IDEA AND PERSPECTIVE

A general framework for effectiveness concepts in mutualisms

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Abstract

A core interest in studies of mutualistic interactions is the 'effectiveness' of mutualists in providing benefits to their partners. In plant-animal mutualisms it is widely accepted that the total effect of a mutualist on its partner is estimated as (1) a 'quantity' component multiplied by (2) a 'quality' component, although the meanings of 'effectiveness,' 'quantity,' and 'quality' and which terms are applied to these metrics vary greatly across studies. In addition, a similar quantity × quality = total effect approach has not been applied to other types of mutualisms, although it could be informative. Lastly, when a total effect approach has been applied, it has invariably been from a phytocentric perspective, focussing on the effects of animal mutualists on their plant partner. This lack of a common framework of 'effectiveness' of mutualistic interactions limits generalisation and the development of a broader understanding of the ecology and evolution of mutualisms. In this paper, we propose a general framework and demonstrate its utility by applying it to both partners in five different types of mutualisms: pollination, seed dispersal, plant protection, rhizobial, and mycorrhizal mutualisms. We then briefly discuss the flexibility of the framework, potential limitations, and relationship to other approaches.

Keywords

Mutualism effectiveness, mycorrhizal mutualisms, plant protection mutualisms, pollination mutualisms, rhizobial mutualisms, seed dispersal mutualisms.

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INTRODUCTION

Mutualistic interactions are widespread in all ecosystems (Bronstein 2015). Key to understanding the ecology and evolution of mutualisms is viewing the interaction as a *process* (e.g. a bee visits a flower, removes pollen, and transports it to another flower) that has both an *immediate effect* (e.g. pollen deposition, the immediate outcome of the interaction) and a *delayed effect* linked to demography and fitness (e.g. seed set, a delayed outcome that is expressed after the interaction has ended) (Fig. 1). Central to all studies of mutualisms is a consideration of the 'effectiveness' of mutualistic partners in performing the studied processes, whether it is the effectiveness of seed dispersing animals in producing seedlings (Loayza & Rios 2014), the effectiveness of pollinating animals in producing seeds (Rodríguez-Rodríguez *et al.* 2013), the effectiveness of ants defending plants from antagonists (Rico-Gray & Oliveira 2007), the effectiveness of rhizobia in providing nitrogen to a legume (Jia *et al.* 2013), or the effectiveness of mycorrhiza in promoting plant growth (Campanelli *et al.* 2014). However, the meaning of effectiveness, and the terminology used to communicate this concept, varies tremendously across studies, which limits our ability to develop a general understanding of mutualistic interactions and their outcomes.

A second limitation lies in the unbalanced approach taken in the studies of mutualisms. Although all mutualistic interactions have fitness consequences for both interacting partners by definition, empirical studies of mutualisms focus only on the fitness consequences for one of the partners. For example, studies of plant-animal mutualisms invariably focus on the effectiveness of animal mutualists in promoting some correlates of plant fitness or population dynamics, whilst ignoring the effectiveness of plant mutualists in promoting success of their animal partners, a form of 'resource provisioning effectiveness (RPE)' with consequences for animal fitness and population dynamics.

Developing a generally applicable framework for studying mutualisms is challenging given the extraordinary variety of mutualisms and diversity of organisms involved. However, this challenge can be lessened by thinking first about commonalities in processes and outcomes of mutualisms. A number of approaches have been taken to categorising mutualisms. Holland & DeAngelis (2010) and Holland (2015) distinguish three classes of mutualisms based on a consumer-resource approach. In bidirectional consumer-resource mutualisms each partner in the interaction is both a consumer and a resource; in mycorrhizal mutualisms, the plant consumes soil resources provided by the fungus and the fungus

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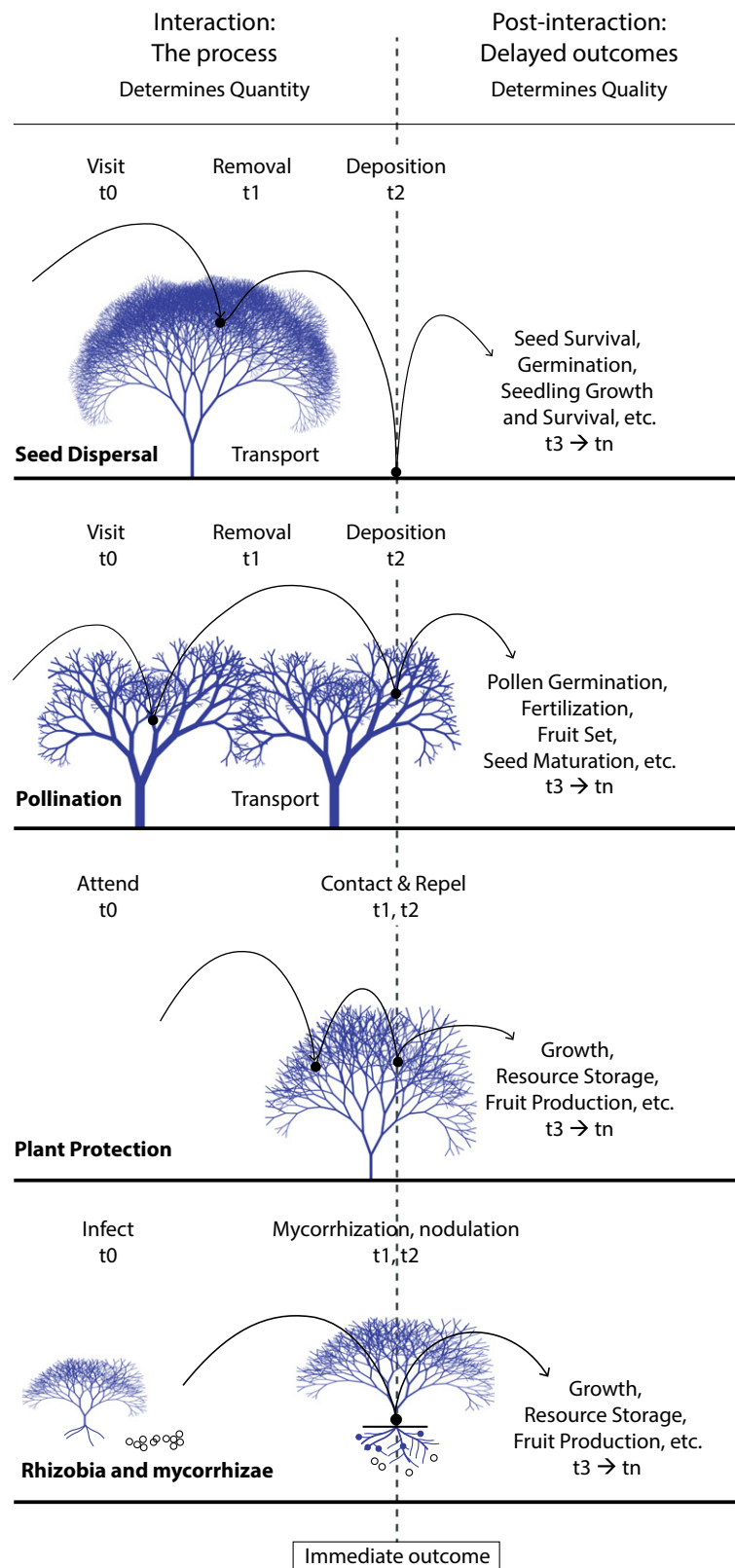
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Figure 1 Distinguishing characteristics of the processes of seed dispersal, pollination, plant protection, and rhizobial/mycorrhizal mutualistic interactions. This figure depicts two sequential stages spanning a temporal sequence $t_0, t_1, \ldots, t_n$ of events (e.g., visitation, removal, deposition). The first stage, which represents the interaction, ends with the immediate outcome (e.g. deposition of a seed; $t_0 - t_2$); this stage determines the quantity component of effectiveness. The post-interaction delayed outcomes ($t_3, \ldots, t_n$), such as seed survival and germination, determine the quality component of effectiveness. In pollination and seed dispersal mutualisms, the transition $t_1 - t_2$ involves the actual transport of plant propagules.

consumes carbohydrates provided by the plant. In unidirectional consumer-resource mutualisms, one partner consumes a resource supplied by the other partner whilst providing that partner with a service, such as a bird consuming a fruit and providing the plant with seed dispersal services. Holland & DeAngelis (2010) also consider indirect consumer-resource mutualisms in which two species receive benefits through indirect interactions with a third species; however, this synthesis is only concerned with mutualisms where partners directly interact, which encompass the vast majority of known mutualisms. Alternatively, mutualisms can be classified in terms of services provided – transportation, protection, and nutritional mutualisms (Bronstein 2015). Further, mutualisms can be viewed from the perspectives of intimacy (symbiotic or non-symbiotic), obligacy (obligate or facultative), or specificity (specialised or generalised) (Bronstein 2015). Despite the great diversity of actual interactions involved in mutualisms, there are clear commonalities in processes (interacting partners receive resources/services from their partners) and in outcomes (the receipt of these resources/services has both immediate and delayed effects with fitness and demographic consequences). These commonalities facilitate the development of a general framework that is broadly applicable to the diversity of individual direct mutualisms found in nature.

In this paper, we take the first steps towards the development of a general effectiveness framework for viewing the processes and outcomes of mutualistic interactions that is based on consistent terminology and a more restricted range of metrics, and that is applicable to both partners in a mutualism. Our framework is not a modelling framework for predicting outcomes, but rather a descriptive framework that (1) provides a consistent, structured approach for thinking about and studying mutualisms to make comparisons easier, (2) consistently describes the processes and outcomes of individual mutualistic interactions, and (3) facilitates exploration of the context dependence of mutualistic outcomes. We believe this framework can be applied in principle to all direct mutualisms, independent of directionality, services provided, intimacy, obligacy, or specificity. Further, we believe that the use of this framework will help clarify the ecological and the evolutionary consequences of mutualisms. For example, it will help address such questions as follows: What is the direction and strength of selection on flowering plant traits when interacting with a generalist assemblage of insects? Which species of fruiting plant contributes most to the population dynamics of a frugivorous monkey, and does that change with ecological context? What are the likely consequences of the loss of a given mutualist species? Our attempt to unify approaches to mutualisms has the goal of fundamentally changing how the processes and outcomes of mutualisms are viewed and studied.

THE FOUNDATIONS OF AN EFFECTIVENESS FRAMEWORK

It has been recognised for decades in pollination (e.g. Stebbins 1970; Schemske & Horovitz 1984; Herrera 1987, 1989; Vázquez *et al*. 2005) and seed dispersal mutualisms (e.g. Herrera & Jordano 1981; Vázquez *et al*. 2005; Schupp *et al*.

2010), and more recently in plant protection mutualisms (e.g. Ness *et al*. 2006), that the total effect of a mutualistic animal on a plant is a function of (1) some measure of the frequency of the interaction (quantity component) and (2) some measure of the effect of that interaction when it occurs (quality component). These two components are viewed as multiplicative (e.g. Schupp 1993). It is also widely recognised in plant-animal mutualisms that animal species vary in the benefits provided to plants, which has implications for the ecology (e.g. effect on plant population dynamics) and evolution (e.g. evolution of specialisation) of the plant (Herrera & Jordano 1981; Schemske & Horovitz 1984; Ness *et al*. 2006). Further, there appears to be broad acceptance of the notion that a framework built on quantity, quality, and total effect can facilitate quantifying the effects of animal mutualists on plant fitness and population dynamics, and thus more thoroughly and rigorously explore the ecological and evolutionary processes and outcomes of plant-animal mutualisms (Ness *et al*. 2006; Ne'eman *et al*. 2010; Schupp *et al*. 2010). In addition, such a framework can help to rigorously assess the pervasive context dependency and variation of mutualisms (Chamberlain *et al*. 2014).

Nonetheless, there are limitations to current approaches that hinder a broader, comparative understanding of mutualisms. One limitation is the widespread disagreement in the literature when it comes to actual frameworks of effectiveness, terminology employed, proxy variables used as measures of quantity, quality, and total effect, and more. Underlying the confusion in the literature is a sea of terms and metrics, with multiple terms applied to the same component and with individual terms used in many different ways (see Appendix S1; Schupp 1993; Inouye *et al*. 1994; Ne'eman *et al*. 2010) – a sea of effectiveness, efficiency, efficacy, goodness, importance, intensity, performance, and more. The problem is most extreme in pollination mutualisms because a huge literature developed addressing the effects of pollinators without concurrent development of a widely accepted framework (Ne'eman *et al*. 2010). Further, to the best of our knowledge no one has attempted to apply a similar quantity-quality-total effect framework to either other types of mutualisms beyond seed dispersal, pollination, and plant protection (e.g. mycorrhizal), or simultaneously to the partner species (e.g. the seed dispersers). This lack of a consistent framework and terminology inhibits comparative studies and the development of generalities on the ecological and evolutionary consequences of mutualisms (Ne'eman *et al*. 2010).

HOW HAVE WE ASSESSED QUANTITY, QUALITY, AND TOTAL EFFECT IN THE LITERATURE?

As noted, quantity × quality = total effect frameworks have frequently been applied to plant-animal mutualisms, in all cases from a phytocentric perspective. However, the structure of these frameworks has varied greatly. Here we provide a brief overview of how quantity, quality, and total effect have been viewed in the seed dispersal and pollination literature, the only types of mutualisms where such frameworks have been extensively applied; this provides context for our general framework. In many cases, we translate original terms into

categories of quantity, quality, and total effect based on our interpretations. More thorough reviews are available (e.g. Schupp 1993; Inouye *et al.* 1994; Ne'eman *et al.* 2010; Schupp *et al.* 2010), and an extended version of this overview is in Appendix S2.

Most seed dispersal studies over the last decades have taken a fairly consistent approach based on the seed dispersal effectiveness (SDE) framework (Schupp 1993; Schupp *et al.* 2010), with some variation because of the logistical constraints and the varying ecologies of interacting organisms. Generally, quantity is the number of seeds dispersed, quality is the probability that a dispersed seed produces a 'recruit', frequently an established seedling, and total effect is the number of new 'recruits' produced by the activities of that disperser species (e.g. Calviño-Cancela & Martín-Herrero 2009; Escribano-Avila *et al.* 2014; Loayza & Rios 2014; Mellado & Zamora 2014; Rother *et al.* 2016). Multiplicative subcomponents of quantity and quality are often considered; e.g. quantity is the number of visits multiplied by the number of seeds dispersed per visit.

In pollination mutualisms, quantity is mostly the frequency of visits to a plant or to individual flowers without considering an immediate outcome of the interaction (e.g. Mayfield *et al.* 2001; Sahli & Conner 2007; Ne'eman *et al.* 2010; Fagua & Ackerman 2011; Sánchez-Lafuente *et al.* 2012; Castro *et al.* 2013; Rocca & Sazima 2013), although more complex indices have been used (e.g. Jacobs *et al.* 2010; Robertson & Leavitt 2011; Rader *et al.* 2012; Rodríguez-Rodríguez *et al.* 2013). Metrics of quality include surrogates thought to affect pollination potential, such as pollen loads (Jacobs *et al.* 2010; Zych *et al.* 2014) or within- vs. between-plant-pollinator movements (Utelli & Roy 2000). Others consider the number of pollen grains deposited on stigmas (Gómez & Zamora 1999; Mayfield *et al.* 2001; Ne'eman *et al.* 2010; Rader *et al.* 2012; King *et al.* 2013; Maldonado *et al.* 2013; Zych *et al.* 2013; Bruckman & Campbell 2014) and/or removed from anthers (Sahli & Conner 2007; Rodríguez-Rodríguez *et al.* 2013; Zych *et al.* 2013) during a single visit by a pollinator to be measures of quality. Lastly, a growing number of studies consider post-pollination consequences, such as germinated stigmatic pollen loads (Rocca & Sazima 2013), ovule fertilisation (Brittainn *et al.* 2013), fruit and seed set (Mayfield *et al.* 2001; Sahli & Conner 2007; Fagua & Ackerman 2011; Robertson & Leavitt 2011; Sánchez-Lafuente *et al.* 2012; Maldonado *et al.* 2013; Rodríguez-Rodríguez *et al.* 2013; Bruckman & Campbell 2014), surrogates of seed vigour such as seed size and germination (Fagua & Ackerman 2011), and offspring survival to flowering (Gómez 2000). Diverse estimates for total effect range from dimensionless scores of combined surrogate metrics (e.g. Zych *et al.* 2014) to immediate outcomes of stigma contacts and pollen deposition on conspecific stigmas (e.g. Rader *et al.* 2012) to various stages of delayed outcomes ranging from pollen germination (Rocca & Sazima 2013) through seed germinability (Fagua & Ackerman 2011) to offspring survival to flowering (Gómez 2000). The common thread is that the total effect is quantified as the product of some measure of quantity, generally the frequency of visits, and some measure of quality, which varies widely across studies (Vázquez *et al.* 2005).

A GENERAL FRAMEWORK

In our framework, we use the term effectiveness for the total effect of a mutualist and the terms quantity and quality for the components of effectiveness. Whilst contrary to other formulations (e.g. Ne'eman *et al.* 2010), we believe this to be the clearest and most appropriate structure of terminology. See Appendix S1 for additional discussion on terminology and a detailed justification for our choices.

Characteristics of an ideal framework

In this paper, we highlight characteristics of a general idealised framework that we believe maximise its value for understanding the ecology and evolution of mutualisms. This framework focusses on the effects of two interacting populations of mutualists, although the approach can be used to consider differences amongst individuals in effectiveness (Schupp *et al.* 2010).

(1) Effectiveness of the mutualistic interaction between two partners is ideally defined as the number of new adults of a partner produced by the activity of the other partner. Therefore, effectiveness must include some measure of the post-interaction, delayed outcomes of the actual interaction (Fig. 1). For example, no matter how many seeds have been dispersed, dispersal has not been effective if no seedlings are produced. Thus, effectiveness ideally is based on measured mean fitness (e.g. the number of new adults recruited) or estimates of population growth rate. However, such an extensive measure is frequently difficult if not impossible to obtain, so more restricted correlates of fitness or vital rates will be used as proxies (see below under Quality for a more thorough discussion). Our measure of effectiveness can have evolutionary implications, when effectiveness is accounted for at the level of individual fitness, and demographic implications, when it is measured at the level of population dynamics of the partners.
(2) Effectiveness is composed of two components, a quantity component and a quality component. Whilst these components are the critical metrics for quantifying effectiveness of a mutualism, assessing subcomponents of quantity and quality improves our understanding of the processes driving effectiveness.
(3) The quantity component of effectiveness is a measure of the number of immediate outcomes of the interaction, not simply the number of interactions. For example, in seed dispersal mutualisms, quantity is the number of seeds dispersed, not the number of visits to the host plant (Schupp *et al.* 2010). Similarly, quantity in pollination mutualisms is the number of pollen grains deposited, not simply the number of floral visits. As noted previously, this contrasts with how quantity is generally viewed in pollination mutualisms.
(4) The quality component of effectiveness incorporates the post-interaction, delayed outcomes of the interaction (Fig. 1). Although in some cases, quality is at least partly determined during the interaction phase – e.g. foraging decisions of a pollinator influence characteristics of the pollen load – this quality can only be expressed post-interaction – e.g. after pollen deposition on a stigma. As with effectiveness, this ideally involves the quantification of fitness or demographic

consequences of the interaction event, such as the probability that an individual interaction event produces a new adult of the interacting organism. However, we must frequently use more restricted correlates of fitness or vital rates in practise. These proxies will provide valuable insight, but the value of that insight increases with each sequential step we follow in the chain of post-interaction outcomes; for pollination mutualisms, the probability a pollen grain fertilises an ovule carries more fitness information than simply the number of pollen grains germinating on the stigma, but the probability that a pollen grain produces a seed that germinates tells even more.

(5) Components and subcomponents of effectiveness are multiplicative. For example, if we calculate SDE for bird species A as quantity (number of seeds dispersed) × quality (probability a dispersed seed produces a 2-year-old recruit) then we have quantified the number of 2-year-old recruits produced by the dispersal activities of species A and the contributions of quantity and quality to effectiveness.

Whilst many plant–animal mutualism studies use frameworks similar to our idealised framework, many others do not. Studies on seed dispersal are most likely to correspond to our framework, largely because our general framework is an extension of the widely accepted SDE framework (Schupp et al. 2010). However, we believe our framework can be used to describe the effectiveness, and what processes contribute to effectiveness, of any direct mutualism, whether unidirectional or bidirectional, symbiotic or non-symbiotic, specialised or generalised, obligate or facultative.

In addition, as we illustrate below, our framework can be used to describe the effectiveness of both partners in a mutualism, which is ultimately necessary if we are to thoroughly understand the evolutionary and ecological consequences of the mutualism.

APPLYING THE FRAMEWORK

We first discuss in very general terms how to apply our effectiveness framework to the breadth of diverse mutualisms in nature. Then, as examples, we specifically apply our framework to both partners in five mutualisms: seed dispersal, pollination, plant protection, rhizobial, and mycorrhizal (Fig. 2). The primary goal is to demonstrate that many distinct types of mutualisms can be addressed with our framework, at least in principle. We then use an outgrowth of our general framework of effectiveness, the effectiveness landscape, inspired by Sewall Wright's (1932) adaptive landscape (Fig. 3), to discuss lessons that can be learnt from our approach to mutualisms.

Application of the framework to individual mutualisms: general approach

Although we believe our framework can be used with all direct mutualisms, there may be methodological limitations to quantifying some relevant components and subcomponents of some mutualistic interactions presently. Nonetheless, using the framework to organise thinking about processes and outcomes of mutualisms is valuable even in such cases, and may even contribute to the development of new methods.

Given the vast variety of types of mutualisms and extraordinary diversity of organisms involved in mutualisms it is impossible to propose firm guidelines on appropriate metrics to use. Consequently, in applying the framework to a given mutualism it is critical to understand thoroughly the biology of the mutualism. Then, based on this knowledge, metrics of the components and subcomponents of effectiveness must be selected that are biologically meaningful and (preferably) feasible to quantify. Effectiveness should be in terms of meaningful proxies for fitness or population dynamics. The chosen metric for quantity should be in terms of immediate outcomes of the interaction (ideally frequency-related), whilst the metric for quality should be in terms of delayed post-interaction outcomes (ideally probability-related).

Application of the framework to individual mutualisms: five examples

To make these examples more relevant, rather than depicting idealised metrics (e.g. number of adults produced by the activities of a mutualist), we present proxy metrics that are realistic, biologically relevant to fitness/population dynamics, and are in many cases data that are collected in studies of mutualisms. These examples are for specific (though partially to completely hypothetical) mutualisms and are not directly applicable to all mutualisms within the given type. Based on the biological characteristics of the partners in any specific mutualism and on logistical feasibility, proxy metrics can be modified to better represent that interaction whilst still maintaining an effectiveness framework that quantifies a fitness- or population-related outcome of the interaction.

Seed dispersal mutualism

Seed dispersal mutualisms are unidirectional consumer-resource (Holland & DeAngelis 2010; Holland 2015) transportation (Bronstein 2015) mutualisms. They involve the removal, transport, and deposition of seeds and the harvest and use of resources provided by plants (Fig. 1; Janzen 1983). Seed dispersal depends on the interaction of a mobile animal with an immobile plant (seed removal) followed by the interaction of that animal with the overall environment (seed deposition) – the 'target' for seed dispersal is diffuse and varies continuously in suitability (Wheelwright & Orians 1982; Schupp 1993). A single interaction with a seed equally affects male and female fitness of the plant. These mutualisms vary from relatively specialised to extremely generalised, and the partners vary greatly in their dependences on the mutualism. Uniquely, seed dispersal is frequently a multi-step process, with primary dispersal followed by biotic or abiotic secondary dispersal.

Figure 2a applies our framework to a seed dispersal mutualism. The left side represents SDE, which here is the number of new plants recruited to the population. Reflecting the diffuse nature of the target, quantity is the number of seeds dispersed, without reference to where seeds arrive. This is a function of the number of visits and the number of seeds dispersed per visit. Quality is the probability that a dispersed seed produces a new recruit, which is a function of the probability that a seed germinates following handling and the
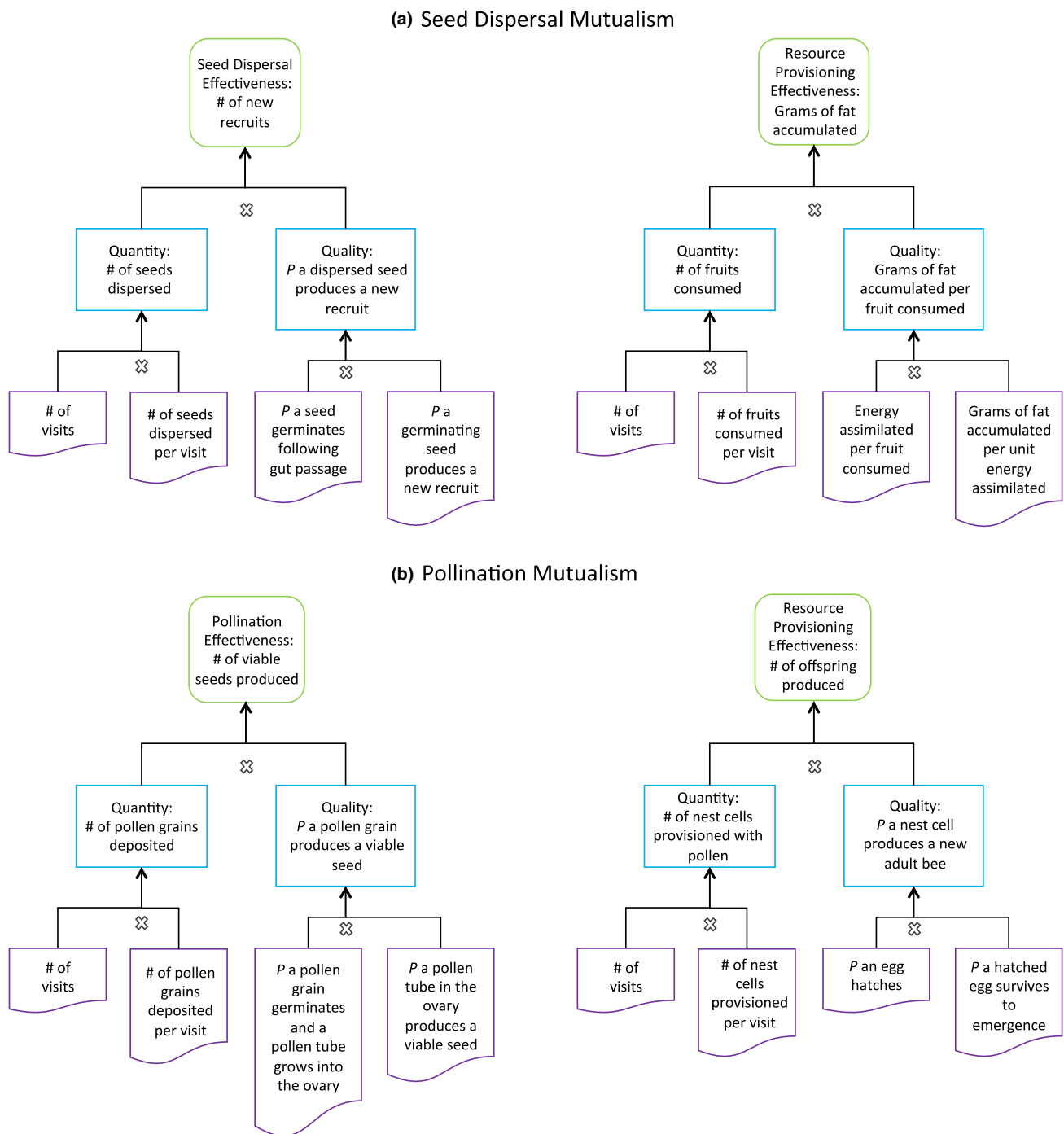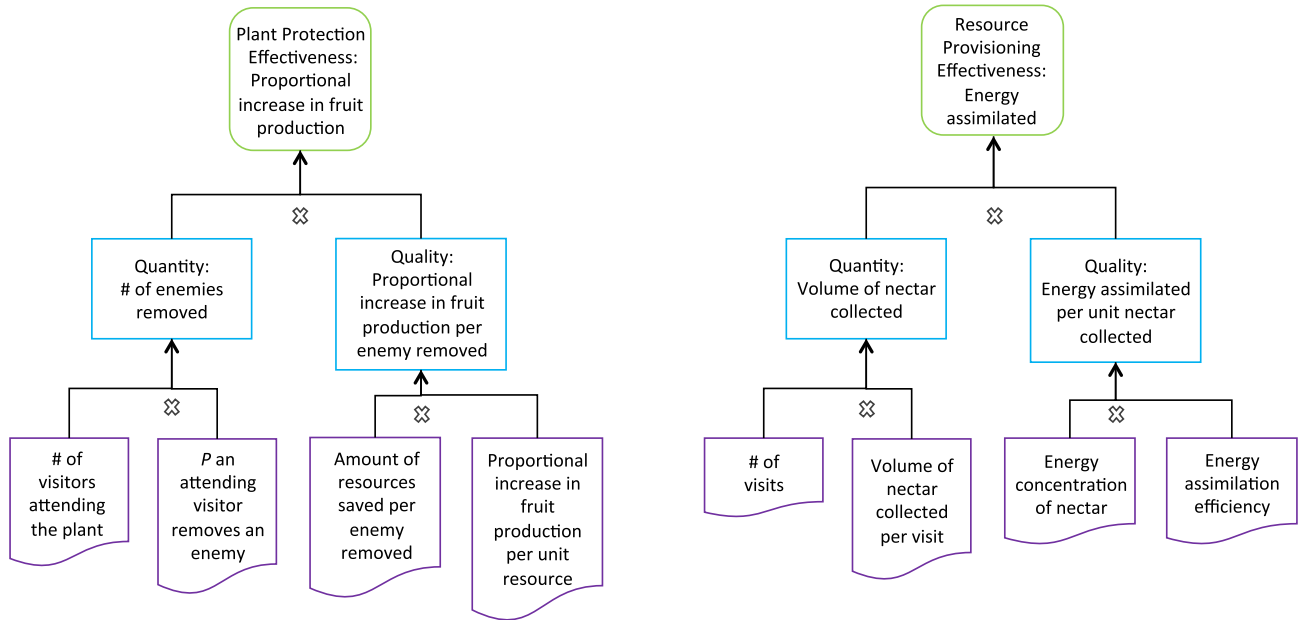
(a) Seed Dispersal Mutualism

(b) Pollination Mutualism

Figure 2 Hypothetical applications of the framework to (a) seed dispersal, (b) pollination, (c) plant protection, (d) rhizobial nitrogen fixing, and (e) mycorrhizal mutualisms that reflect the processes and outcomes depicted in Fig. 1. For each mutualism, we present a flowchart for both interacting partners; e.g. for seed dispersal, we present the effectiveness a plant receives from a disperser species on the left and the effectiveness the dispersal agent receives from the plant species on the right. In all examples, effectiveness measures a proxy of a fitness/demographic outcome of the interaction resulting from multiplying a quantity component, determined by the number of immediate outcomes, by a quality component, determined by post-interaction outcomes. In all examples, the subcomponents of quantity and of quality are also multiplicative (bottom row) and defined by proxy variables that generally can be determined by observation and experimentation. Different colours and shapes of boxes are used to clearly distinguish different hierarchical levels in the flowcharts. P = probability. The X symbol indicates that the connected components or subcomponents are multiplicative.

probability that a germinating seed produces a new recruit, which is largely driven by where in the landscape that seed arrived. This represents the approach taken in many seed dispersal studies where combinations of observations and

experiments provide data to populate these components and subcomponents (e.g. Calviño-Cancela & Martín-Herrero 2009; Schupp *et al*. 2010; Escribano-Avila *et al*. 2014; Loayza & Rios 2014; Mellado & Zamora 2014; Rother *et al*. 2016).

(c) Plant Protection Mutualism

```
Plant Protection
Effectiveness:
Proportional
increase in fruit
production
         ↑
        ⊗
  ┌──────┴──────┐
Quantity:        Quality:
# of enemies     Proportional
removed          increase in fruit
                 production per
                 enemy removed
    ↑                ↑
   ⊗                ⊗
┌───┴───┐        ┌───┴───┐
# of      P an    Amount of   Proportional
visitors  attending resources  increase in
attending visitor  saved per   fruit
the plant removes an enemy      production
          an enemy  removed     per unit
                                resource
```

```
Resource
Provisioning
Effectiveness:
Energy
assimilated
         ↑
        ⊗
  ┌──────┴──────┐
Quantity:        Quality:
Volume of nectar Energy assimilated
collected        per unit nectar
                 collected
    ↑                ↑
   ⊗                ⊗
┌───┴───┐        ┌───┴───┐
# of      Volume of  Energy      Energy
visits    nectar     concentration assimilation
          collected  of nectar   efficiency
          per visit
```

(d) Rhizobial Nitrogen Fixing Mutualism

```
Rhizobial
Effectiveness:
Total height
growth
produced
         ↑
        ⊗
  ┌──────┴──────┐
Quantity:        Quality:
# of nodules     Height growth
produced         produced per
                 nodule
    ↑                ↑
   ⊗                ⊗
┌───┴───┐        ┌───┴───┐
# of CFUs  # nodules  Amount of   Height
(colony    produced   nitrogen    growth
forming    per CFU    fixed per   produced
units)                nodule      per unit
                                  nitrogen
```

```
Resource
Provisioning
Effectiveness:
Descendants
produced
         ↑
        ⊗
  ┌──────┴──────┐
Quantity:        Quality:
# of descendants P an initiated
initiated        descendant produces
                 an established
                 descendant in soil
    ↑                ↑
   ⊗                ⊗
┌───┴───┐        ┌───┴───┐
Quantity of # of      P an initiated  P an
carbon      descendants descendant    undifferentiated
assimilated initiated   remains       descendant is
from plant  per unit    undifferentiated released into the
            carbon                    soil and survives
```
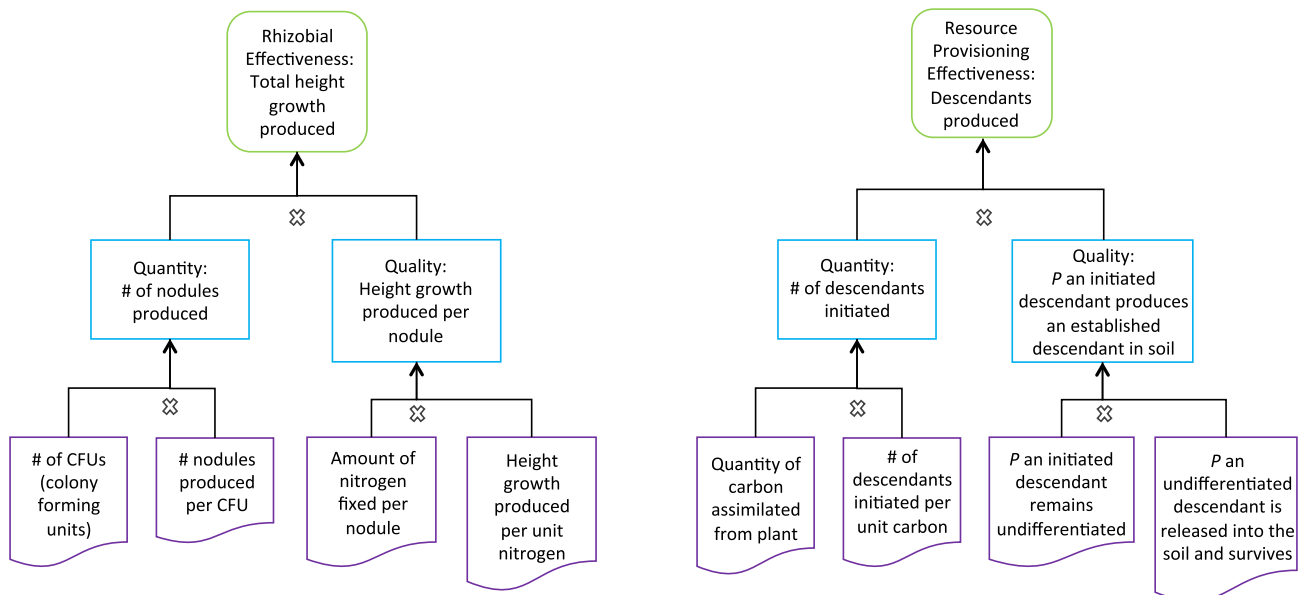
Figure 2 Continued.

Although focussing on established seedlings has limitations, it is frequently all that is feasible, especially with long-lived tree species generally favoured in such studies, and it measures a vital rate linked to population growth and ultimately fitness. Further, there is potential to incorporate population projection models to extend the analysis into later juvenile stages (Godínez-Alvarez & Jordano 2007; Rey & Alcántara 2014) if not the complete life cycle, but this is much more data demanding.

The right side of Fig. 2a represents RPE of a fruiting plant (RPE-Fruiting Plant). We assume a bird is eating fruits to store fat for migration, so RPE-Fruiting Plant is measured as grams of fat accumulated which clearly has implications for survival and perhaps reproduction. Quantity is the number of fruits consumed, which is a function of the number of visits and the number of fruits consumed per visit. Quality is the grams of fat accumulated per fruit consumed, which is a function of the energy assimilated per consumed fruit and the grams of fat accumulated per unit energy assimilated. These metrics can be addressed through observations of fruit consumption combined with feeding experiments (e.g., Jordano 1988). Frugivores eat fruit for more reasons than fat storage, however, so the appropriate proxy metrics must be selected based on understanding of the mutualism.
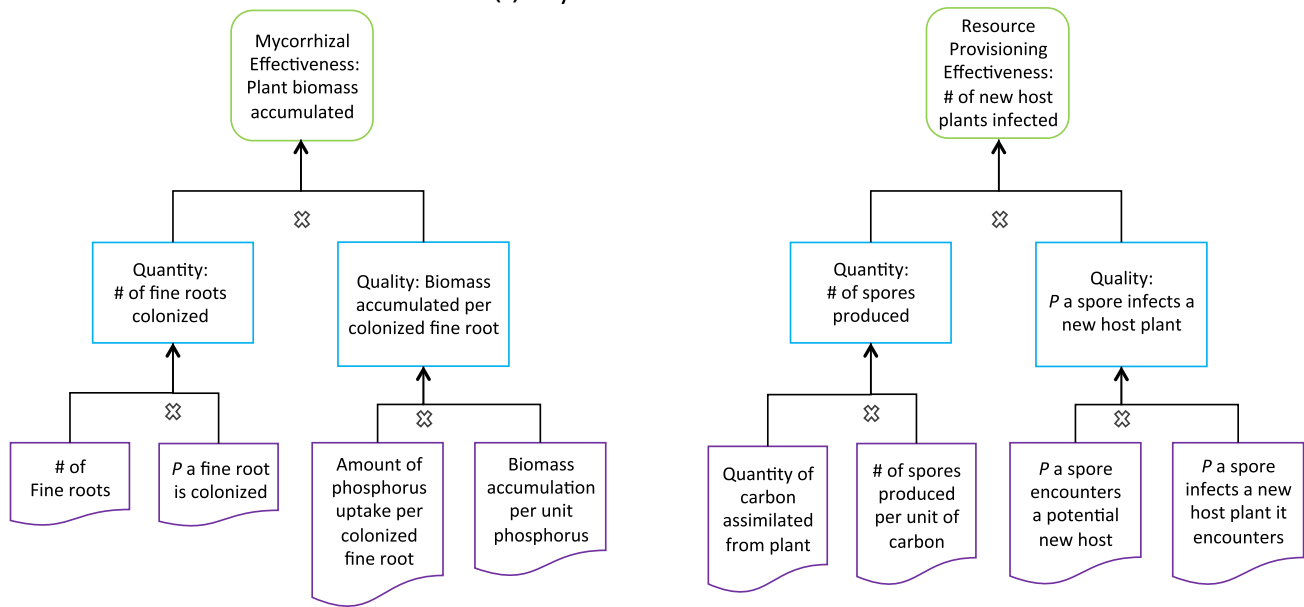
(e) Mycorrhizal Mutualism

Figure 2 Continued.

Pollination mutualism

Pollination mutualisms are also unidirectional consumer-resource (Holland & DeAngelis 2010; Holland 2015) transportation (Bronstein 2015) mutualisms. Similar to seed dispersal, it involves the removal, transport, and deposition of pollen and the harvest and use of resources provided by plants (Fig. 1; Janzen 1983). In contrast to seed dispersal, pollination depends on the interaction of one animal with one flower (pollen removal) followed by the interaction of that animal with a second flower (pollen deposition) of the same (geitonogamous pollen transfer) or a different (allogamous pollen transfer) individual – the 'target' is specific and generally viewed as suitable (compatible conspecific stigma) or not (Wheelwright & Orians 1982), although compatibility is in reality a continuous variable. An interaction with a flower might differentially affect male (pollen removal) and female (pollen deposition) fitness of the plant, and pollinator effectiveness can be viewed from the paternal, maternal, or combined perspective (Ne'eman et al. 2010). Note, however, that at the population level the interaction between an animal and a plant results in equal male and female fitness. There is perhaps even more variation in the degree of specificity and intimacy than in seed dispersal, ranging from super-generalist pollinators to highly specialised bees.

Figure 2b applies the framework to a pollination mutualism. In this study, pollination effectiveness (PE), on the left-hand side, is the number of viable seeds produced, an early stage in the chain of post-interaction delayed effects and a first step to recruitment. Reflecting the specific nature of the target, quantity is the number of pollen grains deposited on compatible stigmas. It is a function of the number of visits and the number of pollen grains deposited per visit. Quality, the probability that a pollen grain on a stigma produces a viable seed, is the probability a pollen grain germinates and a pollen tube grows into the ovary multiplied by the probability

a pollen tube in the ovary produces a viable seed. The number of pollen grains deposited on a stigma in a single visit and some measure of the number of visits are commonly quantified in pollination studies. Although many studies stop with pollen deposition, others quantify post-interaction delayed consequences which can be used as proxies for quality. Note that the subcomponents of quality used here reflect the distinction between pre-zygotic and post-zygotic measures of quality (Alonso et al. 2012). Although the hierarchical structure we promote has not been used fully in pollination studies, similar frameworks have been applied. For example, one measure of pollinator effectiveness derived by Fagua & Ackerman (2011) was visitation rate multiplied by the mean number of seeds produced per visit. While this removes pollen grains deposited per visit from the quantity component and subsumes it into a 'black box' of quality, the overall product is quantifying seed production, the measure of PE used here.

The resource provisioning effectiveness of a flowering plant (RPE-Flowering Plant), on the right, represents a scenario where bees collect pollen for offspring rearing. RPE-flowering plant is thus the number of bee offspring produced, a vital rate linked to population recruitment and fitness. Quantity, the number of nest cells provisioned with pollen, is a function of the number of visits and the number of nest cells provisioned per visit. Quality, the probability a nest cell produces a new adult bee, is a function of the probability an egg hatches and the probability a hatched egg survives to emergence. Although this is complicated by the likelihood of mixed pollen loads, the approach is promising for at least some species such as solitary cavity-nesting bees where contents of nest cells can be quantified and where the probability of producing an adult bee can be quantified on experimental nest cells (e.g. Praz et al. 2008). Because pollinators also collect other resources from flowers for multiple reasons, in many pollination
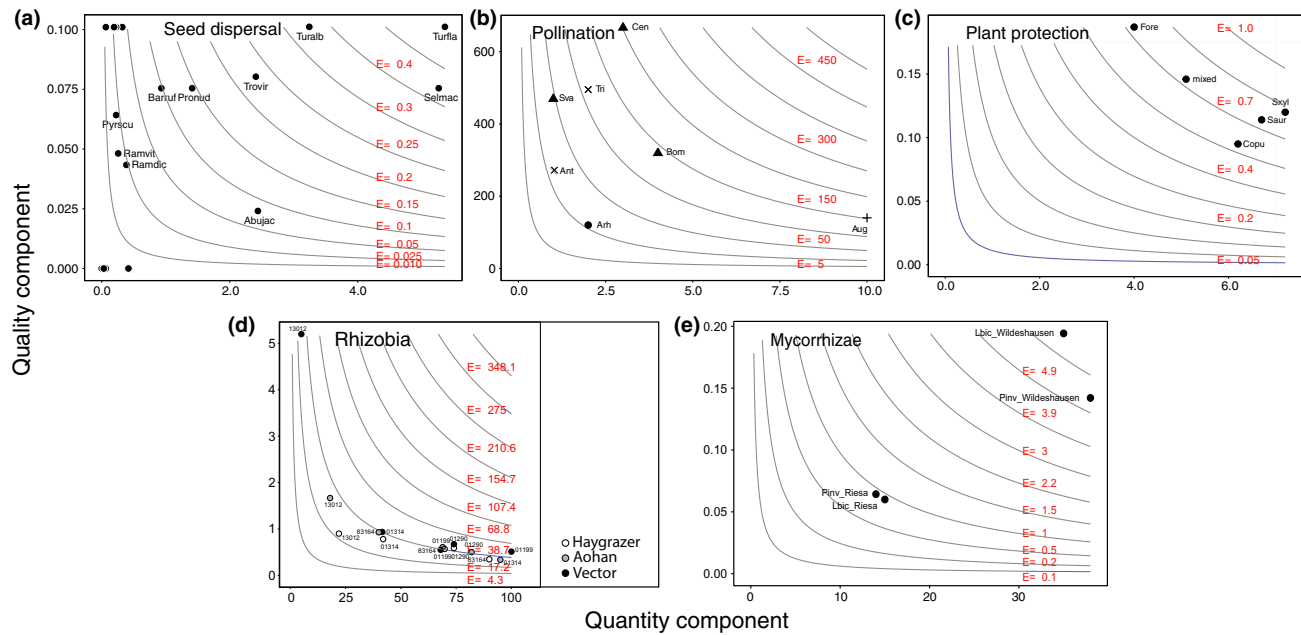
Figure 3 Representative effectiveness landscapes that reflect to a greater or lesser degree the hypothetical mutualisms in Fig. 2. Because all empirical studies on these types of mutualisms take a phytocentric approach, all five of our landscapes portray the effectiveness of multiple mutualists on some measure of plant success. In an effectiveness landscape for a plant species, the x-axis is the quantity component and the y-axis is the quality component. Isoclines represent all combinations of quantity and quality that result in the same effectiveness and are labelled as E = x. Effectiveness landscapes rise in 'elevation' (effectiveness) from the origin to the upper right. Individual mutualist species interacting with the plant are plotted on the landscape based on their quantity and quality components, and their locations on the landscape with respect to the isoclines measure their effectiveness (quantity × quality). (a) A seed dispersal effectiveness landscape (SDE Landscape) derived from birds dispersing the palm *Euterpe edulis* (Rother *et al.* 2016). Quantity is the number of seeds dispersed per 10 h, quality is the probability a dispersed seed produces an established seedling, and SDE is the number of established seedlings produced from 10 h of dispersal activity. Not all disperser species are identified. Abujac = *Aburria jacutinga*, Barruf = *Baryphthengus ruficapillus*, Pronud = *Procnias nudicollis*, Pyrscu = *Pyroderus scutatus*, Ramdic = *Ramphastos dicolorus*, Ramvit = *Ramphastos vitellinus*, Selmac = *Selenidera maculirostris*, Trovir = *Trogon viridis*, Turalb = *Turdus albicollis*, Turfla = *Turdus flavipes*. (b) A pollination effectiveness landscape (PE Landscape) derived from data on bees pollinating the cactus *Opuntia sulphurea* (Maldonado *et al.* 2013). Quantity is the number of pollen grains deposited on stigmas per visit, quality is the probability a pollen grain produces a seed, and PE is the number of seeds produced by the actions of a bee species. Ant = *Anthidium* sp., Arh = *Arhysosage bifasciata*, Aug = *Augochloropsis* sp., Bom = *Bombus opifex*, Cen = *Centris brethesi*, Sva = *Svastrides zebra*, Tri = *Trichoturgus laticeps*. Bee families are distinguished by symbols: Megachilidae = x, Halictidae = +, Apidae = ▲. (c) A plant protection effectiveness landscape (PPE Landscape) calculated from data on ant protection of *Ferocactus wislizeni* (Ness *et al.* 2006). Quantity is the number of surrogate 'herbivores' killed in 30 min, quality is the proportional increase in fruit annual production per 'herbivore' killed, and PPE is the proportional increase in fruit production because of the tending by a given ant species. Copu = *Crematogaster opuntiae*, Fore = *Forelius* sp., Saur = *Solenopsis aurea*, Sxyl = *Solenopsis xyloni*. Mixed = a mixed assemblage that over time was not dominated by any particular ant species. (d) A rhizobial nitrogen fixing mutualism effectiveness landscape (RE Landscape) from data in Jia *et al.* (2013) on five strains of the rhizobium *Ensifer meliloti* (01199, 01290, 01314, 83164, and 13012) inoculating three cultivars of *Medicago sativa* (Haygrazer, Vector, and Aohan). Quantity is the number of nodules developed after experimental inoculation, quality is the plant height growth (mm) 50 days after sowing per nodule, and RE is total plant height growth (mm). (e) A mycorrhizal effectiveness landscape (ME Landscape) using data from Baum *et al.* (2000) for two ectomycorrhizal strains (Lbic = *Laccaria bicolor* and Pinv = *Paxillus involutus*) infecting *Populus trichocarpa* on two different soils (Wildeshausen with higher % sand and Riesa with higher % silt and clay). Quantity is the number of fine roots colonised of 200 examined, quality is increased biomass because of the mycorrhiza per unit root colonisation after 6 months of growth, and ME is increased biomass as a result of mycorrhiza.

mutualisms other resources and fitness proxies (e.g. females inseminated, egg production) are more appropriate.

Plant protection mutualism

Plant protection mutualisms are unidirectional consumer-resource (Holland & DeAngelis 2010; Holland 2015) protection (Bronstein 2015) mutualisms. There is an interaction involving a mobile animal that provides a service and an immobile plant that provides a resource (Fig. 1). However, there is no transport and the interaction involves a third interactor, the enemy (e.g. herbivore). These mutualisms vary greatly from generalist, facultative, non-symbiotic interactions to highly specific, obligate, symbiotic relationships.

Our application of the framework to plant protection mutualisms (Fig. 2c) represents a facultative non-symbiotic interaction. Plant protection effectiveness (PPE), on the left, is the proportional increase in fruit production, a metric of reproduction. Quantity, the number of enemies removed, whether by killing or repelling, is a function of the number of visitors attending the plant and the probability an attending visitor removes an enemy. Quality, the proportional increase in fruit production per enemy removed, is a function of the amount of resources saved per enemy removed and the proportional increase in fruit production per unit resource. Although the numbers of ants tending facultative ant-plants are highly variable in space and time, robust sampling can provide data on

mean visitation. Ness *et al.* (2006) were able to distinguish individual cacti that were predominantly visited by particular species of ants and relate that species-specific tending to fruit production. Other potential proxies of effectiveness include measures of growth, where added resources can be allocated to reproduction or survival, or survival itself.

On the right, RPE represents a mutualism based on ants foraging on an extrafloral nectary-bearing plant for energy (RPE-EFN Plant). The RPE-EFN Plant is the quantity of energy assimilated; this energy can be used for survival or energetic needs of foraging. Quantity, the volume of nectar collected, is determined by the number of visits and the volume of nectar collected per visit. Quality, the amount of energy assimilated per unit volume of nectar, is a function of the energy concentration of nectar and energy assimilation efficiency. These metrics are quantifiable through chemical analysis and physiological measurements. Considering more obligate, symbiotic plant protection mutualisms, additional resources (e.g. food bodies) and benefits (colony growth) may be appropriate.

Rhizobial nitrogen fixing mutualism

Rhizobial nitrogen fixing mutualisms are bidirectional consumer-resource (Holland & DeAngelis 2010; Holland 2015) nutritional (Bronstein 2015) mutualisms. These are symbiotic but not obligate for either partner (Denison & Kiers 2011). When a rhizobium infects a root it massively proliferates in the root nodule by cloning. Some of these cells differentiate into bacteroids which are forms capable of fixing atmospheric nitrogen but which, at least in some systems, lose the ability to reproduce. It is thought that when the nodule senesces, undifferentiated 'descendant' rhizobia capable of reproduction escape to the soil. The primary resource provided by the plant to rhizobia is carbon for energy and building blocks, although energy-rich polyhydroxybutyrate (PHB) and phosphate may also be important resources improving descendant survival. In return, rhizobia provide plants with fixed nitrogen.

Figure 2d represents our application of the framework to the rhizobial nitrogen fixing mutualism. Rhizobial effectiveness (RE), on the left, is height growth achieved by a plant; increased growth provides resources that can be allocated to survival and reproduction. Quantity, the number of nodules produced, is a function of the number of CFUs (colony forming units) and the number of nodules produced per CFU. Quality, the plant height growth produced per nodule, is a function of the amount of nitrogen fixed per nodule and the height growth produced per unit nitrogen. Other fitness proxies include plant biomass and reproduction; we chose height growth in our example to better match the effectiveness landscape presented in Fig. 3. Nodule production and some measure of fitness consequences of nodule production can be quantified (e.g. Jia *et al.* 2013). The proposed subcomponents are more challenging to measure, but these challenges do not appear insurmountable.

The RPE of a legume in symbiosis with rhizobia (RPE-Legume), presented on the right, assumes the primary benefit to the rhizobia is carbon gained. RPE-Legume is the number of descendants released to the soil, which has clear linkages to population growth and individual fitness. Quantity, the number of descendants initiated, is a function of the quantity of carbon assimilated and the number of descendants initiated per unit carbon. Quality, the probability an initiated descendant produces an established descendant in the soil, is a function of the probability an initiated descendant remains undifferentiated into a N-Fixing bacteroid and is thus still capable of reproduction and the probability an undifferentiated descendant is released into the soil and survives. Estimates have been made of the number of rhizobial descendants in individual nodules and whole plants (Denison & Kiers 2011) and it appears feasible to experimentally estimate the release of descendants back into the soil, though to the best of our knowledge this has not been carried out. It is less clear that estimating the proposed subcomponents is technically feasible at this point.

Mycorrhizal mutualism

Mycorrhizal mutualisms are bidirectional consumer-resource (Holland & DeAngelis 2010; Holland 2015) nutritional (Bronstein 2015) mutualisms. Our example is based on the arbuscular mycorrhizal (AM) fungal mutualism, which is symbiotic and is obligate for the fungus but not for the plant (Denison & Kiers 2011). New plant roots are infected by hyphae from germinating spores or infected roots. The primary resource provided by the plant is carbon. In return, the fungus provides a variety of resource (e.g. phosphorous) and non-resource (e.g. protection against pathogens) benefits. This diversity of benefits that mycorrhiza provides complicates any analysis of effectiveness.

Our application of the framework to a mycorrhizal mutualism in Fig. 2e represents a system where the major benefit a plant receives is increased uptake of limited phosphorous. On the left, mycorrhizal effectiveness (ME) is plant biomass accumulated; biomass growth means increased resource availability for allocation to survival and reproduction. Quantity, the number of fine roots colonised, is a function of the number of fine roots and the probability a fine root is colonised. Quality, the biomass accumulated per colonised fine root, is a function of the amount of phosphorous uptake per colonised fine root and the biomass accumulated per unit phosphorous. Reproduction and survival are other desirable and achievable proxies for effectiveness more directly linked to fitness. Fine root colonisation of a subsample of roots and plant biomass, often for colonised and un-colonised plants, are measured in many mycorrhiza studies (e.g. Baum *et al.* 2000). Resource uptake, in this case phosphorous, is also measurable.

The RPE of a plant in symbiosis with mycorrhiza (RPE-Mycorrhizal Plant), on the right, is the number of new host plants infected, which is related to fungal fitness and population growth. This example assumes the primary route to infection of new plants is through spores rather than infected plant roots. However, a similar flowchart could be constructed based on reproduction through growth of the hyphal network. Quantity, the number of spores produced, is a function of the quantity of carbon assimilated from the plant and the number of spores produced per unit of carbon assimilated. Quality, the probability that a spore infects a new host plant, is a function of the probability a spore encounters a potential host and the probability that a spore successfully infects a new host plant it encounters. Both carbon assimilation by fungi

and spore production can be estimated (Denison & Kiers 2011). The feasibility of estimating the rates at which spores encounter roots and the probability a spore infects a root it encounters with present technology is not clear to us.

Effectiveness landscapes

An effectiveness landscape provides an intuitive, visual representation of effectiveness and the relative contributions of quantity and quality to effectiveness (Schupp *et al.* 2010). For example, an effectiveness landscape for a plant species has quantity as the *x*-axis and quality as the *y*-axis. By plotting the positions of animal mutualistic species based on their measured quantity and quality, one sees not only where each species lies in *x*–*y* space, but also where they lie on the effectiveness landscape represented by isoclines delineating all combinations of quantity and quality that yield the same effectiveness; this landscape rises in 'elevation' (effectiveness increases) from lower left to upper right. We present five preliminary effectiveness landscapes based on information extracted and/or calculated from published papers and relatively closely reflecting the respective mutualisms from Fig. 2. Because of the phytocentric bias of empirical work, we can only construct effectiveness landscapes for the left-hand panels of Fig. 2 depicting the effectiveness of an assemblage of mutualistic partners on some correlate of plant fitness. We use these to illustrate useful insights that can be obtained from our framework and related effectiveness landscapes. Code for estimating and plotting effectiveness landscapes with R is in Jordano (2014).

Figure 3a shows a SDE Landscape for the palm *Euterpe edulis* in the Atlantic forest of Brazil based on data in Rother *et al.* (2016). Quantity is the number of seeds dispersed per 10 h and quality is the probability that a dispersed seed produces an established seedling. Thus, SDE is the number of established seedlings produced from 10 h of dispersal activity. Figure 3b is a PE Landscape based on metrics calculated from Table 1 in Maldonado *et al.* (2013) and represents bees pollinating the cactus *Opuntia sulphurea*. Quantity is the number of pollen grains deposited on stigmas in a single visit whilst quality is the probability a pollen grain produces a seed. Thus, PE is the number of seeds produced per visit. Figure 3c is a PPE Landscape based on metrics calculated from the data in Appendix B of Ness *et al.* (2006) on ant protection of *Ferocactus wislizeni* in Arizona. Quantity is the number of 'herbivores' killed in 30 min, where 'herbivores' were experimental surrogate herbivores, quality is the proportional increase in fruit production per 'herbivore' killed, and PPE is the proportional increase in fruit production because of tending activities of a given ant species. Figure 3d is a RE Landscape using data (Jia *et al.* 2013) on five strains of the rhizobium *Ensifer meliloti* inoculating three cultivars of *Medicago sativa*. Quantity is the number of nodules developed after experimental inoculation, quality is plant height growth (mm) 50 days after sowing per nodule, and RE is the total plant height growth (mm). Figure 3e is a ME Landscape for two ectomycorrhizal strains (*Laccaria bicolor* and *Paxillus involutus*) infecting *Populus trichocarpa* on two different soils (Baum *et al.* 2000). Quantity is the number of fine roots colonised of 200

examined, quality is increased biomass per unit root colonisation after 6 month growth, and ME is increased biomass because of mycorrhiza. See Appendix S3 for more detailed explanations of the calculations.

What are the relative contributions of quantity and quality to effectiveness?

A valuable property of our framework as viewed through effectiveness landscapes (Fig. 3) is that it visually reveals the effectiveness structure of an assemblage of mutualists. We can easily see the contributions of quantity and quality to a mutualist's effectiveness. For example, the most effective seed disperser (*Turdus flavipes*, Turfla) has the highest value of SDE because it has high values of both quantity and quality (Fig. 3a). However, the most effective mutualist may be most effective primarily because of its quality, as *Centris brethesi* (Cen) in the PE Landscape (Fig. 3b), or primarily because of its quantity, as *Solenopsis xyloni* (Sxyl) in the PPE landscape (Fig. 3c). Mutualistic species even may be similarly effective for different reasons, as in the PPE Landscape (Fig. 3c); *Forelius* sp. (Fore), the mixed ant species assemblage (mixed), and *S. aurea* (Saur) all had similar PPEs, the first because of high quality, the last because of high quantity, and the mixed assemblage as a result of intermediate values of both. These insights can help tease apart those species that are adapted to their partners, because they presumably will have high values of quality, from those species that are effective simply because they are quantitatively important, perhaps only because they are abundant. This has further implications for the outcomes of mutualisms because at least in many mutualisms such as seed dispersal and pollination, quantity is likely more variable than quality in time, driven by the changes in the population sizes and availability of alternative resources. Thus, one might predict that partners whose effectiveness is determined primarily by quantity will be less consistent in effectiveness over time.

What is the distribution across the effectiveness landscape of an assemblage of mutualists?

Effectiveness landscapes also reveal the functional spread or variation amongst species of mutualists interacting with a single partner. Variation in effectiveness amongst species in an assemblage can be minimal, as in the PPE Landscape (Fig. 3c) and the ME Landscape (Fig. 3e) with less than two-fold variation, or extensive, as in the SDE Landscape (Fig. 3a) with roughly two orders of magnitude variation. These differences have implications for redundancy of services and for vulnerability of the mutualism to loss of particular partners. More revealing than the range in effectiveness is the overall distribution of species on the landscape. It is thought that most multi-specific assemblages are characterised by most species lying close to the lower left corner of the effectiveness landscape, whilst only a relatively small subset will be highly effective (Vázquez *et al.* 2005). None of our landscapes show precisely such an assemblage, although the SDE Landscape (Fig. 3a) suggests the existence of one to a few highly effective species and a larger number of less effective species. However, these landscapes also reveal suites of species with low quantity coupled with high quality; such species can increase their

effectiveness greatly with relatively modest increases in quantity (Schupp *et al.* 2010), for example, with changes in local abundance.

What can effectiveness landscapes reveal about the context dependence of mutualisms?

Effectiveness landscapes are very useful for exploring context dependency of mutualistic interactions, for example, by revealing how a single mutualist species changes its location on the landscape depending on year, population, habitat type, etc. For example, in the ME Landscape (Fig. 3e) both *L. bicolor* (Lbic) and *P. involutus* (Pinv) were more effective on the sandier Wildeshausen soil than on the less sandy Riesa soil. In addition, whilst the two species were equally effective on Riesa soil, *L. bicolor* was the most effective mutualist on Wildeshausen soil. In the RE Landscape (Fig. 3d), both the quantity and quality components of the RE of five strains of the rhizobium *E. meliloti* varied with the cultivar of *M. sativa* infected, though in different ways. For example, strain 13 012 varied primarily in quality whilst strain 83 164 varied primarily in quantity. Interestingly, despite large variation in quantity and quality across the combinations of rhizobial strain and plant cultivar, RE varied only modestly.

Note that as long as subcomponents are multiplicative, landscapes can also be constructed for the components of effectiveness. For example, considering SDE, we can plot a quantity effectiveness landscape with the subcomponent (number of visits) on the *x*-axis and the subcomponent (number of seeds dispersed per visit) on the *y*-axis (Schupp *et al.* 2010).

FLEXIBILITY OF THE FRAMEWORK

The framework is adaptable to more complex mutualistic interactions than discussed so far, such as diplochorous seed dispersal systems where diplochory does not just add one or more additional species of dispersers, but rather adds a separate sequential stage of dispersal (Phase II) that interacts with the original pattern of dispersal (Phase I). For example, it has been used to tease out the contributions of Phase I (bird) and Phase II (ant) dispersal to SDE in *Erythroxylum ambiguum* in a Brazilian Atlantic forest (Camargo *et al.* 2016). Similarly, it has been modified to compare the SDE of Phase I dispersal with the SDE of combined Phase I and Phase II dispersal to quantify the additional fitness benefits of Phase II dispersal in diplochorous systems (Culot *et al.* 2015).

POTENTIAL LIMITATIONS

One potential limitation of our approach is that it focusses on mean responses whilst generally ignoring intraspecific trait variation, an issue that is of growing interest in ecology and evolution (Bolnick *et al.* 2011). For example, intraspecific variation in fruit diameter can influence the probability of a fruiting plant having its seeds dispersed and, if dispersed, whether they are regurgitated or passed through the digestive track (Hernández 2009; Lotan & Izhaki 2013). Second, our approach cannot easily capture potentially critical rare events, such as a long distance pollen dispersal event that alters the probability of seed production. Nonetheless, if sampling is

well-designed we believe our framework can provide a very reasonable quantification of population-level outcomes of the interaction and the processes leading to those outcomes. In addition, whilst most empirical studies of effectiveness do focus on population means, our approach does not preclude the incorporation of variability. Calviño-Cancela & Martín-Herrero (2009) used bootstrapped stochastic simulation models parametrized with field data to acknowledge uncertainty in transition probabilities, resulting in the generation of standard deviations of quantity, quality, and effectiveness. Similarly, Rodríguez-Rodríguez *et al.* (2013, fig. 2) present a PE Landscape with standard deviations for quantity and quality components of effectiveness.

RELATIONSHIP TO INTERACTION STRENGTH

Our effectiveness metric can be related to what in food webs and predator-prey interactions is called interaction strength, a concept recently expanded to mutualisms (Vázquez *et al.* 2015). Although many definitions and measures of interaction strength exist, our effectiveness is perhaps most similar to the notion of interaction strength as the short-term effect of one individual on an individual of another species ('*per-capita* interaction strength' *sensu* Wooton & Emmerson 2005). Nonetheless, there are clear distinctions between an interaction strength perspective of mutualisms and our effectiveness framework. Interaction strength generally focusses on the effects of an individual on either another individual or the average individual in the population, and does this by modelling population growth. Our effectiveness framework primarily focusses on the effects of one population on another population, and does this by quantifying the outcomes of the mutualistic interaction as it exists in the present. In addition, our effectiveness framework can be used in both evolutionary and ecological contexts, if effectiveness is measured in terms of fitness differences or population growth, respectively.

CONCLUSION

Because of inherent complexities of biological interactions, enormous variation of key natural history details, and logistical difficulties, the empirical application of our framework will require flexibility, just as studies of mutualisms in general have always required flexibility. However, we argue that the consistent use of such a framework will help advance our understanding of the ecology and evolution of plant-animal mutualisms. This framework highlights the critical importance of considering fitness and/or demographic consequences of the interaction. It also clearly distinguishes immediate quantitative outcomes of the interaction from delayed, post-interaction qualitative outcomes – both are crucial for understanding these interactions. At least in principle it can quantify the fitness consequences of interactions in a way that can tease apart the relative contributions of different factors. For example, does quantity or quality have a greater impact? And if it is quantity, is this because of a greater number of visits or a greater number of immediate outcomes per visit? In addition, if structured comparably across studies, this framework provides a means to compare effectiveness of mutualisms across

species, within a species across populations, within a population across years, and more. Lastly, maintaining this framework as an overall organising structure for viewing the outcomes of mutualisms does not preclude focussing on only certain aspects of effectiveness. For example, if the interest is in understanding differences amongst flower visitors in pollen deposition and what drives those differences then studying only the quantity component of PE and its subcomponents is valid. However, this should not be confounded with effectiveness. Overall, our effectiveness framework provides a useful conceptual tool to assess the extreme diversity of outcomes in mutualisms, and to properly characterise their enormous context dependency.

AUTHORSHIP

This paper was conceived, developed, written, and revised by all authors.

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