g(P_i)}\right)$$

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

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

$$\frac{dP}{dt} = r_p P + c_p \left(\frac{\alpha_{pa} PA}{h_{pa} + A}\right) - q_p \left(\frac{\beta_p PA}{e_{pa} + P}\right) - d_p P$$

$$\frac{dA}{dt} = r_a A + c_a \left(\frac{\alpha_{ap} PA}{h_{ap} + P}\right) - q_a \left(\frac{\beta_a PA}{e_{ap} + A}\right) - d_a A$$

In consumer–resource models, exponential growth (first term) is regulated by the benefits (second term) and costs (third term) of the interaction, resulting from the production of the resources by each interacting species, with constants c_p, c_a, q_p and q_a representing conversion rates, α_{pa}, α_{ap}, β_{pa} and β_{ap} representing the saturation levels and h_{pa}, h_{ap}, e_{pa} and e_{ap} representing the

Box 1 Continued

half saturation constants; the fourth term represents density-dependent mortality, governed by death rates d_p and d_a. Note that this model has been proposed by Holland *et al.* (2002) and Holland & DeAngelis (2010) for two species P and A, and to our knowledge it has not been extended to multispecies systems.

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

$$\frac{dP_i}{dt} = r_i\left(1 - \sum_l \gamma_l P_l\right)\sum_j e_{ij}\sigma_{ij}V_{ij}(P_i, A_j, \alpha_{ij}) - d_i P_i$$

$$\frac{dA_j}{dt} = \sum_i c_{ij}f_{ij}(R_i, P_i)V_{ij}(P_i, A_j, \alpha_{ij}) - d_j A_j$$

$$\frac{dR_i}{dt} = \beta_i P_i - \phi_i R_i - \sum_j f_{ij}(R_i, P_i)V_{ij}(P_i, A_j, \alpha_{ij})$$

$$\frac{d\alpha_{ij}}{dt} = \frac{G_i}{A_j}\left(c_{ij}f_{ij}(R_i, P_i)V_{ij}(P_i, A_j, \alpha_{ij}) - \alpha_{ij}\sum_{k=1}^m c_{kj}f_{kj}(R_k, P_k)V_{ij}(P_i, A_j, \alpha_{ij})\right)$$

Here, plants exhibit intra and interspecific density-dependence of magnitude γ in their recruitment rate, which is governed by the rate $V_{ij} = P_i A_j \alpha_{ij}\tau_{ij}$ at which pollinators of each species visit the plant. The function α_{ij} is the foraging effort displayed by pollinator j on plant i, which takes values between 0 and 1; the sum of α_{ij} over all plants visited by pollinator j is equal to one. The parameter τ_{ij} is the visitation efficiency of animal j to plant i. The parameter G_j is the basal adaptation rate of foraging α_{ij} of animal j on its plant resources, i.e. the speed of change in α_{ij} when the term within parenthesis in the equation for $d\alpha_{ij}/dt$ is non-zero. The parameter τ_{ij} is the visitation efficiency of animal j to plant i. Animals grow by consumption rate f_{ij} of floral resources R in their visits to host plants. Floral resources R are produced at a rate β, self-limited at a rate ϕ and consumed by animal visitors. Parameters e_{ij}, σ_{ij} and c_{ij} are conversion terms, while r_i and d_i have the same meaning as in other model classes.

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

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

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

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

(see *Quantifying effect strength of plant–animal mutualistic interactions in nature*).

Another approach to the assessment of interaction strength in mutualistic interactions considers phenology as a strong determinant of the outcome of interactions. Encinas-Viso *et al.* (2012), in parallel and with similar arguments to Nakazawa & Doi (2012) for food webs, assumed that the temporal overlap between interacting species, resulting from their phenological dynamics, defines interaction strengths. The rationale is that, as species do not interact uninterruptedly through time in many ecosystems, their interactions are annulled when their active stages (e.g. flowers and active pollinators) disappear temporarily from the system. In addition, as the length of phenophases varies largely among species, it is likely that the length of temporal overlap between phenophases of interacting species explains a large part of the variance in effect strength.

Under this view, instantaneous effect strength is less important for defining annual average effect strength. Remarkably, Encinas-Viso *et al.* (2012) found that phenology, without invoking other biological constraints, can largely explain the main topological properties observed in real plant–animal mutualistic webs, such as high nestedness and limited connectance. In addition, they found that the length of the season affects strongly the stability and diversity of mutualistic webs.

From the preceding paragraphs it is evident that the use of interaction strength concepts in the context of mutualistic interactions has been conceptually and empirically limited, thus providing a motivation for further synthesis. In the remainder of the article, we outline a conceptual scheme for defining effects in ecological interactions in general and in plant–animal mutualistic interactions in particular. This conceptual framework encompasses most previous concepts of

interaction strength proposed in the literature. We illustrate this framework by applying it to a model community of inter-acting plants and pollinators, and give recommendations for its application to data collection in field studies.

A CONCEPTUAL FRAMEWORK FOR ECOLOGICAL EFFECTS IN PLANT–ANIMAL MUTUALISTIC INTERACTIONS

Any interaction between two species can be defined as the reciprocal influence that the species exert on each other. An *interaction* thus involves a bidirectional causal influence, which can be decomposed into its constituent unidirectional *effects* of each species on the other (Fig. 1). More precisely, an effect can be defined as the capacity to transmit changes between variables (species' attributes in this case; Pearl 2009; ArunKumar & Venkatesan 2011). As it is unlikely that the two effects of a pair of interacting species have the same magnitude, the term 'interaction strength' commonly used in the ecological literature is ambiguous, and it is thus more meaningful to refer instead to 'effect strength'. Defining effects also requires specifying the relevant attributes whose change is transmitted from the emitter to the receptor of the effect – usually abundance (n) for the emitter and some property of the temporal trajectory of abundance (τ) for the receptor. In addition, behaviour could also be used as a meaningful variable for both emitter and receptor. Thus, most commonly the ecological effect of species i on species j represents how a change in the abundance of species i (n_i) triggers a deviation in the abundance trajectory of species j (τ_j). While a change in abundance is an easily measurable property of ecological populations, a change in the trajectory of abundance is more elusive, and, as we will see below, depends on the temporal scale at which interaction strength is defined.

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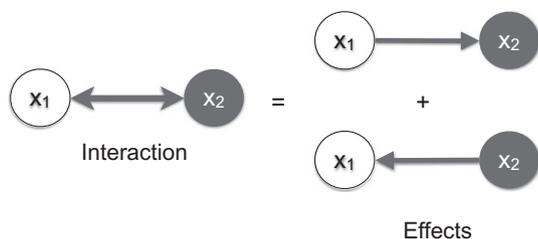
entire system reaches a new steady state. Long-term effects will thus encompass the time needed to reach a new steady state, which will depend on the dynamics of the system and thus on the generation times of the species involved (Yodzis 1988). Therefore, as shown below, long-term effects can be reduced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

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

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

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

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

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

As long as we are interested in the relative strength of effects within a community, the first part of the rightmost expression can be disregarded and we can redefine the long-term (net) effect of species i on species j as

$$L_{ji} = \mathrm{adj}(-\mathbf{J})_{ji} \tag{3}$$

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

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

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

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

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

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

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

In this model, p and q represent the population size or biomass of the generalist and specialist plants, respectively, and a and y represent the population size or biomass of the generalist and specialist pollinators. Parameters r_p, r_q, r_a and r_y are intrinsic rates of population growth of each species. Functions B, E, G and W represent the *per capita* benefits obtained from direct interactions and depend on the population size of the directly interacting species and that of the other species of the guild which could interfere with visitation. For plants, benefits represent enhanced reproduction, survival or growth; for animals, resource (reward) uptake or other fitness gains. For plants, there is a *per capita* cost (C and O) derived from producing and offering rewards, which, like benefits, are functions of the species involved in the visitation rate of each plant species.

Functions s, e, b and m are density-dependence terms, while functions u, h, l and k represent inhibition to population growth derived from direct interspecific competition within a given guild (e.g. space-limitation of plant recruitment and animal nesting). This model includes several fundamental dynamic features of plant–animal mutualistic interactions (see Box 1). First, the population growth rate of each species results from an intrinsic growth rate, the positive effect of the mutualism and negative density dependence (Gause & Witt 1935; Bascompte *et al.* 2006). Second, the positive effects among mutualists are not restricted to a linear relationship respect to the abundance of the partner (Holland *et al.* 2006). Third, there is interspecific competition among plant and among animal species (Bastolla *et al.* 2009). Finally, there is a cost function related to mutualism in the equation of plant species, which leads to explicit consumer–resource dynamics (Box 1, model class 4; Holland & DeAngelis 2010). Of course, the model can be made more sophisticated if multiple state variables are defined for each species (Valdovinos *et al.* 2013).

As discussed above, effect strength can be measured at two contrasting temporal scales. Short-term effects are expressed commonly as the partials of the per capita population growth rate of the receptor species respect to changes in the abundance of the emitter (eqn 1). Long-term effects, in contrast, are often represented by the total derivative of equilibrium abundance of the receptor respect to changes in the abundance of the emitter, which can be calculated from the adjugate of the negative community matrix (eqn 3). Given that for models of even minimal complexity the adjugate can be quite large, which can make calculation of effect strength difficult, it may be more analytically convenient to start with short-term effect strengths, and then use them as the building blocks
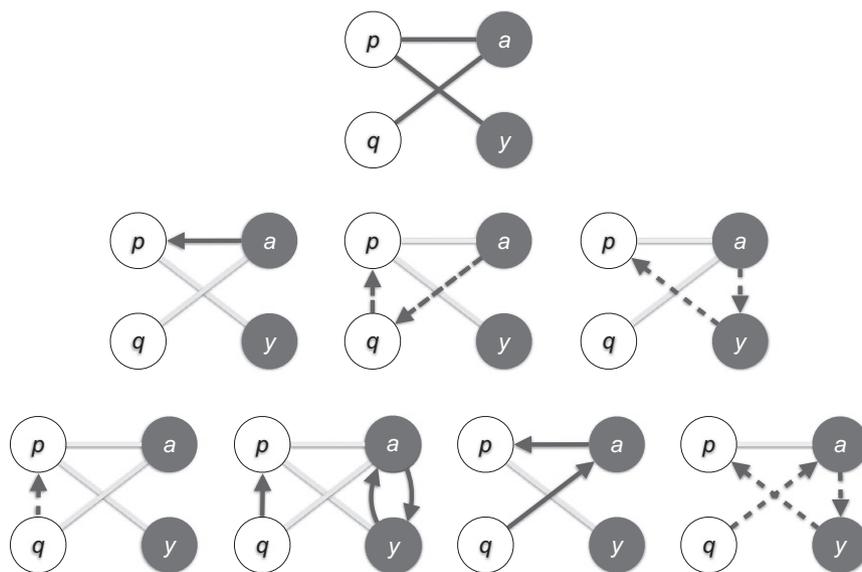
Figure 2 Representation of four-species model community of plants (white circles) and animals (black circles) used to demonstrate the conceptual framework proposed in this paper. Top panel: An idealised mutualistic web composed of a generalist plant (p), a specialist plant (q), a generalist pollinator (a) and a specialist pollinator (y). Links represent mutualistic interactions. Middle panels: Decomposition of the paths that contribute to the net, long-term effect strength of animal a on plant p. Bottom panels: Decomposition of the paths that contribute to the net, long-term effect strength of plant q on plant p. In the middle and bottom panels, continuous and dashed arrows show paths that result in a positive and negative contribution to the net effect respectively; mutualistic links that do not take part of this effect are shown in light tones; self-effects not shown.

of long-term effects. For example, for the general model (eqn 4), short-term effect strength of other species on the generalist plant p are

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

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

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

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 (eqn 4). Specifically, we will consider the effects of an animal on a plant, and between plants, by applying eqn 3 to the Jacobian matrix associated to the system represented by eqn 4. Thus, the long-term effect strength of the generalist animal on the generalist plant is

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

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

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

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

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

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

QUANTIFYING EFFECT STRENGTH OF PLANT–ANIMAL MUTUALISTIC INTERACTIONS IN NATURE

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

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

A second route for calculating long-term effects indirectly by combining a series of short-term effects is to conduct pulse experiments, in which the perturbation occurs once at a specific point in time (Bender *et al.* 1984; Paine 1992). As we have seen above (eqns 6 and 7), each element of L_{ji} is computed as a function of a specific set of elements D_{kl}. For
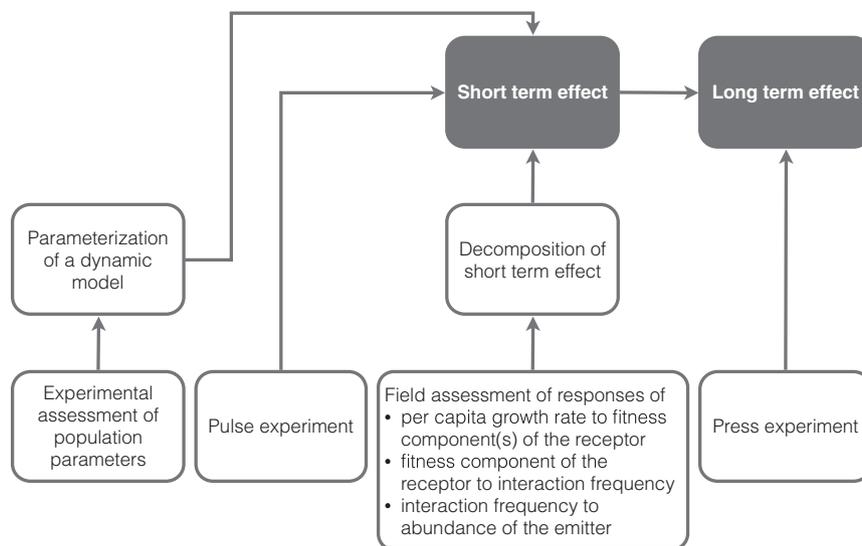
Figure 3 Multiple approaches for estimating short- and long-term effects (filled boxes) in plant–animal mutualistic interactions. Boxes at the base of the diagram indicate the basic empirical measures needed for the assessments. Long-term effects can be assessed directly through press experiments (sustained alteration of the emitter's abundance). Alternatively, long-term effects can be assessed indirectly from short-term effects through the experimental assessment of parameters of dynamic population models, pulse experiments or the field assessment of components of short-term effects (see text for details).

brevity, we define the *per capita* population growth rate as $F_k = dn_k/(n_k dt)$, which can be inserted into eqn 1 to obtain $D_{kl} = \partial F_k/\partial n_l$. The D_{kl} elements represent direct interactions between species that belong to the sphere of influence of L_{ji}. For simplicity, we define this set as $S_{ji} = \{D_{kl}$ for all species k and l that belong to the sphere of influence of $L_{ji}\}$. For computing a given L_{ji} from its D_{kl} components it is necessary to know the species composition and topology of the community. Then, from this information we obtain the community structure represented by the structure of the Jacobian matrix **J** (see details in Box 2). Nevertheless, note that even so a dynamic model is not necessary at this step, as the procedures outlined in Box 2 rest on a specific set of assumptions that lead to the basic structure of effects among the species (i.e. which elements of the Jacobian matrix are zero and which are not); this set of assumptions represents in fact a model. By applying eqn 3 to the **J** matrix we obtain the symbolic expressions for calculating long-term effects, including the set S_{ij}. We can concentrate our experimental effort on measuring each element D_{kl}. Thus, we can perform a pulse experiment for each D_{kl}, after which the change in the *per capita* population growth rate of the receptor, relative to the control, is recorded.

Unfortunately, the use of pulse experiments, although standard in ecology for measuring short-term effects, is not a panacea. Short-term effects should be measured with this method by introducing a constant flux of emitter individuals in the population, which is impossible because organisms come in integers, and then estimating the derivative of abundance with respect to time at the moment of the introduction, which is also often violated because some time after the pulsed introduction is needed for detecting changes in population sizes. To minimise these problems, experimenters should avoid conducting pulse experiments on small populations, and should record the response of the receiver species shortly after the

manipulation. Even more important, experimenters should bear in mind that the errors of these calculations will accumulate when combining several D_{kl} estimates to calculate L_{ji}. That said, Schmitz (1997) has shown that calculating long-term effects through the inverse Jacobian matrix (as shown in eqns 2, 3, 6 and 7) is a useful tool for assessing the qualitative outcome of long-term experiments, even under a considerable amount of variation in the values of the responses. Furthermore, although conducting pulse experiments is certainly possible (see, e.g. Lopezaraiza-Mikel *et al.* 2007; Brosi & Briggs 2013), they still require substantial experimental effort, and in many situations they may be unfeasible, especially for community-wide studies involving many pairs of interacting plant and animal species.

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

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

where F_k is the *per capita* population growth rate of the receptor species k (as defined in eqn 1), Z_k is a fitness component of the receptor likely to respond to the interaction with the emitter species l, V_{kl} is the frequency of interaction events between species k and l, and n_l is the abundance of the emitter species l (see Box 2 for the use of short-term effects to calculate long-term effects, and Box 3 for the derivation and

Box 2 Obtaining the symbolic Jacobian matrix from the adjacency matrix of plant–animal mutualistic networks

For calculating long-term effects by means of eqn 3, we need to have the Jacobian matrix **J** of the network, which can be obtained from the adjacency matrix Δ by making some assumptions, as outlined below.

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

Then we need to compute a symbolic Jacobian matrix **J**, which depends on, but is not equal to, Δ. More precisely, **J** has in general more non-zero elements than Δ. Some of these elements not contained in Δ are, nevertheless, reachable from the topology of mutualistic interactions. We need to follow three basic assumptions. First, the plant–animal mutualistic interactions rest on interaction frequency (visitation) between plants and animals. Second, interaction frequency between plant i and animal j depends on the abundances of the interacting species i and j. Third, the interaction frequency between plant i and animal j depends also on the abundances of the immediate neighbours of i and j. This last assumption is explained by the interference effect of other animal species visiting plant i on the visit to i performed by j, and by the interference of other plants visited by j exerted on j's visits to i. This rationale is illustrated in Fig. 4. Thus, given the bipartite nature of mutualistic networks, for obtaining matrix **J** from Δ we need to uncover the connections of length-two between pair of species of the same guild (i.e. among plants and among animals). This is easily done by calculating the square of Δ. Thus, the symbolic matrix **J** is obtained by labelling all non-zero elements of $\Delta + \Delta^2$. These steps also ensure incorporating self-limitation in every population. To this symbolic **J** we could apply eqn 3 for obtaining the set S_{ij} and the combination of its elements needed for calculating long-term effects. We provide an example of these steps below.

1. The adjacency matrix

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

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

2. Identifying interference effects

For bipartite networks, we can use the square of Δ for obtaining those effects (see main text) that depend on the topology of mutualistic interactions:

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

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

3. Identifying all short-term effects

Integrating direct mutualistic effects (i.e. visitation) and interference effects (which could be considered interaction modifications; see Dambacher & Ramos-Jiliberto 2007), we obtain

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

Box 2 Continued

4. Symbolic Jacobian matrix

All non-zero elements of the latter matrix are given a label, which renders the matrix **J** to be used in eqn 3 for calculating long-term effects.

$$\mathbf{J} = \begin{bmatrix} D_{pp} & D_{pq} & D_{pa} & D_{py} \\ D_{qp} & D_{qq} & D_{qa} & 0 \\ D_{ap} & D_{aq} & D_{aa} & D_{ay} \\ D_{yp} & 0 & D_{ya} & D_{yy} \end{bmatrix}$$
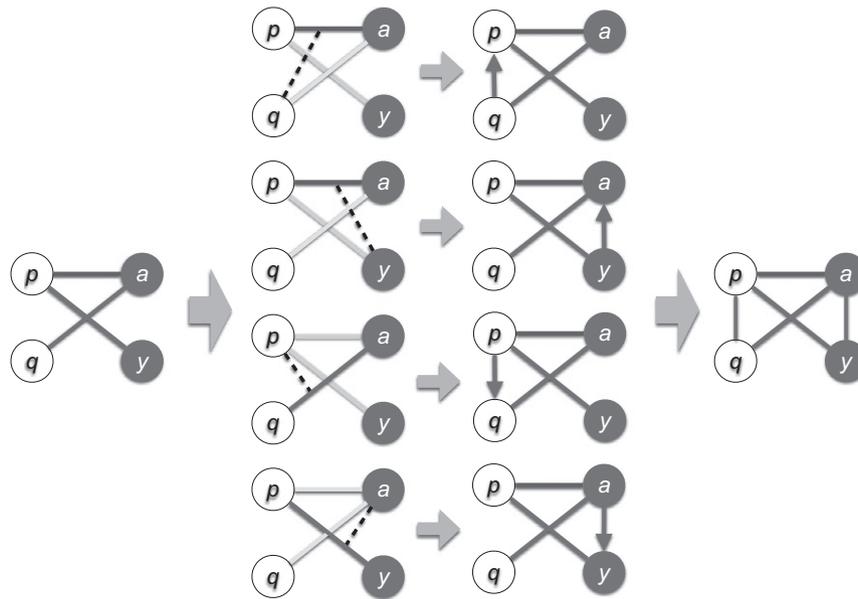
Figure 4 Representation of intra-guild interference effects (competition for mutualists) on mutualistic interactions discussed in Box 2. Left: Graph with only raw mutualistic interactions, equivalent to the adjacency matrix. Middle left: Each of the interference effects, depicted as dashed links from species to each focal interaction (dark grey). Middle right: The resulting species-to-species intra-guild effect. Right: resulting graph of mutualistic and interference interactions, equivalent to the Jacobian matrix.

rationale behind eqn 8). Note that eqn 8 assumes for simplicity that the influence that the abundance of the emitter species n_l exerts on the interaction frequency between the receptor k and its other neighbours (different from l) is negligible (see Box 3). Given that these derivatives are functions that can hardly be assumed to be linear, in practice they must be evaluated at a specific point within the variable's space. This point could be, for example the set of abundances and traits present at the instant of the investigation, or at a future time, when the community reaches equilibrium. Thus, the first (left) term of the rightmost expression of eqn 8 represents the effect that the change in a fitness component of species k exerts on its own *per capita* growth rate, the second term is the effect that the change in the frequency of interaction events between species k and l exerts on the fitness component Z_k, which captures the positive and negative terms of eqn 5, and the third term is the effect that the change in the abundance of species l exerts on the frequency of interaction events between species k and l. Incorporating frequency of interaction in the estimation of D_{kl} makes sense, given that in plant–animal mutual-

isms individuals are involved in multiple interaction events throughout their lifespan (i.e. a bee visits many flowers), a property of plant–animal mutualistic interactions that sets them apart from food webs. Note that, in the context of benefit–cost model discussed in the previous section (eqns 4 and 5), the benefit–cost relationship is implicit in the short-term effects described by eqn 8, as it represents the net benefits that can normally be observed in field studies (i.e. gross benefits minus costs). As a whole, the three types of observations involved in the decomposition of eqn 8 should be substantially simpler to obtain than manipulating the abundances of each emitter species and measuring the response in the receiver species in terms of its overall population growth rate.

The choice of the fitness component Z_k considered as surrogate of F_k is crucial for the assessment of effect strength. Two main criteria should be borne in mind: the *per capita* rate of change of the receptor should be sensitive to the variation in the fitness component, and the fitness component should in turn be sensitive to the variation in interaction frequency. The greater the product of these two sensitivities, the better the chosen fit-

ness component as a surrogate of F_k for the assessment of effect strength. For example, for plant–pollinator interactions an obvious choice of a fitness component is seed production for plants, and either fecundity or survival for animals.

In cases in which *per capita* population growth rate is not uniquely determined by one fitness component involved in the plant–animal interaction under study, several components of F_k should be considered instead (Reed & Bryant 2004; Crone 2001). In this case, it is also necessary to know the effect of changing the value of each chosen fitness component of the receptor species on its own *per capita* growth rate. Thus, each component D_{kl} of the set S_{ji} can be computed as

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

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

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

The next step in the decomposition of short-term effects is to calculate the response of the fitness component Z_k to changes in the frequency of interaction events (the second partial derivative in the rightmost expression of eqns 8 and 9; Fig. 3). For example, for plants we can study the contribution of particular pollinator species to the seed production of a particular plant species, which can be done with pollinator exclusion experiments in which flowers are experimentally exposed to one visit of a particular pollinator species and the resulting seed production is measured afterwards (e.g. Herrera 1987; Olsen 1997; Vázquez *et al.* 2005; Sahli & Conner 2006); equivalent observations can be done for plant–seed disperser interactions (e.g. Fleming & Williams 1990; Wheelwright 1991; Jordano & Schupp 2000). For animals, we can study the contribution of particular plant species to the reproduction of a particular animal species (Vázquez *et al.* 2012).

Finally, we must estimate the response of visitation frequency to changes in the abundance of the emitter species (the rightmost partial derivative in eqn 8; Fig. 3). This can be done easily in the field by counting the number of animal visits to plants (see, e.g. Herrera 1989; Fleming & Williams 1990; Olsen 1997; Jordano & Schupp 2000; Vázquez *et al.* 2005; Sahli & Conner 2006; Vázquez *et al.* 2012), weighing them by the degree of daily, seasonal and interannual temporal overlap

between the interacting organisms, obtained from direct phenological observations (e.g. flowering, fruiting or nesting phenology). Thus, this term will be greater for species with longer daily, seasonal and interannual overlap of their activity periods. In addition, if among-species variation in the frequency of interaction per emitter individual (third derivative) is substantially greater than variation in the fitness response to increments in visitation (the product of the first two derivatives), then the short-term effect strength could be approximated using only information on the frequency of interaction events (Vázquez *et al.* 2005, 2012). Note that the short-term effect D_{ji} as defined here is different from both interaction strength (per visit) and species impact (per population) as defined in Vázquez *et al.* (2012), but that it may be approximated by species impact divided by abundances.

CONCLUDING REMARKS

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

As is clear from our review, most past studies of plant–animal mutualistic interactions, included our own, have considered interaction strength concepts implicitly and imprecisely. Furthermore, antagonistic (e.g. trophic) and mutualistic interactions differ in some obvious ways, which implies that interaction strength concepts developed in the context of antagonistic interactions cannot be automatically applied to mutualistic interactions. For example, whereas in predator–prey interactions prey are assumed to experience only detrimental – either lethal or non-lethal – direct effects from the interactions with their predator, in plant–animal mutualisms the effects of interactions always have potential benefits and costs. Another distinctive attribute of plant–animal mutualisms is that all participant individuals are involved in multiple interaction events throughout their lifespan, which again sets them apart from food webs; visitation frequency is also of paramount practical relevance, as it is this attribute of interactions what is usually recorded in field studies. For these reasons, improving the conceptual framework for defining and measuring interaction strength in plant–animal mutualisms is clearly necessary for further progress.

Our framework emphasises the concept of unidirectional effect as the basic component of ecological interactions. Although this concept is not new, we believe that applying it to the study of the strength of ecological interactions will help clarify its meaning, its quantitative definition and its measurement. We have also emphasised the temporal scale at which effect strength is defined, considering short-term effects as the building blocks of long-term effects. Clearly, quantifying short-term effects will be considerably simpler and less prone to error than quantifying long-term effects. As we have proposed, such short-term effects can be estimated by considering key attributes of plant–animal mutualistic interactions, namely the ability of plant and animal individuals to interact multiple times throughout their

Box 3 Decomposition of short-term effects

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

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

where the focal effect strength is defined in eqn 5b:

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

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

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

$$B(p,q,a,y) = B(Z_{p1}(V_{pa}(p,q,a,y), V_{py}(p,a,y))) \tag{12}$$
$$C(p,q,a,y) = C(Z_{p2}(V_{pa}(p,q,a,y), V_{py}(p,a,y))), \tag{13}$$

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

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

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

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

For simplicity, we assume $\frac{\partial V_{pa}}{\partial a} \gg \frac{\partial V_{py}}{\partial a}$ and neglect the last four lines of eqn 15. Then, grouping terms and dropping the arguments of B y C for readability,

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

Given that all terms other than B and C in eqn 10 are independent from Z_{p1} and Z_{p2}, we 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 Z_{p2}. Then, eqn 16 becomes

> **Box 3 Continued**
>
> $$\frac{\partial F_p}{\partial a} = \frac{\partial F_p}{\partial Z_{p1}} \frac{\partial Z_{p1}}{\partial V_{pa}} \frac{\partial V_{pa}}{\partial a} + \frac{\partial F_p}{\partial Z_{p2}} \frac{\partial Z_{p2}}{\partial V_{pa}} \frac{\partial V_{pa}}{\partial a}, \tag{17}$$
>
> which is equivalent to eqn 9 in the main text for the above two plant fitness components. Finally, by assuming that only a single fitness component Z_{p1} is relevant for determining capita growth rate of species p (as assumed in eqn 8), then eqn 17 reduces to
>
> $$\frac{\partial F_p}{\partial a} = \frac{\partial F_p}{\partial Z_{p1}} \frac{\partial Z_{p1}}{\partial V_{pa}} \frac{\partial V_{pa}}{\partial a}, \tag{18}$$
>
> thus recovering eqn 8 of the main text. In the case that a fitness component under consideration could participate in determining both cost and benefit functions B and C, this development also holds without significant changes.

lifespan, the influence of biological rythms of interacting species that determine frequency of interaction, and fitness components relevant at the level of demography and population dynamics. The relative importance of these components as determinants of effect strength in plant–animal mutualistic interactions in ecological communities stands out as a key avenue for future research. Furthermore, our framework could also be extended to incorporate the spatial and temporal variation in the strength of ecological effects as an inherent feature of ecological interactions, which would help deal with the problem of variability in interaction strengths pointed out by Abrams (2001) for food webs.

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

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