

Research

Resource conversion: a generalizable mechanism for resource-mediated positive species interactions

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Positive species interactions are ubiquitous in natural communities, but the mechanisms through which they operate are poorly understood. One proposed mechanism is resource conversion – the conversion by a benefactor species of a resource from a resource state that is inaccessible to a potential beneficiary species into a resource state that is accessible. Such conversion often occurs as a byproduct of resource consumption, and sometimes in exchange for non-resource benefits to the benefactor species. At least five known classes of interactions, including both facilitative and mutualistic ones, may be classified as resource conversion interactions. We formulated a generalizable mathematical model for resource conversion interactions and examined two model variants that represent processing chain and nurse plant interactions. We examined the conditions under which these conformed to the stress-gradient hypothesis (SGH), which predicts increased interaction benefits in more stressful environments. These yielded four key insights: 1) resource conversion interactions can be positive (towards the resource recipient) only when facilitator-mediated resource conversion is more efficient than the baseline, spontaneous, facilitator-independent resource conversion; 2) the sign of resource conversion interaction outcomes never switches (e.g. from net positive to net negative) with changing levels of resource availability, when all other parameters are kept constant; 3) processing chain interactions at equilibrium can never be positive in a manner that conforms to the SGH; 4) nurse plant interactions can be positive and conform to the SGH, although the manner in which they do depends largely on how resource stress is defined, and the environmental supply rate of surface soil moisture. The first two insights are likely to be generalizable across all resource conversion interactions. The general agreement of the model with empirical studies suggest that resource conversion is the mechanism underlying the aforementioned interactions, and an ecologically meaningful way of classifying these previously unassociated positive species interactions.

Keywords: nurse plant facilitation, nutritional mutualism, processing chain commensalism, stress-gradient hypothesis, substitutable resource

Introduction

Positive species interactions are ubiquitous in natural communities (Stachowicz 2001), but our understanding of them has been poor in comparison to our understanding of negative species interactions such as competition and predation (Bruno et al. 2003, Brooker et al. 2008). This lag in conceptual synthesis is caused in part by 1) the lack of clear distinctions between facilitation and mutualism (Bronstein 2009), and 2) the lack of a mechanistic understanding of many positive species interactions (Soliveres et al. 2015, Michalet and Pugnaire 2016). Furthermore, the sign and magnitude of the interaction effect often change considerably with the environmental contexts, such as resource abundances, environmental stresses, partner densities, etc., in which the interaction occurs. This phenomenon is known as conditionality or context dependency, and poses an additional challenge for the study of positive species interactions because it is often difficult to predict the magnitude and direction of changes in interaction strengths.

The definitions of facilitation and mutualism overlap significantly (Stachowicz 2001, Brooker et al. 2008), and the separation that exists between them owes more to the different historical backgrounds of these fields than to identifiable biological or ecological differences (Bronstein 2009). Bronstein (2009) argued that facilitation is distinguished from mutualism by being restricted to positive species interactions that are local (i.e. interactions that involve cross-community transactions, such as pollination and dispersal, are not classified as facilitative), and that occur between individuals of the same trophic level. It may be added that mutualism refers to interactions that largely benefit both partners in the interaction, while facilitation may encompass interactions that yield primarily one-sided benefits (Bruno et al. 2003). Despite these efforts in clarifying definitions, many positive species interactions still have to be classified as both facilitative and mutualistic (Bronstein 2009, Z  l   et al. 2018).

The lack of a mechanistic understanding of many positive species interactions is especially evident in the correlative/phenomenological approaches taken in many studies of plant–plant facilitation (Michalet and Pugnaire 2016), and in the use of mutualism categories which are insufficiently mechanism-specific. An example of the latter is seen in the category of mutualisms known as ‘nutritional symbioses/mutualisms’. Nutritional symbioses/mutualisms are a large group of positive species interactions encompassing plant–mycorrhizal, coral–zooxanthellae, bark beetle–fungus, fungus–leaf cutter ant mutualisms, etc. and entail the partner-facilitated resource acquisition of at least one species in an interaction (Bronstein 2015). However, it was recently pointed out that interactions previously grouped under this broad category actually operate through at least two distinct mechanisms, which may be termed resource exchange and resource conversion (Lam and Tan 2019). This distinction better reflects the ecological, resource-mediated mechanisms that stabilize both subcategories of interactions.

Resource exchange mutualisms include the plant–mycorrhizal and coral–zooxanthellae symbioses, and have been shown to be bidirectional mutualisms that involve the mutual trade of essential resources (Schwartz and Hoeksema 1998, Hoeksema and Schwartz 2003, McGill 2005, de Mazancourt and Schwartz 2010). Essential resources are resources which must be consumed by a species for survival, and that cannot be substituted with alternatives (Tilman 1980, Chase and Leibold 2003). In such interactions, each species supplies its partner with an essential resource which is limiting to the fitness of its partner, but which it is able to acquire in excess (Schwartz and Hoeksema 1998, Hoeksema and Schwartz 2003, de Mazancourt and Schwartz 2010). Resource conversion mutualisms include hemiptera–ant and gut microbiota–host interactions, and involve the conversion of a resource from a resource state that is inaccessible to one species into a resource state that is accessible to it, by its partner. This conversion often occurs as a byproduct of resource consumption by the resource processor, which in turn often receives some non-resource benefits such as protection or domicile from the resource recipient. Importantly, resource conversion mutualisms operate through substitutable (with respect to the resource recipient) rather than essential resources (Lam and Tan 2019). Two resources are substitutable if population growth can be maintained in the absence of either by consumption of the other (Tilman 1980, Chase and Leibold 2003). In hemiptera–ant interactions, hemiptera feed on sugar-rich phloem sap, and excrete a portion of these sugars in the form of honeydew, which is collected by ants (Way 1963). The ants do not supply the hemiptera with any resources, but instead provide them with the non-resource benefit of protection from predators (Way 1963). Ants are unable to harvest phloem sap without assistance from hemiptera, but are known to abandon their hemiptera partners and/or prey upon them when offered alternative sugar sources (Offenberg 2001), which clearly demonstrates the substitutable nature of this resource (sugars or carbohydrates) with respect to the ants.

Resource conversion is also the underlying mechanism in several other types of positive species interactions, although these have not previously been classified as nutritional symbioses/mutualisms in the literature (Table 1). In processing chain commensalisms (Fig. 1b; hereafter referred to as processing chain interactions for generalizability), an ‘upstream consumer’ (the resource processor) converts an inaccessible resource into a more accessible one, typically through its excrement or byproducts of the consumption process, for a ‘downstream consumer’ (the resource recipient) (Heard 1994b). In nurse plant facilitation (Fig. 1c; hereafter referred to as nurse plant interactions for generalizability), a nurse plant increases surface soil moisture under its canopy as it draws up groundwater deep in the soil using tap roots, and thus facilitates seedling and/or herbaceous species recruitment around it (Prieto et al. 2010, 2011, Armas et al. 2012). As deep groundwater sources are largely inaccessible to shallow-rooted seedlings or herbaceous plant species, a nurse

Table 1. Types of resource conversion interactions (rows), examples of them, and the modifications to the basic model required to model each of these (a tick represents the inclusion of the relevant process in the model). The first two interactions (which do not involve non-resource benefits) are commensal or unidirectional in nature, while the last three (which all involve non-resource benefits) are mutualistic or bidirectional in nature.

Type of substitutable resource facilitation	Examples	Facilitator-independent resource conversion (arrow a in Fig. 1a)	Non-resource benefits (arrow b in Fig. 1a)	Environmental supply of resource 2 (S_2 in Fig. 1a)	Other modification (arrow c in Fig. 1a)
(a) Commensalistic interactions					
Processing chain commensalism	Midge–mosquito larva ¹ Scirtid–mosquito larva ² Ammonia oxidizing–nitrite oxidizing bacteria (nitrification cycle) ³	✓			
Nurse plant facilitation	Nurse plant–seedling ⁴	✓		✓	
(b) Mutualistic interactions					
Classical nutritional-protective mutualism	Fungal–leaf cutter ant ⁵ Hemipteran–ant ⁶ Lycaenidae–ant ⁷		✓		
Prey capture facilitation	Bat–pitcher plant ⁸ Crab spider–pitcher plant ⁹	✓	✓		
Digestive mutualism	Fungus–bark beetle ⁵ Gut microbiota–host ¹⁰ Hemiptera–Roridula ¹¹ Inquiline–pitcher plant ¹²	✓	✓		✓

¹ Heard 1994a

² Paradise 1999.

³ Prosser 1990.

⁴ Prieto et al. 2010, 2011, Armas et al. 2012.

⁵ Bronstein 2015.

⁶ Way 1963.

⁷ Pierce et al. 2002.

⁸ Schöner et al. 2017.

⁹ Lam and Tan 2019.

¹⁰ Bäckhed et al. 2005.

¹¹ Ellis and Midgley 1996.

¹² Lam et al. 2017.

plant effectively converts an inaccessible resource state into one that is accessible to its partners. In classical nutritional-protective mutualisms (Fig. 1d), such as the ant–hemiptera interaction described above, one species makes an inaccessible nutritional resource available to its partner in exchange for a non-resource benefit such as protection/domicile. In prey/resource capture facilitation (Fig. 1e), a free-living species shares the resource pool with its partner, but is more efficient in capturing this resource, and benefits the resource recipient through a nutritional byproduct of resource capture in exchange for non-resource benefits such as protection/domicile (Schöner et al. 2017, Lim et al. 2018). Digestive mutualisms (Fig. 1f) are like processing chain interactions in which the resource processor is an endosymbiont or inquiline species that lives in/upon its host, the resource recipient, and processes food resources that are consumed/captured by its host (Anderson and Midgley 2003). In each of these cases, the resources are substitutable with respect to the resource recipient, and are often merely different states of a single underlying resource ‘currency’ (Lam and Tan 2019), yet the resource recipient is hindered from directly consuming the upstream resource for reasons that are specific to each system.

Processing chain and nurse plant interactions are seldom recognized as cases of ‘nutritional mutualisms’, perhaps because the benefit in such interactions is often unidirectional, but the underlying mechanism of resource conversion between them and the other classes of interactions described above is clearly analogous (Lim et al. 2018). Some authors have observed that many evolutionarily independent interspecific interactions are mechanistically convergent – a phenomenon that has come to be known as ‘convergent interactions’ (Bittleston et al. 2016) – and this appears to be so with the examples of resource conversion reviewed here. Such a convergence offers itself as a unifying mechanism that could promote conceptual syntheses and generalization between systems.

Conditionality, or context dependency, is a hallmark of positive species interactions (Bronstein 1994, Chamberlain et al. 2014), and is well reported in both mutualism and facilitation (Bronstein 2009). The stress-gradient hypothesis (SGH) is a product of plant–plant facilitation research (Bertness and Callaway 1994, Brooker et al. 2008, Maestre et al. 2009), and predicts that positive species interactions are stronger and more abundant in communities experiencing high stress. In this regard, the SGH may be understood as

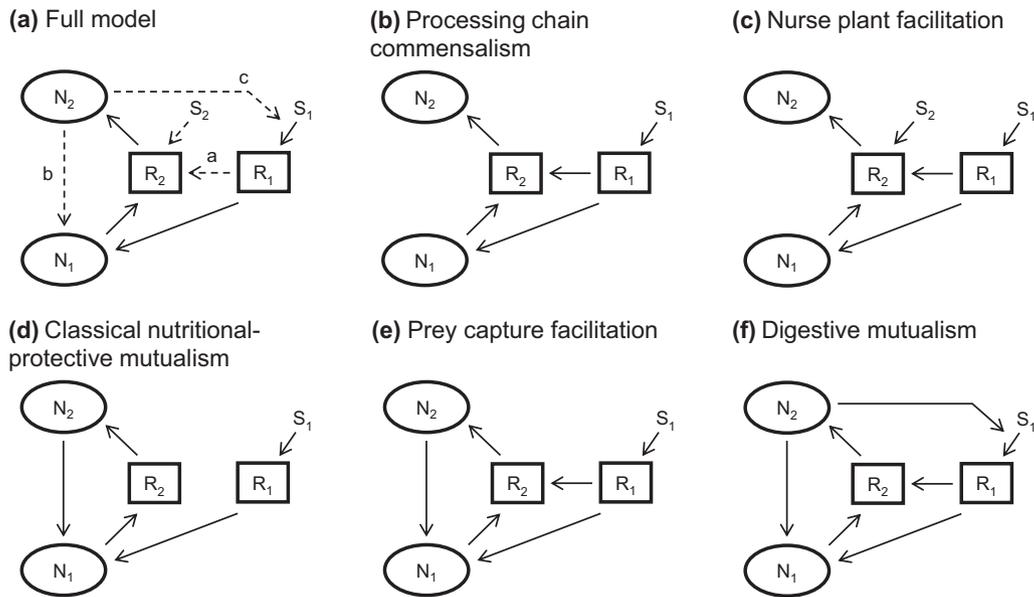


Figure 1. Box and arrow conceptual diagrams of the underlying mechanism behind resource conversion interactions. In panel (a), the full model with all possible secondary processes is shown, with solid lines representing processes which are common across all resource conversion interactions, and dashed arrows to processes which are specific to subsets of them. In panels (b–f), five variants of the full model, representing the types of interactions shown in Table 1, are shown. N_1 = population density of the resource processor, species 1; N_2 = population density of the resource recipient, species 2; R_1 = density of the resource or resource state that is inaccessible to the resource recipient species; R_2 = density of the resource or resource state that is accessible to the resource recipient species; S_1 or S_2 = supply rate of resource 1 or 2.

‘a phenomenological perspective of a specific case of context dependency, where the context considered is the intensity of environmental stress’ (Lim et al. 2018). Stress may be divided into categories of resource (e.g. soil moisture in a xeric plant community) or non-resource (e.g. salinity in an intertidal invertebrate community) stress, and stress-ameliorative facilitation in these two categories of interactions may differ significantly (Maestre et al. 2009). Although the SGH was originally applied to positive species interactions (Bertness and Callaway 1994), it has been used extensively to describe the weakening of negative species interactions under conditions of increasing stress as well (Fugère et al. 2012, He et al. 2013), albeit in interactions that presumably could be positive under certain circumstances. We thus follow this practice throughout this study, and include reductions in competition or ammensalism with increasing stress within the definition of the SGH.

Convergence between mutualistic and facilitative resource conversion interactions suggests that the SGH or context dependency phenomena resulting from them should be similarly convergent (at least under a subset of conditions), and empirical studies have largely found this to be true. Greater net benefit under conditions of greater resource stress, as predicted by the SGH, has been demonstrated in processing chain interaction (Fugère et al. 2012), nurse plant facilitation (He et al. 2013), prey capture facilitation (Lim et al. 2018), nutritional–protective mutualism (Offenberg 2001) and digestive mutualism (Sanders et al. 2017, Leong et al. 2018). However, empirical studies do not reveal if these interactions, and the phenomena resulting from them, are ecologically stable, or if they are non-equilibrium transitory states (e.g.

time stages in succession, positive interactions with recently introduced alien species, etc.), or merely incidental/spurious findings (e.g. if sampled populations occur within ecological traps and thus provide benefit for partners in unsustainable ways). This is because it is often logistically impossible to follow the populations of interacting species through multiple generations to observe the long-term outcomes of interactions. Consumer–resource type models are dynamic models which describe the population densities of species as functions of resource availabilities, and are widely used in competition and niche theory to evaluate the potential of competing species to coexist (Tilman 1980, Chase and Leibold 2003). Consumer–resource models have been adapted increasingly for the modelling of positive species interactions in recent years (Gross 2008, de Mazancourt and Schwartz 2010, Lee and Inouye 2010, Butler and O’Dwyer 2018, Dangles 2019, Johnson and Bronstein 2019). Consumer–resource type models of resource trade mutualisms predict that such interactions yield greater net nutritional benefits for both partners when environmental resource abundances are low (de Mazancourt and Schwartz 2010) – a prediction that agrees well with the SGH. However, the only comparable model of resource conversion known to date is the processing chain model developed by Heard (1994a), but this model has not been developed or applied to systems other than processing chain commensalisms. It is thus the aim of this study to develop a generalizable, population-based mechanistic model for resource conversion interactions, and to evaluate the conditions under which a net positive effect and the SGH can occur in such a model.

The model

Specifying the model

The model involves two species with population densities N_i and two substitutable resources with resource densities R_j (Fig. 1). Species 1 is the resource processor, and converts a resource (R_1) which is inaccessible (difficult to capture or process) to species 2, the resource recipient, into a resource that is more accessible to it (R_2) in the process of feeding on it. Several variants of the model may be implemented, representing different types of resource conversion interactions (Table 1). Differences between these models are reflected in the varying combinations of secondary processes (Table 1; dashed arrows labelled a, b, c and S_2 in Fig. 1a) acting alongside the primary underlying mechanism (solid arrows in Fig. 1a). We identify five principle types of resource conversion interactions, namely processing chain commensalism, nurse plant facilitation, classical nutritional–protective mutualism, prey capture facilitation and digestive mutualism (Table 1, Fig. 1). Two of these, namely processing chain commensalism and nurse plant facilitation, are primarily commensal or unidirectional (Table 1, Fig. 1b–c), while three, namely classical nutritional–protective mutualism, prey capture facilitation and digestive mutualism, are primarily mutualistic or bidirectional (Table 1, Fig. 1d–f).

Processing chain interaction

Processing chain interactions are most extensively studied in aquatic invertebrate detritivore communities (Heard 1994a, Paradise and Dunson 1997, Daugherty and Juliano 2002, Juliano 2009). The feeding activities of the resource processor (species 1 in our model; also known as the ‘upstream consumer’ in the literature) results in the production of a downstream resource or resource state (often smaller particles of detritus) that can be fed upon by the resource recipient (species 2 in our model; also known as the ‘downstream consumer’ in the literature). Resource conversion may also occur spontaneously via microbial decomposition and/or geochemical processes (Heard 1994a, Daugherty and Juliano 2002). The model (Fig. 1b) is very similar to the one proposed by Heard (1994a), except that a resource loss term for the downstream resource is not included in this model.

$$\begin{aligned}\frac{dN_1}{dt} &= N_1 (f_{11}\alpha_{11}R_1 - d_1) \\ \frac{dN_2}{dt} &= N_2 (f_{22}\alpha_{22}R_2 - d_2) \\ \frac{dR_1}{dt} &= c_1(S_1 - R_1) - f_{11}N_1R_1 - nR_1 \\ \frac{dR_2}{dt} &= mf_{11}N_1R_1 + nR_1 - f_{22}N_2R_2\end{aligned}\quad (1.0)$$

The model is adapted from the consumer–resource family of models (Tilman 1980), which underlie contemporary niche models (Chase and Leibold 2003). For simplicity, the linear variant (rather than the Monod variant) of the model is used. That is, population growth is a linear (rather than saturating) function of a species’ consumption of a resource.

In this model, f_{ij} is the per capita feeding rate of species i on resource j ; α_{ij} is the efficiency at which species i converts each unit of resource j consumed into new individuals of species i ; d_i is the per capita mortality rate of species i ; c_1 is the resource 1 turnover rate constant; S_1 is the supply rate of resource 1; n is the efficiency of spontaneous, unfacilitated conversion of resource 1 into resource 2; and m is the efficiency of conversion of resource 1 into resource 2 by species 1 (Supplementary material Appendix 1 Table A1). All parameters in this model are positive, with the additional restrictions $0 \leq m < 1$ and $0 \leq n < 1$ as these parameters represent proportions.

We solved the system at steady state by setting the right-hand sides of all four equations to zero, yielding two equilibria. We term the first the species 2-dominant equilibrium, although it must be noted that the absence of species 1 from this equilibrium is caused by the values of its growth parameter with respect to the supply of resource 1, and not by competitive exclusion by species 2, since the latter does not consume resource 1 and thus cannot compete with species 1:

$$\begin{aligned}\bar{N}_{1,\text{sp2.dom}} &= 0 \\ \bar{N}_{2,\text{sp2.dom}} &= \frac{nc_1S_1\alpha_{22}}{(n+c_1)d_2} \\ \bar{R}_{1,\text{sp2.dom}} &= \frac{c_1S_1}{n+c_1} \\ \bar{R}_{2,\text{sp2.dom}} &= \frac{d_2}{f_{22}\alpha_{22}}\end{aligned}$$

The second may be termed the coexistence equilibrium:

$$\begin{aligned}\bar{N}_{1,\text{coexist}} &= \frac{c_1S_1\alpha_{11}}{d_1} - \frac{n+c_1}{f_{11}} \\ \bar{N}_{2,\text{coexist}} &= \frac{((n-mn-mc_1)d_1 + mc_1f_{11}S_1\alpha_{11})\alpha_{22}}{d_2f_{11}\alpha_{11}} \\ \bar{R}_{1,\text{coexist}} &= \frac{d_1}{f_{11}\alpha_{11}} \\ \bar{R}_{2,\text{coexist}} &= \frac{d_2}{f_{22}\alpha_{22}}\end{aligned}$$

The local stability of each equilibrium was then examined using a Jacobian matrix, and the stability criteria were found to be (Supplementary material Appendix 1):

Species 2-dominant equilibrium:

$$\frac{c_1 S_1}{n + c_1} < \frac{d_1}{f_{11} \alpha_{11}} \quad (1.1)$$

Coexistence equilibrium:

$$\frac{c_1 S_1}{n + c_1} > \frac{d_1}{f_{11} \alpha_{11}} \quad (1.2)$$

These two conditions are mutually exclusive, and are furthermore equivalent to $\bar{R}_{1,sp2.dom} \leq \bar{R}_{1,coexist}$ (Eq. 1.1) or the reverse (Eq. 1.2), respectively. $\bar{R}_{1,sp2.dom}$ is analogous to Tilman's (1980) R^* . Condition 1.2 is also equivalent to the condition for the coexistence equilibrium to be well defined (all state variables positive; the trivial equilibrium is always well-defined). In Tilman's models, the condition for persistence of a species is that $R_i^* < S_i$ – that is, the supply rate of the resource exceeds its R^* or the minimum density of that resource required by the species for its death rate to be perfectly balanced by growth/birth resulting from resource consumption (Chase and Leibold 2003). In this model, the condition determining the persistence of species 1 (species 2 always persists) is similar, except that the availability of resource 1 is reduced by its natural loss through resource turnover (c_1) and facilitator-independent conversion into another resource state (n). Thus the condition for species 2's persistence is not $\frac{d_1}{f_{11} \alpha_{11}} < S_1$ (as in Chase and Leibold 2003) but instead (Eq. 1.2).

We evaluated the conditions under which the interaction has a net positive effect on species 2 (the resource recipient or downstream consumer). This may be calculated as either an absolute or relative effect – both types of effects are commonly reported in the literature, and the choice of absolute or relative effect can affect the interpretation of the SGH (Holmgren and Scheffer 2010). The absolute effect (AE) is simply the increase in the resource recipient's equilibrium population density as a result of its interaction with species 1:

$$AE = \bar{N}_{2,coexist} - \bar{N}_{2,sp2.dom}$$

$$AE = \frac{(mn + mc_1 - n)(c_1 f_{11} S_1 \alpha_{11} - (n + c_1) d_1) \alpha_{22}}{(n + c_1) d_2 f_{11} \alpha_{11}} \quad (1.3.1)$$

The relative effect may be calculated using the relative interaction index (RII) (Armas et al. 2004):

$$RII = \frac{\bar{N}_{2,coexist} - \bar{N}_{2,sp2.dom}}{\bar{N}_{2,coexist} + \bar{N}_{2,sp2.dom}} \quad (1.3.2)$$

$$= \frac{(mn + mc_1 - n)((n + c_1) d_1 - c_1 f_{11} S_1 \alpha_{11})}{(n + c_1)(mn + mc_1 - n) d_1 - c_1 f_{11} S_1 \alpha_{11} (n + mn + mc_1)}$$

For the interaction to have a net positive effect on species 2, Eq. 1.3.1 and/or 1.3.2 must be positive, and the coexistence conditions must be satisfied – that is, Eq. 1.2 must hold. In this model, the signs of both AE (Eq. 1.3.1) and RII (Eq. 1.3.2) are determined by one common condition:

$$m > \frac{n}{n + c_1} \quad (1.4)$$

To interpret this condition biologically, observe that in the baseline scenario where species 1 is absent (i.e. at the species 2-dominant equilibrium), the loss of resource 1 is governed only by its turnover rate and facilitator-independent processing, and the baseline conversion efficiency of resource 1 to resource 2 is

$$\text{Baseline conversion efficiency} = \frac{n R_1}{n R_1 + c R_1} = \frac{n}{n + c}$$

which is the right-hand side of Eq. 1.4. Similarly, the conversion efficiency of species 1 can be calculated as

$$\text{Species 1 conversion efficiency} = \frac{m f_{11} N_1 R_1}{m f_{11} N_1 R_1 + (1 - m) f_{11} N_1 R_1} = m$$

which is the left-hand side in Eq. 1.4.

Thus, the condition in Eq. 1.4 states that the absolute (AE) and/or relative (RII) effect of species 1 on species 2 is positive when species 1's resource conversion efficiency is higher than the baseline facilitator-independent conversion efficiency. This finding is intuitive, and in agreement with that of Heard (1994a).

Obligacy is a special case of positive interspecific effect when species 2 is so reliant on species 1 that it cannot survive without it. Mathematically, obligacy occurs when $N_{2,sp2.dom} < 0$, given that the conditions for stable coexistence hold (Eq. 1.2). In the processing chain model, this reduces to the condition that $n = 0$, which means that spontaneous conversion of the resource does not occur – a condition which is arguably true for such processing chain interactions as found in the nitrification cycle (Prosser 1990).

Context dependency

The outcome of positive species interactions tends to be context dependent (Chamberlain et al. 2014), that is, the positive effects of an interaction may be accentuated or lost according to the environmental contexts in which an interaction occurs. To examine this, we obtained the partial derivatives of AE and RII with respect to the environmental supply of resource 1 (i.e. S_1):

$$\frac{\partial AE}{\partial S_1} = \frac{c_1 (mn + mc_1 - n) \alpha_{22}}{(n + c_1) d_2} \quad (1.5.1)$$

$$\frac{\partial RII}{\partial S_1} = \frac{(mn + mc_1 - n)((n + c_1) d_1 - c_1 f_{11} S_1 \alpha_{11})}{(n + c_1)(mn + mc_1 - n) d_1 - c_1 f_{11} S_1 \alpha_{11} (n + mn + mc_1)} \quad (1.5.2)$$

Equation 1.5.1–2 were then evaluated under coexistence equilibrium conditions, that is, when Eq. 1.2 holds. Both Eq. 1.5.1–2 were found to be negative when a single condition is fulfilled:

$$m < \frac{n}{n + c_1}$$

This is exactly the reverse condition of Eq. 1.4, which is the condition necessary for the interaction to have a net positive effect on species 2. This means that when $m < \frac{n}{n + c_1}$ (i.e. species 1's resource conversion efficiency is lower than the baseline resource conversion efficiency), the interaction outcome is always negative (ammensalistic with respect to species 2), and becomes increasingly negative with increasing S_1 (Fig. 2). Conversely, when $m > \frac{n}{n + c_1}$ (i.e. species 1's resource conversion efficiency is higher than the baseline resource conversion efficiency), the interaction outcome is always positive (commensalistic with respect to species 2), and increases with S_1 (Fig. 2). Because the RII is an asymptotic index (Armas et al. 2004), in both cases RII asymptotes at $\frac{mn + mc_1 - n}{n + mn + mc_1}$ at high values of S_1 (Fig. 2). The SGH – an increasing interaction effect value with decreasing resource supply (S_1) – can only hold when the interaction has a net negative effect on the resource recipient species (Fig. 2).

Nurse plant model

Nurse plant interaction is a type of plant–plant interaction that is prevalent in arid–semi-arid habitats. The term is also used for cushion plants in alpine or arctic environments. However, in those cases, the stress factor (cold) and facilitative mechanism (wind shielding) are categorically different, and we thus refer only to water resource facilitation in arid–semi-arid habitats in our interpretations of our model here. Nurse plants are usually larger, xeromorphic plant species that are capable of tolerating dry conditions, and are able to draw up groundwater resources through deep tap roots (Beltran et al. 2012). The utilization of such groundwater resources inadvertently leads to the leakage of some moisture to surface soils around nurse plants through a process known as hydraulic lifting (Prieto et al. 2010, 2011, Armas et al. 2012). Plants growing under the nurse plant often have shallow root systems that are unable to access deep groundwater resources, but instead utilize this surface soil moisture and thus benefit from the presence of the nurse. Water movement through the soil column also occurs spontaneously via capillary action, at a rate that varies significantly across different soil profiles (Rushton 2005). The model includes this process as a facilitator-independent resource conversion term (n), which is simply a constant proportional rate of the density of the ground water resource. Although the supply of ground and surface soil water is arguably linked to precipitation rates, the two resources are modelled with separate supply processes ($c_j(S_j - R_j)$) because the geographical processes determining the availabilities of these water resources to plants often vary independently of each other (Rushton 2005), which is also why most hydrological models model groundwater and surface soil moisture separately (Graham and Butts 2005).

For example, occasional heavy rains interspersed by long periods of drought over a sandy-soil habitat can lead to high groundwater tables (large S_1) but low water availabilities in the surface soils (low S_2). Nurse plants may utilize surface soil moisture to a small degree as well, but we omit such a term (f_{12}) from the model for tractability. Instead, the resource conversion rate (m) in our model should be understood as a rate that has already been offset by a small amount of resource consumption by the nurse plant.

Conceptually, the nurse plant model is simply a processing chain model (Eq. 1.0) with an additional term on the dR_2/dt equation representing environmental cycling of resource 2 (Fig. 1c):

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 (f_{11}\alpha_{11}R_1 - d_1) \\ \frac{dN_2}{dt} &= N_2 (f_{22}\alpha_{22}R_2 - d_2) \\ \frac{dR_1}{dt} &= c_1 (S_1 - R_1) - f_{11}N_1R_1 - nR_1 \\ \frac{dR_2}{dt} &= c_2 (S_2 - R_2) - f_{22}N_2R_2 + mf_{11}N_1R_1 + nR_1 \end{aligned} \quad (2.0)$$

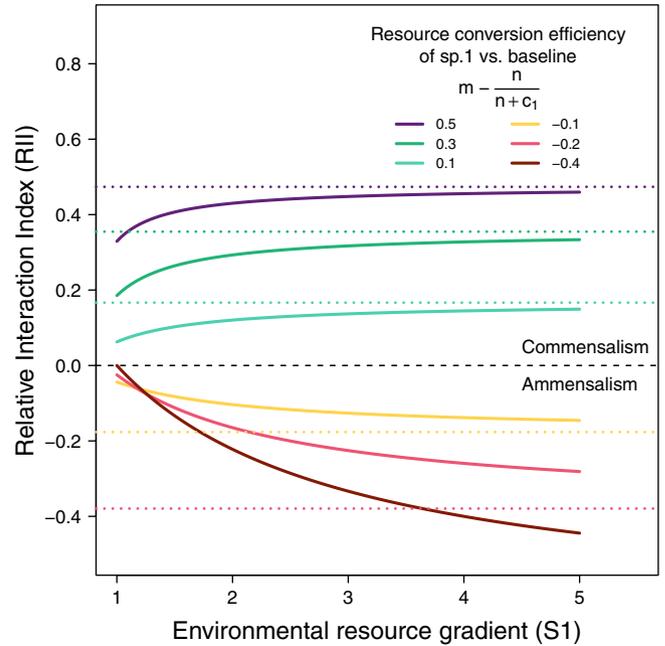


Figure 2. Relative effect (relative interaction index (RII)) of species 2 in a processing chain interaction, along a gradient of resource 1 supply rates (S_1). Continuous lines represent model predictions under varying parameter value combinations, and dotted lines represent asymptotic limits of predictions. Cool colors represent the parameter combinations where species 1's resource conversion efficiency is greater than that of the baseline, while warm colors represent parameter combinations where the baseline resource conversion efficiency is greater. Parameter values used to construct this and the next figure are: $c_1 = 0.5$, $d_1 = 0.5$, $d_2 = 0.5$, $\alpha_{11} = 1$, $\alpha_{22} = 1$, $f_{11} = 1$, $f_{22} = 1$.

All parameters in this model are positive, with the additional restrictions $0 \leq m < 1$ and $0 \leq n < 1$.

We solved the system at steady state by setting the right-hand sides of all four equations to zero, yielding four equilibria.

The first is the trivial equilibrium:

$$\begin{aligned}\bar{N}_{1,\text{trivial}} &= 0 \\ \bar{N}_{2,\text{trivial}} &= 0 \\ \bar{R}_{1,\text{trivial}} &= \frac{c_1 S_1}{n + c_1} \\ \bar{R}_{2,\text{trivial}} &= \frac{nc_1 S_1}{(n + c_1)c_2} + S_2\end{aligned}$$

The trivial equilibrium is always well-defined, and it can be shown (Supplementary material Appendix 2) that its stability criteria are:

$$\begin{aligned}\frac{c_1 S_1}{n + c_1} &< \frac{d_1}{f_{11}\alpha_{11}} \\ \frac{nc_1 S_1}{(n + c_1)c_2} + S_2 &< \frac{d_2}{f_{22}\alpha_{22}}\end{aligned}$$

It is evident that equilibrium resource densities are determined by the presence of their consumers (species 1 consumes only resource 1, and species 2 consumes only resource 2), thus they may be rewritten in terms of Tilman's (1980) R^* , the minimum equilibrium resource requirements of their consumers:

$$\begin{aligned}R_{1,\text{sp1}}^* &\equiv \frac{d_1}{f_{11}\alpha_{11}} \\ R_{2,\text{sp2}}^* &\equiv \frac{d_2}{f_{22}\alpha_{22}}\end{aligned}$$

The stability criteria of the trivial equilibrium may thus be expressed also as:

$$\begin{aligned}\bar{R}_{1,\text{trivial}} &< R_{1,\text{sp1}}^* \\ \bar{R}_{2,\text{trivial}} &< R_{2,\text{sp2}}^*\end{aligned}\quad (2.1.1)$$

The second equilibrium is the species 1-dominant equilibrium:

$$\begin{aligned}\bar{N}_{1,\text{sp1.dom}} &= \frac{c_1 S_1 \alpha_{11}}{d_1} - \frac{n + c_1}{f_{11}} \\ \bar{N}_{2,\text{sp1.dom}} &= 0 \\ \bar{R}_{1,\text{sp1.dom}} &= \frac{d_1}{f_{11}\alpha_{11}} \\ \bar{R}_{2,\text{sp1.dom}} &= \frac{mc_1 S_1 + \frac{(n - mn - mc_1)d_1}{f_{11}\alpha_{11}}}{c_2} + S_2\end{aligned}$$

For this equilibrium to be well-defined (none of the state variables may be negative under biologically valid conditions), we must have

$$S_1 > \frac{d_1(mn + mc_1 - n)}{c_1 f_{11} m \alpha_{11}} - \frac{c_2}{mc_1} S_2$$

This condition is equivalent to $\bar{R}_{2,\text{sp1.dom}} > 0$ and guarantees $\bar{N}_{1,\text{sp1.dom}} > 0$ (since $\frac{d_1(mn + mc_1 - n)}{c_1 f_{11} m \alpha_{11}} - \frac{c_2}{mc_1} S_2$ is necessarily less than $\frac{d_1(n + c_1)}{c_1 f_{11} \alpha_{11}}$).

It can be shown (Supplementary material Appendix 2) that the stability criteria for the species 1-dominant equilibrium are

$$\begin{aligned}R_{1,\text{sp1}}^* &< \bar{R}_{1,\text{trivial}} \\ \bar{R}_{2,\text{sp1.dom}} &< R_{2,\text{sp2}}^*\end{aligned}\quad (2.1.2)$$

The third equilibrium is the species 2-dominant equilibrium:

$$\begin{aligned}\bar{N}_{1,\text{sp2.dom}} &= 0 \\ \bar{N}_{2,\text{sp2.dom}} &= \frac{nc_1 S_1 \alpha_{22}}{(n + c_1)d_2} + c_2 \left(\frac{S_2 \alpha_{22}}{d_2} - \frac{1}{f_{22}} \right) \\ \bar{R}_{1,\text{sp2.dom}} &= \frac{c_1 S_1}{n + c_1} \\ \bar{R}_{2,\text{sp2.dom}} &= \frac{d_2}{f_{22}\alpha_{22}}\end{aligned}$$

This equilibrium has the stability criteria (these same criteria guarantee the equilibrium is well defined)

$$\begin{aligned}\bar{R}_{1,\text{trivial}} &< R_{1,\text{sp1}}^* \\ R_{2,\text{sp2}}^* &< \bar{R}_{2,\text{trivial}}\end{aligned}\quad (2.1.3)$$

The final equilibrium is the coexistence equilibrium:

$$\begin{aligned}\bar{N}_{1,\text{coexist}} &= \frac{c_1 S_1 \alpha_{11}}{d_1} - \frac{n + c_1}{f_{11}} \\ \bar{N}_{2,\text{coexist}} &= \frac{\left(mc_1 S_1 + \frac{(n - mn - mc_1)d_1}{f_{11}\alpha_{11}} \right) \alpha_{22} + c_2 \left(S_2 \alpha_{22} - \frac{d_2}{f_{22}} \right)}{d_2} \\ \bar{R}_{1,\text{coexist}} &= \frac{d_1}{f_{11}\alpha_{11}} \\ \bar{R}_{2,\text{coexist}} &= \frac{d_2}{f_{22}\alpha_{22}}\end{aligned}$$

The stability criteria for this equilibrium are (again these same criteria guarantee the equilibrium is well defined)

$$R_{1,sp1}^* < \bar{R}_{1,trivial}$$

$$R_{2,sp2}^* < \bar{R}_{2,sp1.dom} \quad (2.1.4)$$

It is evident, since $R_{1,sp1}^* \equiv \bar{R}_{1,sp1.dom} \equiv \bar{R}_{1,coexist} = \frac{d_1}{f_{11}\alpha_{11}}$ and

$$R_{2,sp2}^* \equiv \bar{R}_{2,sp2.dom} \equiv \bar{R}_{2,coexist} = \frac{d_2}{f_{22}\alpha_{22}},$$

that the stability criteria of the four equilibria are mutually exclusive of each other, and are furthermore consistent with those of the processing chain model (Table 2). We can thus summarize the results of the stability analysis verbally as follows: species 1 will be present at equilibrium if and only if the R^* value of species 1 is lower than the level to which resource 1 equilibrates in the absence of either species; species 2 will be present at equilibrium if either 1) species 1 is absent and the R^* value of species 2 is lower than the level to which resource 2 equilibrates in the absence of either species; or 2) species 1 is present and the R^* value of species 2 is lower than the level to which resource 2 equilibrates in the presence of just species 1. Thus the conditions for persistence of species 1 are independent of whether species 2 is present or not, but the conditions for persistence of species 2 are contingent on species 1. This is consistent with the biological interpretation of the nurse plant model, insofar as only resource-mediated interactions are considered.

We evaluated the conditions under which the interaction has a net positive effect on species 2. As for the processing chain model, this may be calculated as an absolute or a relative effect. The absolute effect (AE) is again the difference between species 2's population densities at the coexistence and species 2-dominant equilibria:

$$AE = \bar{N}_{2,coexist} - \bar{N}_{2,sp2.dom} \quad (2.2.1)$$

The relative effect may be calculated using RII as done in the previous model again as:

$$RII = \frac{\bar{N}_{2,coexist} - \bar{N}_{2,sp2.dom}}{\bar{N}_{2,coexist} + \bar{N}_{2,sp2.dom}} \quad (2.2.2)$$

If the interaction has a net positive effect on species 2, then Eq. 2.2.1 or (equivalently) Eq. 2.2.2 must be positive. This condition is fulfilled when $m > \frac{n}{n+c_1}$, and fails when $m < \frac{n}{n+c_1}$. This result is the same as that shown for the processing chain model (Eq. 1.4).

Obligacy in the nurse plant model occurs when $N_{2,sp2.dom} < 0$, given that the conditions for stable coexistence hold (Eq. 2.1.4). This reduces to the condition $\bar{R}_{2,trivial} < R_{2,sp2}^*$. This corresponds to the scenario where the availability of the inaccessible resource (via environmental supply and spontaneous conversion) is lower than the minimum resource requirement of species 2, thus driving the resource recipient to extinction in the absence of species 1.

The SGH predicts that the net benefit of an interaction is greater in environments of high stress, or low resource availability. There are two externally supplied resources in the nurse plant model, and thus the SGH may be evaluated in terms of gradients of S_1 or S_2 , as well as in terms of absolute (AE) or relative (RII) effect. We first consider the SGH with respect to S_1 . If we interpret the SGH in terms of absolute effect (AE), the criterion for the SGH to hold is that the partial derivatives of the AE with respect to S_1 are negative. If $m > \frac{n}{n+c_1}$ we will always have $\frac{\partial AE}{\partial S_1} > 0$, and the SGH thus would not hold. But if $m < \frac{n}{n+c_1}$ we will always have $\frac{\partial AE}{\partial S_1} < 0$, and the SGH would thus always hold (Supplementary material Appendix 3). When net effect is evaluated in relative rather than absolute terms, the SGH with respect to S_1 holds when $\frac{\partial RII}{\partial S_1} < 0$. It can be shown (Supplementary material Appendix 3) that if $m > \frac{n}{n+c_1}$, we require that $S_2 < \frac{d_2}{f_{22}\alpha_{22}} - \frac{nd_1}{c_2 f_{11}\alpha_{11}} \equiv S_{2,crit}$ (Fig. 3a, 4a), and if $m < \frac{n}{n+c_1}$ we require $S_2 > S_{2,crit}$ (Fig. 3b, 4a).

Next, we consider the SGH with respect to S_2 . As the term S_2 does not occur in AE, $\frac{\partial AE}{\partial S_2} = 0$, and the SGH never holds when net effect is evaluated in absolute terms. However, when it is evaluated in relative terms, then it can be shown (Supplementary material Appendix 4) that, under coexistence conditions (Eq. 2.1.4), $\frac{\partial RII}{\partial S_2} < 0$ when $m > \frac{n}{n+c_1}$ (Fig. 4b). Conversely, when $m < \frac{n}{n+c_1}$, then $\frac{\partial RII}{\partial S_2} > 0$, and the SGH with respect to S_2 never holds (Fig. 4b).

Collectively, these results show that facilitation (i.e. a net positive effect of species 1 on species 2) and competition (i.e. a net negative effect) are both possible outcomes of

Table 2. Mutually-exclusive combinations of the parameter value conditions and their resultant equilibria in the (a) processing chain and (b) nurse plant models. A tick represents the fulfilment of a specified condition, a cross represents the fulfilment of the inverse of that condition, and a dash denotes that a specified condition does not apply to that equilibrium.

Equilibrium	$R_{1,sp1}^* < \bar{R}_{1,trivial}$	$R_{2,sp2}^* < \bar{R}_{2,trivial}$	$R_{2,sp2}^* < \bar{R}_{2,sp1.dom}$
(a) Processing chain model			
Species 2 dominant	×	–	–
Coexistence	✓	–	–
(b) Nurse plant model			
Trivial	×	×	–
Species 1 dominant	✓	–	×
Species 2 dominant	×	✓	–
Coexistence	✓	–	✓

coexistence in the nurse plant model, and that this net interaction outcome is determined solely by whether $m > \frac{n}{n+c_1}$ or the reverse (Fig. 3). Furthermore, the SGH with respect to S_1 is possible under both facilitation and competition scenarios as well, being determined solely by whether $S_2 < S_{2,crit}$ or the reverse (Fig. 4). The SGH with respect to S_2 is also possible, and occurs only when facilitation also occurs.

Discussion

Resource conversion is the underlying mechanism for at least five different types of positive species interactions: processing chain commensalism, nurse plant facilitation, classical nutritional-protective mutualism, prey capture facilitation and digestive mutualism (Fig. 1, Table 1). The former two interactions are primarily commensal or unidirectional, while the latter three are primarily mutualistic or bidirectional. In this study, we formulated a generalizable consumer-resource model and applied this to the first two of these interactions, viz. processing chain and nurse plant interactions. The models were solved analytically to show that the persistence of a species is only possible if its R^* value for the resource it consumes is lower than the equilibrium density of that resource

through processes external to that species (Table 2) – a finding that is consistent with R^* and consumer-resource theory (Tilman 1980, Chase and Leibold 2003). Furthermore, coexistence equilibria with net positive effects on the resource recipient species could be obtained in both models, which meant that positive interactions in these models were ecologically stable outcomes, rather than non-equilibrium transitory phenomena.

The two models yielded four key insights. The first two insights apply to both processing chain and nurse plant interactions: 1) resource conversion interactions can yield net positive effect to the resource recipient only when facilitator-mediated resource conversion (m) is more efficient than the baseline, spontaneous, facilitator-independent resource conversion ($\frac{n}{n+c_1}$), and 2) the sign of resource conversion interaction outcomes never switch (e.g. from a net positive to a net negative interaction) with changing levels of resource availability, when all other parameters are kept constant. The next two insights are specific to the interaction being modelled: 3) processing chain interactions at equilibrium can never have a positive effect and conform to the SGH at the same time (Fig. 2); and 4) nurse plant interactions can have a positive effect and conform to the SGH at the same time, although the manner in which they do so depends largely on

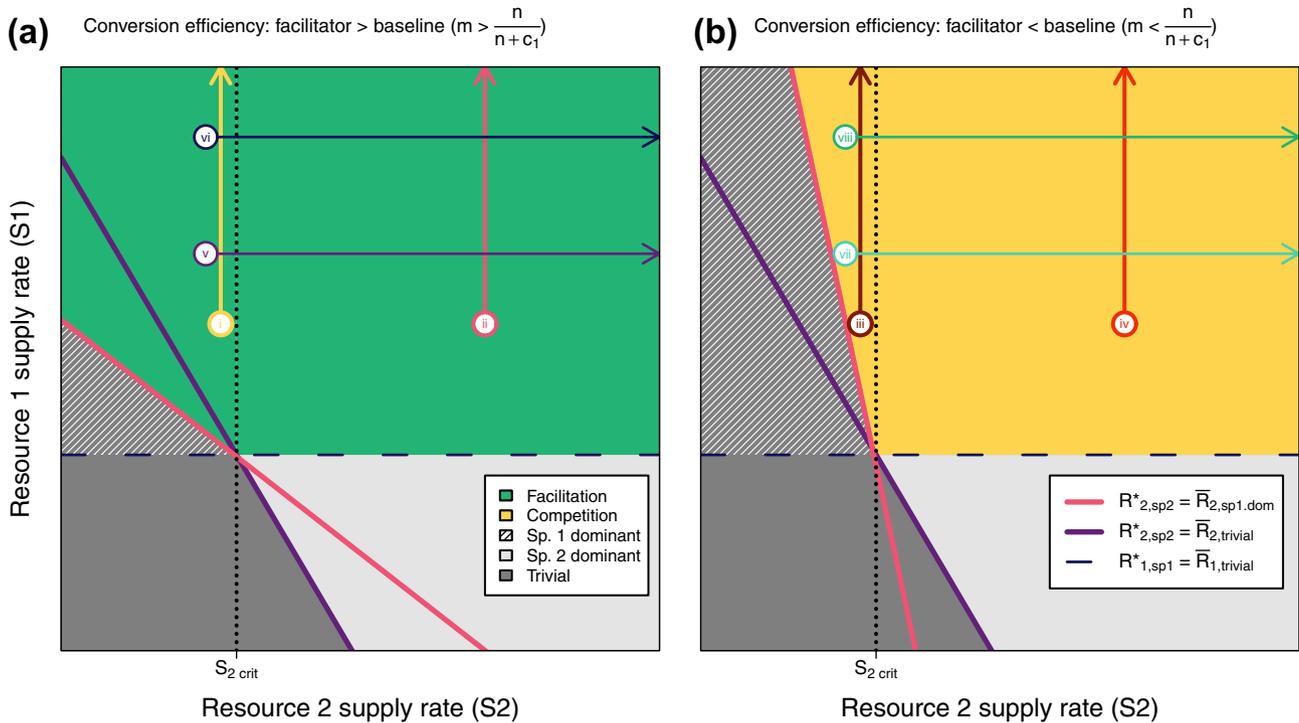


Figure 3. Interaction outcomes (denoted by the colors of the shaded regions) of the nurse plant interaction are determined by the resource supply rates, S_1 (y axes) and S_2 (x axes) and the relative efficiencies of facilitator-mediated conversion (m) and baseline, facilitator-independent conversion ($\frac{n}{n+c_1}$) of resource 1 (in panel a, $m > \frac{n}{n+c_1}$, while this condition is reversed in panel b). The purple and red lines in the figures represent the zero net growth isoclines (ZNGIs) of species 2 under the species 2-dominant and coexistence equilibria, respectively. The roman numerals (i–viii) identify regions of resource space (gradients along S_1 and S_2 that are marked by vertical and horizontal arrows, respectively) that are explored further in Fig. 4. Parameter values used to construct this and the next figure are: $c_1 = 0.51$, $c_2 = 0.52$, $d_1 = 0.53$, $d_2 = 0.49$, $\alpha_{11} = 1.1$, $\alpha_{22} = 0.7$, $f_{11} = 0.8$, $f_{22} = 1.2$.

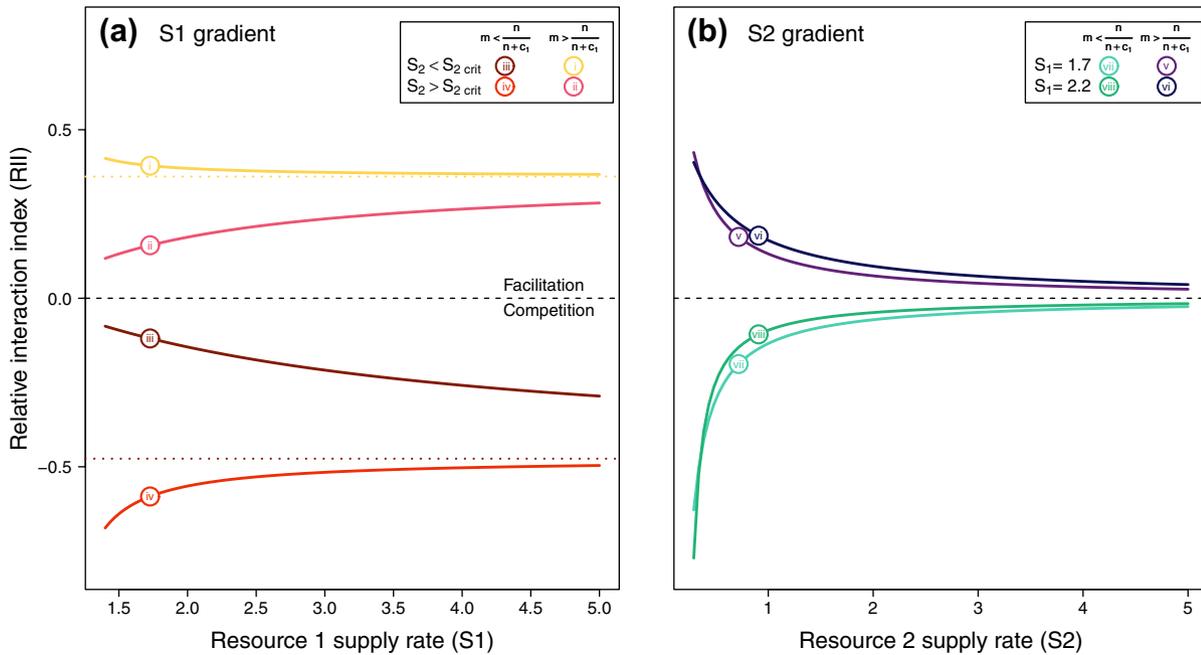


Figure 4. Relative effect (relative interaction index (RII)) of species 2 in the nurse plant model, along gradients of (a) resource 1 supply rates (S_1) and (b) resource 2 supply rates (S_2). Continuous lines represent model predictions under varying parameter value combinations, which correspond to the roman numerals in Fig. 3; dotted lines in (a) represent the asymptotes to which RII values approach at high levels of S_1 . Roman numerals i, ii, v and vi represent the parameter combinations where species 1's resource conversion efficiency is greater than that of the baseline (i.e. $m > \frac{n}{n+c_1}$), and thus facilitation occurs, while roman numerals ii, iv, vii and viii represent parameter combinations where the baseline resource conversion efficiency is greater, and thus competition occurs. The SGH (increasing benefit with increasing stress) occurs in the lines denoted by roman numerals i, iii, v and vi (note that resource stress decreases with increasing resource supply rates).

how resource stress is defined, and the environmental supply rate of surface soil moisture (S_2).

Generalizable principles

In both the processing chain and nurse plant models, the net effect of the resource processor (species 1 in the models) on the resource recipient (species 2 in the models), whether measured in absolute or relative terms, is positive only when the resource processor's efficiency at processing the inaccessible resource (resource 1 in the models) exceeds the efficiency with which that resource is converted into the accessible resource condition (resource 2 in the models) by spontaneous, facilitator-independent processes. This finding had been made by Heard (1994a) earlier in processing chain interactions. Intuitively, growth of the resource recipient is directly proportional to the availability of the accessible resource, and since conversion of the resource from inaccessible to accessible states can occur even in the absence of a resource processor, the presence of this resource processor will only benefit the resource recipient if it can increase the net resource conversion rate. We hypothesize that this result generalizes beyond the specific model used here: higher conversion efficiency by the resource processor is a necessary condition for net positive effect on the resource recipient in all resource conversion

interactions where spontaneous, facilitator-independent resource conversion is possible (i.e. the arrow a of Fig. 1a is present in the model, e.g. prey capture facilitation (Fig. 1e) and digestive mutualism (Fig. 1f)).

A key observation made for both models is that varying supply rates of resources alone cannot cause switches in sign of the interaction. However, interaction sign switches are a common observation in empirical studies of context dependency or the SGH (Bertness and Callaway 1994, Bronstein 1994, He et al. 2013, Chamberlain et al. 2014). The discrepancy between model predictions and reality may be interpreted in two ways. Firstly, if models have successfully captured the key processes in real-world resource conversion interactions, then these findings suggest that the other model parameters seldom stay constant over the entire gradients of resource supplies. For example, resource conversion efficiency (m) or per capita feeding rates of the resource processor (f_{11}) may decrease under conditions of low resource stress, thus leading to net negative impacts on the resource recipient. Alternatively, the absence of switching in our models may be an artefact of the linear resource uptake terms used. It is possible that switching would occur if non-linear population growth models were used instead – that is, if population growth as a function of resource availability were to slow down or plateau at high resource levels, as in the classic

Monod model of resource use (Tilman 1982, Lobry et al. 1992). Comparing the predictions of linear and non-linear population growth models in resource conversion interactions should be a focus of future studies.

An important caveat to the findings concerning interaction strength and the SGH is that, in this study, we considered interaction strength/outcome to be the stable, long-term outcome of only coexisting populations of species. This is the most ecologically-meaningful way of understanding interspecific interactions and is the approach taken by most theoretical studies (de Mazancourt and Schwartz 2010, Butler and O'Dwyer 2019, Dangles 2019), but is not always the interaction strength/outcome described in empirical studies of mutualism/facilitation. Many empirical studies examine: 1) individual rather than population performance, although this can result in observations of 'transient facilitation' (Brooker et al. 2006) or ontogenetic stage-confined effects which do not translate to equivalent population effects (Valiente-Banuet and Verdu 2008); 2) interactions occurring within short time frames, although these may not fully capture demographic stochasticity and/or environmental variation through time (Flores-Torres et al. 2019); 3) interactions that occur in systems in a transitory state – particularly, communities which are in the process of being invaded (Simberloff and Von Holle 1999), although these may result in the eventual extinction of facilitator species. We have avoided examining interactions in non-equilibrium time points in this study.

Processing chain model

Contrary to the predictions of the SGH, our processing chain model predicted that the SGH occurs in processing chain interactions only when the net outcome of the interaction is negative, and, correspondingly, that the SGH never occurs when the interaction has a net positive effect on the resource recipient (Fig. 2). Although many empirical studies have tested the SGH or context dependency with respect to other variables in processing chain interactions (reviewed by Fugère et al. 2012), we know of only two that presented statistically significant findings concerning the SGH with respect to a resource quantity/density gradient in a processing chain interaction (Paradise 1999, Dangles et al. 2018). In their experimental study, Dangles et al. (2018) found that the *Anomalocosmoecus*–*Hyallolella* processing chain interaction (two aquatic detritivorous trichopteran larvae) had a net negative impact on the resource recipient, *Hyallolella* sp., at high resource levels (low resource stress), but this negative impact was lost at very low resource levels (high resource stress) (Dangles et al. 2018) – a result which agrees qualitatively with findings of our model. Paradise (1999), however, found that leaf-shredding scirtid beetle larvae in a tree hole community facilitated *Aedes triseriatus* culicid larvae via a processing chain interaction in a manner that conforms to the SGH in regard to leaf litter detrital resource abundance – a finding which contradicts predictions of our processing chain model. However, in that study, positive growth rates

(and a net positive effect of scirtids on culicids) were detected even in the treatment in which leaf litter resources were not supplied at all – an observation that clearly demonstrated the presence of alternative food resources. While our models show that a net positive processing chain interaction cannot conform to the SGH, the presence of alternative resources is likely to change these findings, just as the two-resource nurse plant model permits a net positive effect and the SGH.

When tested against other stress gradients such as resource quality or habitat quality gradients, processing chain interactions can sometimes both have a positive effect and conform to the SGH (Fugère et al. 2012). This means that the manner in which 'stress' is defined can result in very divergent predictions even within the same system, and supports the suggestion by Maestre et al. (2009) that predictions of the SGH may be altered significantly depending on whether resource or non-resource stress gradients are being considered.

Nurse plant model

Unlike the processing chain model, the nurse plant interaction can simultaneously have a positive effect and conform to the SGH with respect to the inaccessible resource (S_1), albeit under a restricted range of conditions – when the environmental resource supply of the accessible resource S_2 falls below a critical threshold ($S_{2,crit}$; Fig. 3a, 4a). Since the accessible resource in this case represents surface soil moisture, which is supplied directly by precipitation, this corresponds to the scenario where water supply through rainfall or fog is low, but a considerable amount of groundwater (S_1) remains available to deep-rooted nurse plant species. On the other hand, the model predicts that the SGH with respect to the accessible resource (S_2) always holds when the interaction is positive (Fig. 4b).

These findings largely agree with empirical observations of nurse plant systems (He et al. 2013), in which stress is often measured as the inverse of precipitation (Armas et al. 2011). Nevertheless, we know of no studies in which groundwater and surface soil moisture were quantified separately, nor of studies that compared the efficiencies of hydraulic lifting with baseline rates of water movement through soil strata. These empirical studies of nurse plant facilitation thus cannot be taken as validation for the model without clearer definitions of the conditions under which facilitation and/or the SGH are observed. Future empirical studies of nurse plant interactions and the SGH should thus seek to test the predictions of this model by explicitly quantifying the variables and processes represented by it.

Another important observation that can be made from the nurse plant model is that the interaction cannot simultaneously have a net positive effect on the resource recipient and conform to the SGH unless the interaction effect is quantified in relative rather than absolute terms. Other authors have argued qualitatively that the predictions of the SGH can be significantly altered by whether interaction effect is measured in absolute or relative terms (Holmgren and Scheffer 2010).

The results of this study thus provide concrete proof for these otherwise qualitative arguments.

Caveats and future directions

It must be highlighted that the inferences drawn in this study are true only insofar as the dominant facilitative mechanism between resource processor and resource recipient species in either processing chain or nurse plant interactions is mediated by the mechanism of resource conversion. This may not always be the case, for example, between nurse plants and their beneficiary species in arid–semi-arid habitats. Indeed, many studies of plant–plant facilitation have emphasized multifaceted stress-ameliorating effects of nurse plants (Brooker et al. 2008). While ‘stress’ in arid–semi-arid habitats necessarily includes water resource stress that may be ameliorated through below-ground water supplementation via hydraulic lifting (the resource conversion mechanism examined in this study; Prieto et al. 2010, 2011, Armas et al. 2012), above-ground stress amelioration via shading (temperature stress amelioration) and humidification (desiccation stress amelioration) are also important facilitation mechanisms (Armas and Pugnaire 2005). Indeed, it is unlikely that nurse plants in arid–semi-arid climates facilitate beneficiary species via below-ground resource supplementation without also inadvertently contributing to above-ground stress amelioration (Armas and Pugnaire 2005, Soliveres et al. 2015), or that hydraulic lifting occurs in all instances of nurse plant interactions (Barron-gafford et al. 2017), and a model that only considers the below-ground resource-based component of such an interaction is thus undoubtedly a simplification of reality. Nevertheless, the utility of our model is not in providing completely realistic predictions of specific interaction outcomes. Rather, the model provides an insight into the isolated effect of a clearly defined mechanism, and in so doing provides an unambiguous prediction against which empirical data can be compared. To validate the model proposed in this study, future empirical studies should measure densities of both resources/resource states (e.g. coarse and fine particulate matter in processing chain interactions, and groundwater table and surface soil moisture in nurse plant interactions) and mortality rates of interacting species, in addition to their population sizes/growth as is commonly done. Studies should also seek to establish if interacting populations are in a state of equilibrium or not.

Furthermore, we argue that the generalizability of mechanism across biological systems (Fig. 1) and across the historically divergent research fields of facilitation and mutualism (Bronstein 2009) will permit greater syntheses and the derivation of ecological principles. Although we recognized five different types of interactions within the category of resource conversion interactions (Table 1, Fig. 1), only two, unidirectional/commensal ones could be examined within the scope of this study (Table 1a, Fig. 1b–c), leaving the last three, bidirectional/mutualistic ones remaining unexplored (Table 1b, Fig. 1d–f). The SGH (which originated from facilitation research) has not been applied extensively to mutualistic

interactions, but both prey capture (Lim et al. 2018) and digestive (Leong et al. 2019) ones have been shown to conform to SGH’s predictions under experimental (short term) conditions, with the former study also predicting switching at high resource levels. We thus encourage future work to extend our analyses to mutualism models that include bidirectional interactions, and to analytically explore the conditions under which such models may simultaneously yield both a positive interaction effect and conform to the SGH.

Speculations

Models for bidirectional/mutualistic resource conversion interactions differ from unidirectional/commensal ones mainly in the inclusion of a positive effect of the resource recipient upon the resource processor (arrow b in Fig. 1a) via, for example, a reduction of the recipient’s mortality rate. Our preliminary simulations done using a modified species 1 mortality term ($\frac{d_1}{k + N_2}$ instead of d_1) suggested that the two generalizable principles described earlier apply to bidirectional/mutualistic resource conversion interactions in the same way as they did to the interactions examined in this study. However, as was the case in the processing chain model, we could not obtain a positive effect which occurred simultaneously with the SGH. We speculate that, for any resource conversion interaction to simultaneously have a net positive interaction on the resource recipient and conform to the SGH, either 1) species growth responses must be non-linear or 2) there must exist an environmental supply rate for the inaccessible resource (R_2), as was the case in the nurse plant model.

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Author contributions – WNL conceived the study design. RAC and WNL performed the analyses. WNL wrote the first manuscript draft, and RAC contributed to revisions.

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Supplementary material (available online as Appendix oik-06672 at <www.oikosjournal.org/appendix/oik-06672>). Appendix 1–4.