

Expanding comparative-advantage biological market models: contingency of mutualism on partners' resource requirements and acquisition trade-offs

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We expand the comparative-advantage biological market-modelling framework to show how differences between partners, both in their abilities to acquire two resources and in their requirements for those resources, can affect the net benefit of participating in interspecific resource exchange. In addition, the benefits derived from resource trading depend strongly on the nature of the trade-off between the acquisition of one resource and the acquisition of another, described here by the shape (linear, convex or concave) of the resource acquisition constraints of the individuals involved. Combined with previous results, these analyses provide a suite of predictions about whether or not resource exchange is beneficial for two heterospecific individuals relative to a strategy of non-interaction. The benefit derived from resource exchange depends on three factors: (i) relative differences between the partners in their resource acquisition abilities; (ii) relative differences between the partners in their resource requirements; and (iii) variation in the shape of resource acquisition trade-offs. We find that such an explicit consideration of resource requirements and acquisition abilities can provide useful and sometimes non-intuitive predictions about the benefits of resource exchange, and also which resources should be traded by which species.

Keywords: mutualism; resource acquisition; biological market; comparative advantage

1. INTRODUCTION

While the ubiquity and importance of interspecific mutualisms are becoming well understood, there remain many unanswered questions regarding the conditions favouring the evolution and maintenance of mutualisms (Hoeksema & Bruna 2000; Bronstein 2001*a,b*). A diversity of modelling approaches has recently been applied to interspecific mutualisms, including game-theoretical models (e.g. Doebeli & Knowlton 1998), population-dynamics models (e.g. Ringel *et al.* 1996; Holland & DeAngelis 2001; Holland *et al.* 2002) and biological market models (Noe & Hammerstein 1994, 1995; Schwartz & Hoeksema 1998; Hoeksema & Schwartz 2001; Noe 2001). The latter may be particularly useful for explicit analyses of the costs and benefits of potentially mutualistic interactions. Mutualisms are increasingly being seen as interactions that, often being the net result of mutual exploitation, can easily fluctuate along a continuum from mutualism to parasitism (Herre *et al.* 1999). As such, a careful consideration of the costs and benefits involved, and the factors causing them to vary, may lead to a better understanding of these interactions.

One recent biological market approach to modelling mutualisms uses concepts from the economic theory of comparative advantage. This theory was originally developed in the nineteenth century by the economist David Ricardo

to explain the benefits of international trade (Hoeksema & Schwartz 2001; Schwartz & Hoeksema 1998). In the biological version of the comparative-advantage model (Hoeksema & Schwartz 2001; Schwartz & Hoeksema 1998), the resource acquisition abilities of potential trading partners are considered explicitly to show that resource exchange is beneficial for heterospecific individuals if they exhibit relative differences in their abilities to acquire two resources. However, the underlying economic theory also predicts that differences in *requirements* for two resources can make trade beneficial (e.g. Leighton 1970). The biological equivalent of these differing requirements may be consistent differences among species in ratios of required resources in their tissues or metabolic processes.

We have two objectives. First, after summarizing the basic model, we show how differing relative requirements for resources among heterospecific individuals can impact the benefit of interspecific resource exchange within the context of mutualisms. Second, we integrate these results with previous results, presenting a synthesis of when resource exchange is expected to be beneficial and mutualism facilitated, versus when resource exchange mutualism is not favoured.

2. RESOURCE ACQUISITION CONSTRAINTS

Schwartz & Hoeksema (1998) modelled resource exchange between heterospecific individuals to demonstrate how mutualism can be promoted by differences between partners in their relative *abilities to acquire* two resources. We provide an abbreviated summary of the model of Schwartz & Hoeksema (1998) and then expand

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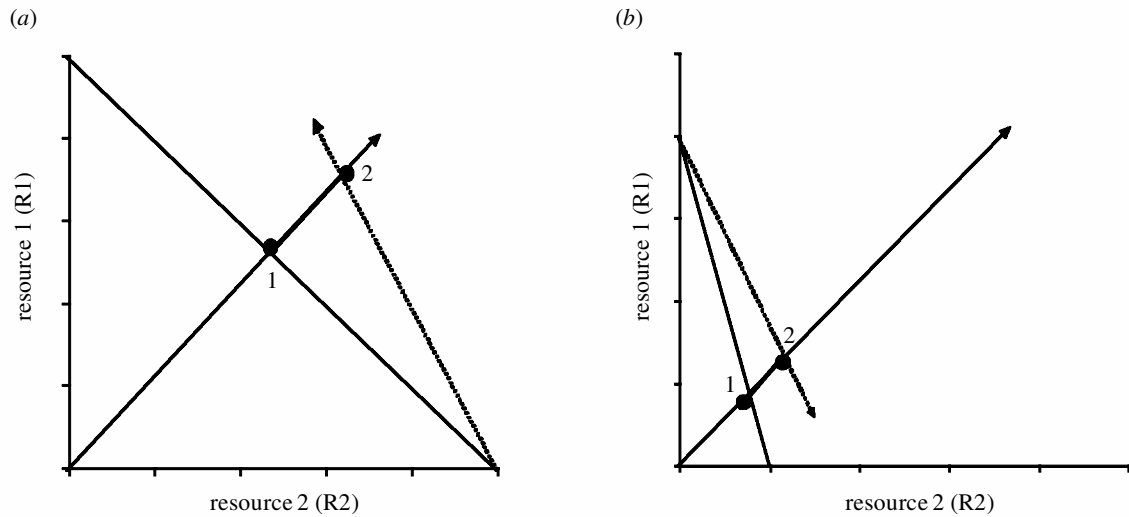


Figure 1. Graphical depiction of conditions for a potential interaction between two individuals, one of (a) species A and one of (b) species B. Both A and B require resource 1 (R1) and resource 2 (R2). The ability of A and B to acquire R1 and R2 in the absence of resource exchange is described by an acquisition constraint (solid lines intersecting both axes). Note that A is absolutely better than B at acquiring both resources, since its acquisition constraint intersects both axes further from the origin. However, B is relatively better than A at acquiring R1, since the slope of its acquisition constraint favours acquisition of R1 over R2, more than does the acquisition constraint of species A. The optimal ratio of the two resources that each individual requires for its metabolism is depicted by the optimal consumption vector (solid arrows), which is identical for A and B. A and B, in the absence of resource exchange, will acquire resources at the point of intersection between their consumption vector and their acquisition constraint (points 1). Under a resource exchange scenario, B specializes on acquisition of R1, A specializes on acquisition of R2, and A and B exchange R1 and R2 at a price (depicted by the slope of the dotted line) that is favourable for both. Both A and B increase total net resource acquisition (points 2), and the benefit from resource exchange is indicated by the distance between points 1 and points 2 along the consumption vector.

this model to consider differences between individuals in their relative resource *requirements*.

The original comparative-advantage mutualism models developed by Schwartz & Hoeksema (1998) are characterized by two important attributes, which we retain for this work. First, we assume that two heterospecific individuals (hereafter A and B) can acquire, and require from the environment, both of two resources (hereafter R1 and R2). Second, the model assumes that potential trading partners have mechanisms by which to assure fair trade (i.e. they are not susceptible to cheaters). Although these models could be used to analyse costs of cheating and the structures to prevent cheating, this is beyond the scope of the current paper.

We use a two-dimensional graphical approach, the axes of the graph being the total amounts of R1 and R2 acquired or consumed by an individual per unit time (figure 1). There is a trade-off in acquisition of these two resources, such that increased acquisition of one resource requires decreased acquisition of the other. This trade-off in resource acquisition is described by a resource acquisition constraint (referred to by Schwartz & Hoeksema (1998) as the isolation acquisition isocline, or IAI) for both individuals A and B, which intersects both axes away from the origin and can be linear, concave or convex. The shape of this curve depends on the extent to which the acquisition of one resource either interferes with, or is a by-product of, the acquisition of the other resource (figure 2). Furthermore, as we will demonstrate below, the shape of this curve has an important impact on when resource exchange is mutually beneficial.

We assume that absolute fitness (e.g. biomass gain or reproductive output per unit time) is an increasing function of acquisition of R1 and R2, such that an individual maximizing absolute fitness will acquire resources at some point along its acquisition constraint, rather than at any point closer to the origin. A linear acquisition constraint describes a constant-cost trade-off in the acquisition of two resources such that the same amount of one resource must be sacrificed in order to acquire one unit of the other resource anywhere along the acquisition constraint. Thus, an individual acquiring resources along its acquisition constraint near the R1 axis is experiencing the same cost ratio as it would be if it were acquiring resources near the R2 axis. By contrast, nonlinear acquisition constraints (convex or concave to the origin) describe trade-offs in the acquisition of two resources such that the cost ratio for the two resources changes depending on the amounts of the two resources being acquired. Specifically, an acquisition constraint that bulges away from the origin, to which we refer here as concave (reversing our previous usage of concave and convex; Schwartz & Hoeksema 1998; Hoeksema & Schwartz 2001), describes the situation when two resources are acquired to some degree as by-products of each other—total acquisition is higher when the two resources are acquired together, whereas specialization on acquisition of one resource comes at a relatively high cost in acquisition of the other resource. For example, near the R1 axis, a large amount of R2 acquisition must be sacrificed for each additional unit of R1 acquisition. An example of such an acquisition constraint, when two resources are acquired to some degree

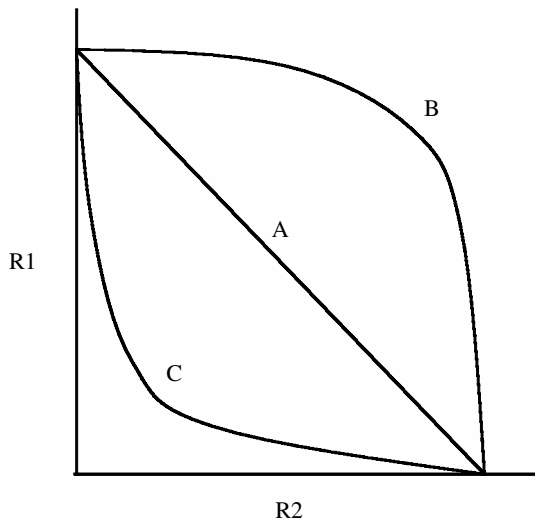


Figure 2. Variation in the shape of the acquisition constraint (referred to as the isolation acquisition isocline, or IAI, by Schwartz & Hoeksema (1998)). If the acquisition constraint is straight (line A), then acquisition of additional units of one resource always results in the same cost in acquisition of the other resource. If the acquisition constraint is concave, i.e. bulging away from the origin (line B) or convex, i.e. bulging toward the origin (line C), then the cost in one resource to acquire an additional amount of the other resource is not constant along the acquisition constraint. Specifically, when the acquisition constraint is concave (line B), acquisition of one resource is to some degree a by-product of acquisition of the other resource. If the acquisition constraint is convex (line C), then acquisition of one resource interferes with acquisition of the other, the opposite of a by-product relationship. In both of these cases of nonlinear acquisition constraints, if an individual is acquiring resources near one of the axes then the cost ratio is more extreme—a large amount of one resource must be given up for a small additional amount of the other resource.

as by-products of one another, is the acquisition of soil resources by plants. Allocation to roots increases the plant's ability to acquire, for example, both nitrate and phosphate and acquisition of one may not diminish potential acquisition of the other.

An acquisition constraint that is convex, i.e. bulges toward the origin, describes a condition when the acquisition of one resource interferes with the simultaneous acquisition of the other resource. This situation could occur, for example, if two resources are patchily distributed, the two resources never occur together in the same patch, and the patches are widely distributed (Tilman 1982). Another example occurs when two resources are nutritionally antagonistic, such that when consumed together neither provides as much nutritional value as when they are consumed separately. In these cases, acquiring both resources together is more costly than acquiring a larger amount of either resource alone. Specialization on acquisition of one resource comes at a relatively low cost in acquisition of the other resource.

Schwartz & Hoeksema (1998), applying concepts from the economic theory of comparative advantage, showed that if the acquisition constraints of two heterospecific individuals were linear and differed in slope (indicating differing resource acquisition abilities), then both benefit from specializing in the acquisition of one resource and

then trading with each other to acquire the other resource (figure 1). Both individuals acquire more resources when using a strategy of resource trade compared with a strategy of mutual non-participation in the interaction. Although Schwartz & Hoeksema (1998) noted that the shape of the acquisition constraint affects the degree to which resource exchange is beneficial, they did not formally analyse this aspect of the model.

3. RESOURCE CONSUMPTION VECTORS

We define the application of acquired resources toward fitness potential with an optimal resource consumption vector, which is the set of points representing the ratio of the two resources for the metabolism of the organism to optimize fitness (solid arrows; figure 1). Each individual, in the absence of resource exchange, will acquire resources at the point of intersection between its optimal consumption vector and its acquisition constraint.

Prior models have assumed that potential trading partners have identical resource requirements (i.e. identical consumption vectors). However, the economic theory of comparative advantage shows that differences in resource requirements can also affect whether trade is beneficial (e.g. Leighton 1970). We use this concept to examine how differences between two heterospecific individuals in the slopes of their consumption vectors could make resource exchange beneficial in a biological market model. To understand the effect of different resource requirements on trade, imagine two individuals that have identical relative abilities to acquire two resources (their acquisition constraints are identical) but different resource requirements to optimize growth or reproductive output (their consumption vectors are different). Because these individuals require different relative amounts of the two resources, they acquire resources at different points along their shared acquisition constraint. As a result, they experience different cost ratios of the two resources (the amount of R1 that must be sacrificed for additional R2, or the rate of transformation). In our example, individual A requires more of R1 than R2, B requires more of R2 than R1, and thus the two individuals have different consumption vectors that intersect the acquisition constraint (which is identical for A and B) in different places (points 1 and 2; figure 3). Since this acquisition constraint is nonlinear (specifically, concave to the origin), the cost ratio for R1 and R2 is different at these two points (i.e. the tangents to the acquisition constraint at these two intersection points have different slopes). Thus, A and B are experiencing different cost ratios of the two resources, despite having identical acquisition constraints. The result is that in the absence of trade, A is acquiring R1 at a point along the acquisition constraint where it is very costly—large quantities of R2 must be given up to acquire a small additional amount of R1 (e.g. four units of R2 for one unit of R1). On the other hand, B is acquiring R2 at a point along the acquisition constraint where it must give up large quantities of R1 to acquire a small additional amount of R2 (e.g. four units of R1 for 1 unit of R2).

If A and B both choose to acquire less of their preferred resource (becoming less specialized with respect to resource acquisition), and instead acquire an excess of their less-preferred resource with which to trade to each

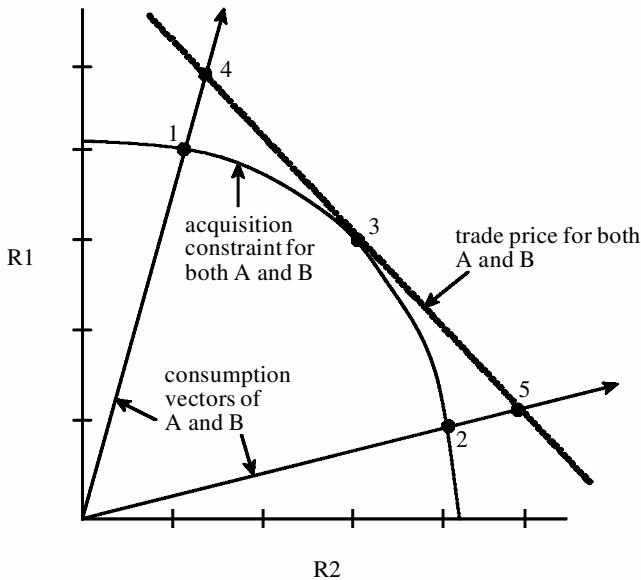


Figure 3. Market conditions for two heterospecific individuals (A and B) having the same concave acquisition constraint (solid line intersecting both axes), but different consumption vectors (solid arrows). A requires a higher ratio of resource 1 (R1) to resource 2 (R2) than does B, as indicated by their differing consumption vectors. In the absence of resource exchange, A acquires resources at a point (point 1) along the acquisition constraint where R1 is very expensive (i.e. a large amount of R2 must be sacrificed for an additional amount of R1), while Species B acquires resources at a point (point 2) along the acquisition constraint where R2 is very expensive. If both A and B acquire less of their preferred resource (R1 for A and R2 for B), acquiring resources instead at point 3, then both acquire excess of their non-preferred, or less-needed resource (R2 for A and R1 for B). If they trade this excess to each other at a price more favourable to both (such as the 1 : 1 cost ratio depicted by the trade acquisition constraint, i.e. the dotted line), both A and B acquire more of both resources (A at point 4 and B at point 5) than in the absence of resource exchange.

other, both individuals end up with more of both resources. Both benefit from resource exchange, and thus interact as mutualists. For example, if A acquires one less unit of R1, it can instead acquire two additional units of R2 (point 3 instead of point 1 in figure 3). Similarly, if B chooses to acquire one less unit of R2, it can instead acquire two more units of R1 (point 3 instead of point 2 in figure 3). If the partners trade R1 and R2 at a price of 1 : 1, each trading two units of its non-preferred resource for two units of its preferred resource (this trade price of 1 : 1 being depicted by the dotted line in figure 3, which is effectively a new trade acquisition constraint), then each will end up with larger amounts of both resources than they could have acquired on their own. The net resource acquisition point for each individual under the scenario of resource exchange is the point of intersection between their respective consumption vectors and the new trade acquisition constraint (points 4 and 5; figure 3). The net result is that under the resource exchange scenario, both A and B end up acquiring resources (partially on their own and partially through trade) at a point along their consumption vector further from the origin than under a scenario of mutual non-interaction (points 4 and 5 com-

pared to points 1 and 2; figure 3). If we assume that individuals are maximizing fitness and that absolute fitness (e.g. growth or reproductive output) is an increasing function of resource acquisition along the consumption vector, then each has benefited by participating in resource exchange rather than acquiring resources on their own.

It is important to note that we have not specified a mechanism for the determination of the price of trade (indicated by the slope of the new trade acquisition constraint: 1 : 1 in the above example, dotted line in figure 3). We assume only that the two individuals trade at a price intermediate between their respective isolation prices (these isolation prices being the slope of the tangent to the point of intersection between the acquisition constraint and the consumption vector of an individual). In reality, the exact trade price could be determined by a variety of mechanisms and may not be exactly intermediate between the isolation prices of the two individuals; however, trade is beneficial to both individuals as long as the price of trade is somewhere between the isolation prices of the two individuals (Schwartz & Hoeksema 1998).

4. INTEGRATING VARIATION IN RESOURCE ACQUISITION AND CONSUMPTION

Thus far we have described three attributes that may vary in the comparative-advantage market model of mutualisms: (i) the shape of resource acquisition isoclines (linear, concave or convex); (ii) differences between partners in resource acquisition constraints; and (iii) differences between partners in consumption vectors. Addressing the variety of possible combinations of these attributes allows us to explore the full spectrum of when mutualisms are predicted to arise from resource exchange. To better understand the implications of the comparative-advantage market model, we analysed the 12 qualitatively different scenarios in the comparative-advantage biological market model framework based on these three factors (summarized in figure 4).

The first important result of considering this spectrum of scenarios (figure 4) is the degree to which the three variables interact to determine whether or not resource exchange results in mutualism. For example, if we assume that both trading partners have the same acquisition constraints (middle row of figure 4), then it can be seen that whether or not mutualism is promoted by the partners differing in resource requirements is completely contingent on the shape of the acquisition constraints. With convex acquisition constraints for both species (indicating that the acquisition of one resource interferes with acquisition of the other resource), resource exchange can still be beneficial, but the benefit is greatest when the resource requirements of the two individuals are most similar (figure 5a). This benefit gradually diminishes as the consumption vectors of the two individuals become more different (figure 5b). Thus, differing consumption vectors between potential trading partners have the opposite effect when acquisition constraints are concave than when they are convex.

The second major result that emerges from a consideration of the full spectrum of scenarios is that when two trading partners differ in their resource acquisition abilities (bottom row in figure 4), then differing resource require-












							
shape of acquisition constraint							
							
consumption vectors similar or different							
acquisition constraints similar or different	similar	 mutualism (trade of either resource is beneficial)	(resource trade is NOT beneficial)	(resource trade is NOT beneficial)	(resource trade is NOT beneficial)	(resource trade is NOT beneficial)	 mutualism (trade of less-needed resource is beneficial)
	different	   mutualism (trade of more easily acquired resource is beneficial)	mutualism (trade of more easily acquired resource is beneficial, especially if it is also the less-needed resource)	mutualism (trade of more easily acquired resource is beneficial)	mutualism (trade of more easily acquired resource is beneficial, especially if it is also the less-needed resource)	(resource trade is NOT beneficial)	mutualism (trade of less-needed resource is beneficial, especially if it is also the more easily acquired resource)

Figure 4. Summary of predicted outcomes of interactions between two heterospecific individuals in a comparative-advantage biological market. The outcome, i.e. whether or not trade is beneficial, depends on the shape of the acquisition constraints (concave, straight or convex) and whether or not acquisition constraints and consumption vectors differ between the two individuals. The scenarios in each cell are presented as being qualitatively different, but can be viewed as extreme endpoints on a multi-dimensional continuum.

ments between partners cause the benefit of resource exchange to become contingent on the relationship between the consumption vector and acquisition constraint of each partner. Specifically, it depends on whether or not the individual that is relatively better at acquiring one resource (according to the differences in acquisition constraints) is also the individual that has a higher relative requirement for that same resource (according to differences in resource consumption vectors). If this is true, then there will be little benefit to specialization and trade—the effects of differing acquisition constraints and differing consumption vectors counteract each other. According to the difference in acquisition constraints, each individual should specialize on acquisition of the resource that it acquires relatively more efficiently than the other. However, according to the difference in consumption vectors, each individual should become less specialized, acquiring more of the resource for which it has less of a requirement. In the opposite situation, when the individual that is relatively better at acquiring a resource is also the individual that needs relatively less of that resource, then trade is beneficial and the outcome is clear. In this situation, both individuals should acquire relatively more of the resource that they are relatively better at acquiring and that they need relatively less of, and then

trade with each other to increase total resource acquisition compared to the scenario of mutual non-interaction.

Among these 12 qualitative cases, there are seven in which resource exchange results in a mutual benefit to the partners (figure 4). It is important to note that the cases we discuss are presented as qualitatively different conditions, but in actuality are extreme points on a multi-dimensional continuum. The net benefit of resource exchange is determined by the dominant traits of the interaction. For example, if two individuals have moderately different acquisition constraints but extremely different consumption vectors, then the difference in consumption vectors should have a much stronger effect on the benefit of resource exchange between them. A less intuitive, but nonetheless interesting, example occurs when acquisition constraints are concave (bulging away from the origin), and one individual is slightly better than its partner at acquiring R1 but has a much higher relative requirement for that resource than its partner. In this case, it may be beneficial for the individual to specialize in the acquisition and trade of R2, despite perceiving a relative acquisition disadvantage for that resource. Finally, the only qualitative scenarios we do not analyse specifically here involve two individuals that differ in the shape of their acquisition constraints (straight versus concave versus convex). These

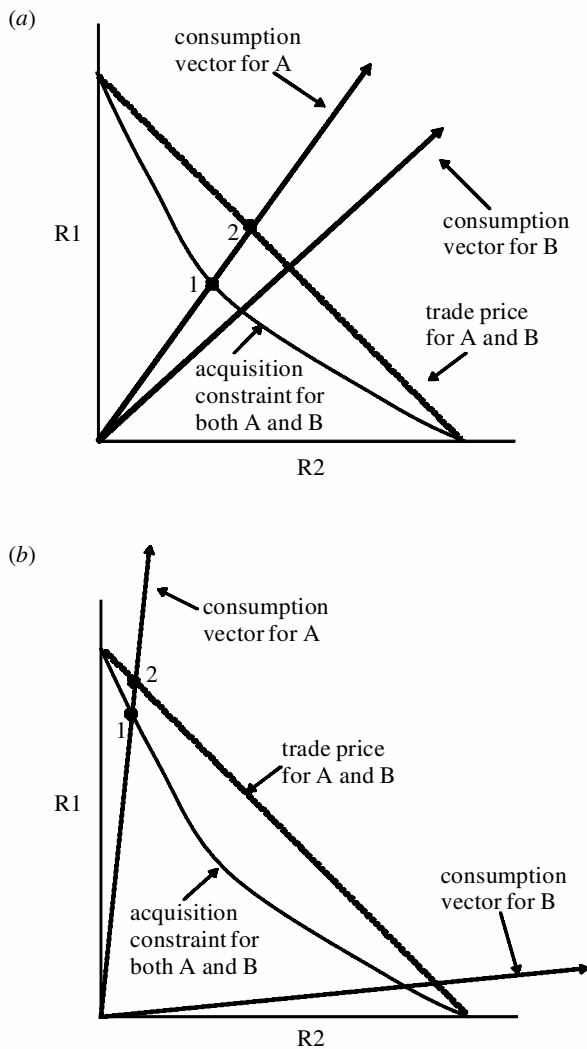


Figure 5. Market conditions for two heterospecific individuals (A and B) having an identical, convex acquisition constraint, and either similar consumption vectors (a) or very different consumption vectors (b). In a resource exchange scenario, A and B agree to trade R1 and R2 at a cost ratio (indicated by the trade acquisition constraint, i.e. the dotted line) that is more favourable for both. When the consumption vectors of A and B are very different (b), the benefit of trade (e.g. for individual A, the distance from point 1 to point 2) is less than when consumption vectors are more similar (a).

scenarios have more complicated outcomes, and in general will be relatively asymmetric, with each trading partner experiencing a qualitatively different benefit from trade. For example, consider two individuals that have identical consumption vectors, but very different acquisition constraints, with one having a straight acquisition constraint and the other having a concave acquisition constraint. In this case, trade will be relatively beneficial to the former individual but not very beneficial to the latter individual.

5. DISCUSSION

The analysis presented here suggests how consideration of the resource requirements and acquisition abilities of potential mutualists can lend insight into the benefits likely to be gained from mutual resource exchange. One

prediction is that differences among species in their relative resource requirements can influence which resources should be traded, and the degree to which such trade is beneficial. Do such differences in resource requirements between species exist in nature? In fact, such differences seem to be prevalent. For example, Rhee & Gotham (1980) showed that eight species of freshwater algae differ substantially from each other in their relative requirements for nitrogen and phosphorus. Such differences may be even more extreme when comparing distantly related organisms.

In general, plants have a higher ratio of carbon to both nitrogen and phosphorus in their tissues and metabolic processes than do fungi (Hurst & Wagner 1969; Perry 1994; Tian *et al.* 1992). Similarly, fungi usually have higher ratios of carbon to nitrogen and phosphorus than do bacteria, due in part to the composition of chitin in fungal cell walls relative to the composition of the mureoproteins in the cell walls of bacteria (Hurst & Wagner 1969; Perry 1994; Woods *et al.* 1982). If we assume comparable respiration rates, then such differences in compositional C : N, for example, imply that bacteria have a relatively higher requirement for nitrogen than fungi. To predict how such interspecific differences should impact the benefits of resource exchange, we also need information about the shapes of the trade-offs in acquisition of the two resources experienced by the potential mutualist partners. Such data may be difficult to collect, since we might expect to see few individuals in nature acquiring resources at the extreme ends of their acquisition constraints. However, hypotheses about the qualitative nature of these trade-offs, i.e. whether acquisition constraints are concave or convex, may be possible in some cases and would allow qualitative predictions about the likely benefits of resource exchange among certain taxa.

Imagine, for example, two hypothetical soil microbe species, a bacterium and a fungus. Assume that for both species the acquisition of carbon is to some extent a by-product of the acquisition of nitrogen, since both carbon and nitrogen can sometimes be acquired as the products of organic matter decomposition. In this case, both the bacterium and the fungus should benefit from a relationship where bacteria trade carbon to fungi for nitrogen, and fungi trade nitrogen to bacteria for carbon (see figure 4). This trading relationship would be driven by the differences between bacterial and fungal individuals in relative requirements for the two resources. Such a trading relationship would be even more favoured if the bacterium had a relative advantage over the fungus for carbon acquisition compared to nitrogen acquisition.

One interesting prediction of the model presented here is that even in some cases where trade is predicted to be beneficial, complete specialization on acquisition of one resource is not predicted—both partners are predicted to retain some ability to acquire both resources on their own. This scenario arises when acquisition of the two resources exhibits a by-product type trade-off, i.e. the acquisition constraint bulges away from the origin, and resource exchange is predicted to be beneficial either due to differing consumption vectors between the two individuals or due to differing acquisition constraints between the two individuals (figure 4). The intuitive explanation for this result is that when there is a by-product relationship between the two resources, increasing specialization on

acquisition of one or the other resource always results in increasing costs. For example, if an individual is acquiring R1 and R2 at a point along a concave acquisition constraint close to the R1 axis, then R1 is being acquired at a point where it is very expensive relative to R2—a large amount of R2 acquisition must be sacrificed to acquire a small additional amount of R1. Thus, when two resources have a by-product relationship, it is always more efficient to acquire the two resources simultaneously than to specialize. This result predicts that when resources are acquired as by-products of each other, mutualist species trading those resources should be less specialized with respect to resource acquisition. Both partner species should have the ability to obtain resources in two different ways—both in trade and on their own. The species involved in such mutualisms may be more robust to fluctuations in each other's abundance over space and time since required resources can be obtained in the absence of a mutualist partner. By contrast, complete resource specialization is predicted when trading partners have linear or convex acquisition constraints, and similar consumption vectors.

We have built upon earlier results, to show that the degree to which two individuals can benefit from a trading relationship can be strongly influenced by differences between the individuals, not only in their relative abilities to acquire two resources, but also their relative requirements for two resources, and that these benefits are contingent on the shape of the trade-off in acquisition between those two resources. Interestingly, variation among partners in resource requirements may also be relevant to cooperation between individuals of the same species, with a Prisoner's Dilemma being avoided when individuals have different relative requirements for cooperative services (Johnson *et al.* 2002). Based on the results derived here, a suite of predictions can be made about whether or not resource exchange is beneficial compared with a strategy of mutual non-interaction (figure 4). These predictions make clear the necessity of an explicit consideration of the resource requirements and acquisition abilities of potential trading partners, in order to understand when mutualistic resource exchange has the potential to occur. What will be most important in assessing the relevance of these results to real interactions in nature are empirical assessments of the degree to which biological interactions exhibit the characteristics of markets (e.g. the cleaner fish–client fish mutualism (Bshary 2001); and the ant–lycaenid mutualism (Noe 2001)). Most importantly, interspecific interactions functioning as biological markets will involve organisms that are able to accurately perceive differences in the relative benefits being offered by competing potential trading partners (i.e. individuals of another species), and choose partners based on those offers.

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