

## Commentary

# Overyielding and stable species coexistence

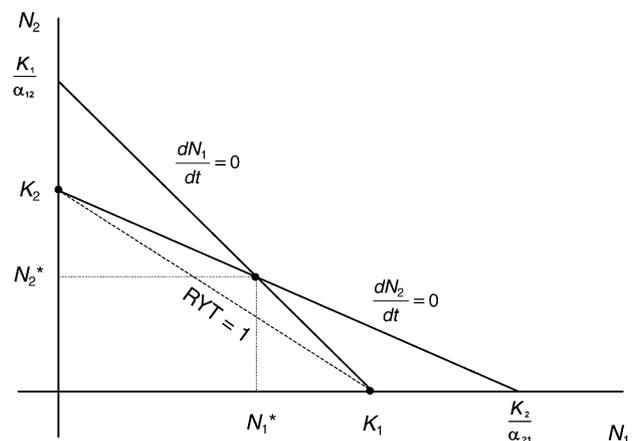
The concept of overyielding originated in plant sciences in the 1950s and 1960s and was widely used in the following decades to assess whether mixtures of plants performed better than expected when compared with monocultures. Overyielding has re-emerged in the last few years as an important method in the analysis of biodiversity experiments (Hector, 1998; Loreau, 1998; Loreau *et al.*, 2001, 2002; Hooper *et al.*, 2005) and other new research areas (Bernasconi *et al.*, 2003). Biodiversity experiments manipulate community diversity (while holding other factors constant) to investigate impacts on ecosystem functioning. Previously, use of the overyielding concept has been limited mainly to the analysis of community ecology experiments on species interactions and in agricultural research, particularly intercropping. However, there has been relatively little work that assesses the overyielding concept in the context of community ecology theory. Loreau (2004) used the classical Lotka–Volterra competition model to investigate overyielding and functional redundancy of species in the context of theory on the stable coexistence of species (Fig. 1). In this issue, Beckage & Gross (pp. 140–148) also use Lotka–Volterra competition models to assess the frequency and degree of overyielding of theoretical communities.

### Overyielding and relative yields

The concept of overyielding is based on the measures of relative yield and relative yield total. These measures were devised and pioneered in Wageningen during the 1950s and 1960s by De Wit (1960). The measures were devised for the analysis of traditional experiments in plant ecology (Harper, 1977) and agriculture (Vandermeer, 1989) where species were grown in monocultures and mixtures. The relative yield of a species is simply its yield in mixture compared with that in monoculture where the null expectation is the monoculture yield times the starting proportion in mixture (e.g. in a two-species mixture where species were planted or seeded at equal density the expected yield of each species is 50% of its monoculture value). The relative yield of a species is a measure of its performance under conditions of intra- and interspecific interactions relative to when only experiencing intraspecific interactions. An important additional consideration is the density under which species start growing. Biodiversity experiments have tended to use a substitutive approach where total

density is held constant and in a two-species mixture plants of another species are substituted for half of the conspecifics of the monoculture. In biodiversity experiments, the monocultures provide the obvious null expectation as the situation with no effective biodiversity (at least at the species level and above). However, substitutive designs alter both diversity and individual species densities at the same time. Additive designs preserve monoculture density while adding plants from other species; a common application is in investigating the effects of weeds on crop yields. Density and diversity can be independently manipulated in a response surface approach which varies the density of both species as orthogonal design variables.

Relative yields tell you about individual species responses but not about the performance of the whole community. The relative yield total (RYT) is simply the sum of the individual relative yields. The null expectation is a value of one, as increases in the relative yields of some species are exactly compensated by declines in others. In a simple resource competition framework,  $RYT = 1$  is consistent with a zero-sum game where a fixed amount of resource is divided up amongst species.  $RYT > 1$  indicates increases in the relative yield of some species which are not exactly compensated for by



Zero-growth isoclines for the Lotka–Volterra competition model when there is stable coexistence between the two species (solid lines). Stable coexistence occurs when  $K_2/\alpha_{21} > K_1$  and  $K_1/\alpha_{12} > K_2$ . In this case, the stable equilibrium point ( $N_1^*$ ,  $N_2^*$ ) lies above the line  $RYT = 1$  (dashed line) which connects the two monoculture equilibria ( $K_1, 0$ ) and  $(0, K_2)$ .

**Fig. 1** Overyielding in the framework of the Lotka–Volterra competition model. Stable equilibrium points above the relative yield total ( $RYT$ ) = 1 line are stable communities that overyield (as in this case). (Reproduced from Loreau (2004) (along with original legend), with permission from Blackwell Publishing Ltd.)

declines in the relative yields of others. This could occur for various reasons, including resource partitioning in which species' resource requirements do not exactly overlap and a mixture of species can therefore exploit resources more completely than any species alone. However, other processes could also produce  $RYT > 1$ , including facilitation where one species benefits another.  $RYT > 1$  could also occur as a result of more indirect processes, such as reduced incidence or severity of pests or pathogens in mixtures relative to monocultures.

Mixtures of species are said to overyield when  $RYT > 1$  (De Wit, 1960; Harper, 1977; Vandermeer, 1989). However,  $RYT > 1$  does not mean that the mixture of species will necessarily outperform the monocultures of all of the constituent species. Whether this occurs or not depends on the balance between the yield-enhancing effects that cause  $RYT > 1$  and the dilution effect caused by substituting individuals of the species with the best performing monoculture with those from species with lower-yielding monocultures. When the yield-enhancing effects outweigh the monoculture-dilution effect such that the mixture outproduces the highest yielding monoculture, a mixture is said to show 'transitive overyielding' (Harper, 1977; Vandermeer, 1989, but see Hector *et al.*, 2002).

### An additive partitioning of biodiversity effects

Relative yield totals have proved very useful but they have a number of limitations. The RYT gives an indication (subject to caveats like those above) of collective community performance (resource partitioning, etc.). However, it gives no collective indication of how abundant species are in mixture and how this relates to their monoculture performance. From an analytical perspective, the scaling of the RYT to a null value of one has the disadvantage that it imposes the asymmetry of a floor at zero but an open ceiling. The additive partitioning method (Loreau & Hector, 2001) extended the relative yield approach to define an overall net effect and to partition this into two additive components: a complementarity effect and a selection effect. The 'net biodiversity effect' (for a community formed from species started at equal densities) is simply the difference between the observed yield of the mixture and the average of the monoculture yields. The complementarity effect is based on changes in relative yields (or rather differences in observed relative yields vs their null expectation values) and is linearly related to RYT but scaled to a value of zero (so as to avoid the asymmetry mentioned above and for the convenience that ANOVA and related methods usually automatically test vs a null value of zero). Complementarity effect values  $> 0$  are consistent with resource partitioning, facilitation and related effects as described above, while values  $< 0$  indicate interference competition. The other half of the partition is a covariance term which was inspired by the Price equation from evolutionary genetics (although the additive partitioning

method and Price equation are not equivalent). The selection effect measures the covariance between a species trait (e.g. monoculture biomass) and its performance in mixture. In this scenario, positive selection effect values indicate dominance of communities by species with greater than average monoculture biomass and negative values indicate the converse.

### A tripartite extension of the additive partition

One limitation of the additive partition is that it assumes, as do relative yields, that complementarity is distributed equally across species. This means that it may underestimate total complementarity, some of which falls under the selection effect (Petchy, 2003). Recently, Fox (2005) has extended the partition by adding a further split. The new extension removes the trait-dependent complementarity from the selection effect, leaving a pure dominance effect that quantifies changes in relative abundance resulting from pure resource competition. Interpreting the new trait-dependent complementarity effect is a little less straightforward, but Fox (2005) provides some possible biological interpretations. One simple application would be to view the new term simply as a correction factor. A new total complementarity effect could be defined as the sum of trait-dependent and trait-independent terms from the tripartite partition (the latter being the complementarity effect from the original partition). The dominance effect from the tripartite partition quantifies shifts in relative abundance resulting from pure resource competition, and the selection effect from the two-way partition quantifies shifts in relative abundance resulting from resource competition and all other species interactions.

### Transitive overyielding

As Beckage & Gross point out, there is some debate about how best to define transitive overyielding in biodiversity experiments. The situation in an agricultural setting is relatively clear: for a farmer the question is whether a mixture can overyield the most productive monoculture. However, in a nonagricultural setting the choice is less clear, because, in principle, every monoculture provides a potential benchmark for comparison (Hector *et al.*, 2002). When would it not make sense to select the species that is highest yielding in monoculture as the benchmark? One situation occurs when the species that is highest yielding in monoculture is not highly abundant in mixture. Abundance is often taken as being inversely related to extinction risk (small populations are usually more likely to become extinct) so that a species that is not highly abundant in the original community may be one of the species that is lost. In this case, it would make no sense to take this species as a benchmark, no matter how high yielding it is in monoculture, since it is not present in the later depauperate community (Hector *et al.*, 2002).

## Overyielding and species coexistence: future perspectives

The new theoretical analysis by Beckage & Gross produces results largely in accord with Loreau (2004): a striking parallel between the conditions necessary for stable coexistence and those that generate overyielding. However, transitive overyielding will only occur under certain conditions, and situations are possible in which diversity and ecosystem functioning are not positively linked (Mouquet *et al.*, 2002; Loreau, 2004). Further exploration of the conditions necessary for both overyielding and coexistence in different theoretical frameworks will provide a solid basis for the interpretation of biodiversity experiments and help to put the experimental results into the broader framework of community ecology.

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## Letters

# What is the link between carbon and phosphorus fluxes in arbuscular mycorrhizas? A null hypothesis for symbiotic function

Arbuscular mycorrhizal (AM) fungi (Phylum: Glomeromycota) are obligate symbionts that obtain their carbon nutrition entirely – as far as is known – from a host plant. The key functional benefit to the plant is a supply of phosphate, a nutrient for which the dominant available forms in soil

(orthophosphate ions) are very poorly mobile because of the abundance of cations such as  $\text{Ca}^{2+}$ ,  $\text{Fe}^{3+}$  and  $\text{Al}^{3+}$  (Tinker & Nye, 2000). Although other functional interactions are known, including defence against pathogens and improved water relations (Newsham *et al.*, 1995a), these may have evolved more recently. It is likely that phosphate uptake was the original selective advantage offered, and that the symbiosis evolved contemporaneously with the land plant flora before the evolution of roots, at a time when acquisition of poorly mobile phosphate ions from soil must have been a major challenge to plants. The evolution of the mycorrhiza may have been a critical stage in the evolution of the land flora (Pirozynski & Malloch, 1975; Brundrett, 2002).

The diagnostic feature of the symbiosis is the arbuscule, a haustorium that penetrates root cortical cells and invaginates the plasma membrane, creating a large surface area for exchange. There is good evidence that the arbuscule is the site of phosphate transfer from fungus to plant, and rates of

plant P uptake can be correlated with the development of arbuscules in the root system. A plant phosphate transporter (MtPt4) is expressed specifically on the peri-arbuscular membrane in *Medicago truncatula* (Harrison *et al.*, 2002), and is assumed to be responsible for plant capture of phosphate from the fungus. Similar transporters have been identified in other species (Glassop *et al.*, 2005; Nagy *et al.*, 2005).

In contrast, the mechanism and location of the reciprocal transfer of C from plant to fungus remain unclear. It is likely that fixed C moves as hexose, probably principally glucose and fructose (Pfeffer *et al.*, 1999). The arbuscule could be the site of both hexose and phosphate transfer, and a model for how this might work has been proposed (Blee & Anderson, 1998). However, there is as yet no evidence for a fungal hexose transporter expressed on the arbuscular membrane (Smith *et al.*, 2001). An alternative explanation is that the intercellular fungal hyphae that grow between and among the cortical cells are the principal organs of fungal hexose uptake (Smith *et al.*, 2001). If this is true, a simple model of phosphate and sugar movement can explain many features of the symbiosis.

Arbuscular mycorrhizal fungi typically colonize roots as defined and restricted patches, ranging from a few tenths of a millimetre to as much as a centimetre of cortex (Cox & Tinker, 1976), and surrounded by other colonization units that may belong to other mycelia. An effective mechanism for symbiotic function must therefore stimulate the plant to deliver sugars to these localized patches within the root. There are two possible mechanisms: either the plant can recognize the presence of the fungus; or it can detect the increased phosphate supply created by the fungus. The former is an evolutionarily unstable mechanism as it is open to 'cheat' fungi that can mimic the signals of a beneficial symbiont without delivering any benefit, whereas the latter ensures that sugar will only be exchanged for phosphate.

Recognizing locally increased P supply is something that many plants can do, as they respond to it by the local proliferation of roots (Drew, 1975; Williamson *et al.*, 2001). Root proliferation – expressed either as an increase of initiation or elongation of laterals, or both – is a tightly regulated response, as root growth is inhibited either side of zones of stimulation (Linkohr *et al.*, 2002). How plants detect locally enhanced phosphate acquisition is unknown, but by analogy with the response to nitrate, where the nitrate ion itself appears to be the signal molecule (Zhang & Forde, 1998), it is likely to be based on the phosphate ion.

We can therefore postulate that when an AM fungus develops an arbuscule inside a root cell and begins to move phosphate ions across the peri-arbuscular membrane, the plant will detect this increased P flux, which will stimulate increased C allocation to a localized region around the arbuscule; such fine-scale pattern in C flux may be detectable by labelling experiments. The challenge for the fungus is now to acquire the extra C, rather than it being used for new root growth. Root cortical cell membranes are leaky to

sugars, which are abundant components of exudates to the rhizosphere (Jaeger *et al.*, 1999). The increased sugar supply will therefore increase the sugar concentration in the apoplast. Although root cells do reabsorb sugars that move into the apoplast, all that is now required is that the fungus has a hexose transporter with a greater capacity for hexose acquisition than the plant, ensuring a one-way valve.

A threat to the fungus would occur if the plant were to initiate new lateral roots at the sites of colonization: these would use sugars and disrupt fungal growth in the cortex. Mycorrhizal colonization can suppress lateral development (Fitter, 1977), consistent with this model. The recent report (Olah *et al.*, 2005) that a diffusible signal from the extraradical mycelium of an AM fungus stimulates lateral formation in *M. truncatula* is not inconsistent with the idea that the intraradical mycelium will suppress lateral growth, as new colonization may be favoured by the development of new laterals, even if growth of existing colonization units is not.

The mechanism proposed here is that C–P exchange in the arbuscular mycorrhiza is regulated by the transport of phosphate across the arbuscule interface, directly stimulating the supply of C by the plant to a spatially defined location in the root, with the fungus capturing hexoses that consequently leak into the apoplast. This mechanism would be resistant to invasion by cheat fungi: if they fail to supply phosphate through the development of arbuscules, they will not stimulate an increased sugar supply. Such fungi could still colonize roots, but would have to scavenge for sugars at the normal and typically low concentrations in the apoplast. In contrast, a mechanism based on recognition processes between plant and fungus within the root (for example at the peri-arbuscular membrane) would be highly susceptible to invasion by cheats, as it would always be possible for a fungus to possess the recognition signals but to offer no benefit. There will have been strong selection pressure for such a recognition mechanism to be active before colonization of the root (Gianinazzi-Pearson & Brechenmacher, 2004; Akiyama *et al.*, 2005).

Numerous plant mutants (and indeed species) are known in which the fungus fails to develop arbuscules and therefore fails to deliver phosphate to the root. This outcome could be explained by the plant regulating fungal growth where there is no benefit, but is as likely to be caused by the fungus aborting the development of colonization where there is no reciprocal response by the plant in the form of an increased sugar supply. Some of these mutants may therefore have a restricted root-proliferation response to phosphate.

A mycorrhizal symbiosis can supply the entire P uptake of a colonized plant, even when there is no growth stimulation and when root development and P availability suggest that the plant would be capable of acquiring substantial amounts of phosphate directly across root cell membranes (Smith *et al.*, 2003). This finding supports the model proposed here, as a successful fungus must continue to provide the plant with P through the arbuscules, in order to maintain a reciprocal C

flux. However, the variation in P inflow to plants colonized by different AM fungi, shown by Smith *et al.* (2003) and by Jakobsen's group (e.g. Munkvold *et al.*, 2004), raises an important question: if C acquisition is determined by P supply, why would fungi vary in the amount of P they supply? The question cannot be answered definitively, but a likely explanation is that fungi (like all organisms) vary in growth strategy and therefore in their demand for C.

This model explains a number of other features of AM symbioses, notably the controversy over C transport from plant to plant via fungi. Although it has been suggested that C may move in the reverse of the normal direction (that is, from fungus to plant), the only firm evidence for this phenomenon in the AM symbiosis is in achlorophyllous plants for which the fungus is the sole source of C (Leake, 1994; Bidartondo, 2005). An explanation for the reversal of C flux in these systems might be that the plant cells have such low sugar concentrations that the flux of hexose from cortex to apoplast is less than from fungus to apoplast, and that the plants have evolved a transport system with an even greater hexose acquisition capacity than the fungus. There are a few other cases where C movement has been postulated from fungus to a green plant, usually where the plant was in deep shade or experiencing intense C demand. In only one case involving an AM fungus has a substantial flux been quantified (Lerat *et al.*, 2002); the plants were tree seedlings rapidly expanding their leaves in spring, and a bulbous plant with a large C store in the bulb. Typically, although C can move from root system to root system through the mycelium, it remains in fungal tissues and is not transferred to the plant (Fitter *et al.*, 1998; Pfeffer *et al.*, 2004).

Another striking feature of AM symbioses is the common existence of multiple colonization of a single root system by a number of different fungi, often closely co-located in the root (Abbott, 1982; Clapp *et al.*, 1995; Merryweather & Fitter, 1995). Multiple colonization might occur frequently if the recognition systems for colonization were generic, and if fungal success within the root varied with their ability to supply phosphate to the plant. Although there could potentially be competition for colonization sites within the roots, selection pressures would act principally on the external mycelium that exists in the highly variable environment of soil. We can predict, therefore, that AM fungi will show substantial interspecific variation in their response to soil factors. We already know that they vary in response to pH (Wang *et al.*, 1993) and disturbance (Helgason *et al.*, 1998); it is likely that many more ecological differences of this sort await discovery.

This model suggests that cheats, fungi that gain C from their host without supplying benefits in return, will be rare. Although some plants – notably achlorophyllous mycoheterotrophs – apparently cheat their fungal partner (Bidartondo, 2005), the evidence for fungal cheats is less clear. Depression of plant growth in experimentally synthesized AM symbioses, especially when the partners do form mycorrhizas in nature

(Klironomos, 2003), is often taken to suggest the existence of fungal cheats. However, no experimental design can explore all the possible conditions under which the symbiosis might be mutualistic. Newsham *et al.* (1995b) found that the *Vulpia ciliata* ssp. *ambigua* / *Glomus* BEG6 mycorrhiza did not promote P acquisition by the plant. Instead, protection from a pathogen was the real plant benefit, but to demonstrate that required an explicit test in the presence of a specific pathogen. The number of potential experimental conditions required to eliminate the possibility that there is some benefit, under some set of environmental conditions, at some stage in the life cycle, is legion.

Cheat fungi might still persist under this model. As already noted, colonization units of distinct fungi may be closely co-located in roots, so stimulation of C supply by one fungus to a region of the root might allow another fungus to benefit from improved sugar supply. We can predict, therefore, that colonization of the root by one fungus may stimulate colonization by another. In a model where the symbiosis is controlled internally by a recognition process between plant and fungus, such behaviour would be hard to explain.

Finally, Mosse (1973) was the first of many to demonstrate that plants can reject new colonization by AM fungi if they have plentiful phosphate, but that they do not eliminate existing colonization units. Similarly, existing colonization can suppress new colonization in the other half of a split-root system (Catford *et al.*, 2003). That outcome is what would be predicted from the current model: as long as the fungus continues to supply phosphate, even if in excess of plant need, it should stimulate sugar supply.

In this simple model for symbiotic function in arbuscular mycorrhizas, the fungus supplies phosphate to the host across the arbuscular interface, and in so doing stimulates a response from the plant by which sugars are transported to the region around the arbuscule. The mechanism involves no unknown biology; explains many patterns of behaviour in the symbiosis; and is evolutionarily stable in being resistant to invasion by cheat fungi. In addition, it offers a number of clear predictions about the biology of the symbiosis, including that:

- all AM fungi have the capacity to transport P across the arbuscular interface;
- C uptake occurs from the cortical apoplast;
- plants respond to colonization by localized C transport, as they do to local nutrient enrichment;
- AM fungi have hexose transporters with a greater capacity to acquire sugars from the apoplast than those on the plant cell membranes;
- colonization of the root by one fungus should locally promote colonization by others;
- late stage nonmycorrhizal mutants may be unable to proliferate roots in response to a localized P supply;
- there will be greater differentiation among AM fungi in traits of the extraradical mycelium than of the mycelium inside the root.

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