Coevolutionary Adaptation in Mutualisms

Gregory Wyatt
St John's College
University of Oxford

A thesis submitted for the degree of
Doctor of Philosophy

Trinity Term 2014

I dedicate this thesis to my first academic mentor, Professor Robert Seymour, who died on July 24, 2012. He supervised my 4th year undergraduate project when he was under no obligation to do so. I had given up on the first project I had begun, and my supervisor for the second had gone on sabbatical. He expended time and effort to support me on a topic some distance from his area of expertise. In so doing, he inspired my passion for academic research. He was the first to suggest that I should consider doctoral studies, and unfortunately his illness prevented me from pursuing research with him. This thesis would never have happened without his support.

Table of Contents

Declaration

Chapter 2 has been published as: Wyatt, G. A. K., Kiers, E. T., Gardner, A., and West, S. A. 2014. A biological market analysis of the plant-mycorrhizal symbiosis. Evolution 68:2603-2618. ETK suggested that studying the cooperativeness of mycorrhizal fungi under different nutrient conditions would be useful. I conceived the model and wrote the manuscript. I received feedback from ETK, AG, and SAW. The published version is included as an Appendix to this thesis.

Chapter 3 was submitted to Nature Communications as an Article. I developed the idea and wrote the manuscript. I received feedback from ETK, AG, and SAW.

Chapter 4 is being prepared for publication as a research article. I developed the idea and wrote the manuscript. I received feedback from ETK, SAW, and AG.

Chapter 5 has been published as: Wyatt, G. A. K., West, S. A. and Gardner, A. 2013. Journal of Evolutionary Biology 26:1854-1865. SAW and AG suggested the idea of developing an explicit model to test whether or not natural selection could favour altruism between species. I conceived the model and led the write-up of the paper with assistance from AG. I received feedback from SAW and AG. The published version is included as an Appendix to this thesis.

Chapter 6 is being prepared for publication as a research article. Andy Gardner suggested this area of research. I then developed an analysis of the problem and wrote a manuscript. Rufus A. Johnstone commented on the manuscript, pointed out mistakes and sent me unpublished on the same problem. I then corrected the manuscript and received feedback from RAJ, Alasdair I. Houston and John M. McNamara. I wrote the version presented here and the mathematical treatment is my own, but I have incorporated the visual explanation and the example from RAJ's manuscript. I also had access to unpublished work by E. M. K. Wilson on the same topic. I was only sent this after the version presented here was written. I made some small changes based on results presented in EMKW's work.

Acknowledgements

First billing must go to my supervisors, Stu and Andy, who gave me help, support and prompt feedback on my projects. It is easy to take their expertise and guidance for granted on a day-to-day basis, so while I cannot do justice to their efforts on this page, I hope that my efforts in producing this thesis go some way to providing a reward for theirs. I am extremely grateful for their work in opening up the magical universe of social evolution to me. I will never see life in the same way again.

Toby has earned her own paragraph and really deserves no less credit than my two official supervisors. Having Toby as a “third supervisor” is a privilege that I could not have dreamed of when I started. Her willingness to help was unrivalled throughout and, as she wrote, I am sure that nobody else was thinking of fungal inhibition of plant P uptake at just after midnight in Amsterdam on Sunday June 8th 2014. Praising only her efforts, however, is completely insufficient. I have not met anyone else in academia that so effortlessly juggles the empirical and conceptual sides of science. The detail she provided for all of my work was invaluable, and if today my ability to “think about the biology” has improved, it is largely down to her.

I thank the BBSRC for providing me with a doctoral training grant.

Too many senior academics to mention by name have given me time, support, and shown interest in my work, but three deserve particular credit. Laurent Lehmann was the first academic to actively support my ambitions for a doctoral degree and without this I may never have got started. He gave me time and support despite my decision to head elsewhere for my studies. It is a credit to him that despite having thoroughly enjoyed my four years at Oxford, I have always known that I passed up a fantastic opportunity. Alan Grafen provided inspiration and one of the greatest regrets during my time at Oxford is that I missed the opportunity to work with him. The brief interactions that I had with him proved both the thoroughness of his mind and the high standards to which he holds his collaborators. I cannot think of a better combination under which to develop. Ford Denison certainly will not expect to be recognised here, but his exemplary treatment of me at the Evolution conference in Ottawa in the summer of 2011 deserves particular recognition. He immediately showed enthusiasm in my work and sat me down in the middle of the conference centre to discuss it.

Too many peers and aspiring academics deserve credit to mention here, but it would be wrong not to mention the following by name: Barbara, my companion during my Oxford career; Adam, my civil partner; Lorenzo, my moral compass; Dan, Ben, Max and Philip, the lads of the theory office; Jay, my academic mentor; Shana and Melanie, who were kind enough to copy edit some of my thesis; Dave, my 6am psychiatrist; and Max, the Eurochic Frankenstein I created but can no longer control.

Finally, I would like to thank my family for supporting me even as Woody and Buzz Lightyear came flying dismembered out of the pram. Through highs, lows, and spectacular tantrums, I am so grateful to know that you will always be there.

Abstract

Natural selection favours those individuals that respond best to novel features of their selective environment. For many, a critical challenge is responding to evolutionary change in mutualistic species. These responses create complex feedbacks, so only coevolutionary approaches are able to fully answer key questions about the maintenance or disruption of mutualistic behaviour, and explain the range of mechanisms that allow individuals to benefit from these associations. I first consider the hypothesis that economic models studying multiple classes of traders, where each trader seeks to optimise its own payoffs will yield insights into mutualistic systems. I show that individuals can be favoured to discriminate amongst potential partners based on the price for which they provide resources. Then, I show that market mechanisms can maintain cooperation and drive specialisation in mutualistic systems. I extend this market model to allow individuals to restrict a mutualistic partner's access to resources, and show that this strategy can stabilise cooperation and increase the fitness of both partners. I also explicitly incorporate relatedness in my market model. I show that high relatedness sometimes increases cooperativeness in members of a mutualistic species, but sometimes decreases cooperativeness as it narrow the scope for partner choice to maintain cooperation. Having studied market mechanisms, I consider indiscriminate costly help to members of another species. I discover that this trait can be favoured by natural selection and can be classified as either altruism between or altruism within species. Finally, I consider a framework for analysing coevolved phenotypic responses to a partner's cooperativeness, a challenging process to model. I demonstrate that this framework can yield firm predictions about behaviour whenever partners hold private information about their costs and benefits.

1

Introduction

1.1 Overview

In this chapter, I provide background to the conceptual framework and modelling approaches used in this thesis (Section 1.2). I then outline the structure of this thesis, provide readers with an introduction to each chapter, and point out links between them (Section 1.3).

1.2 Economic Approaches in Biology

In this thesis, I study biological problems using many modelling tools and assumptions that are widely applied in both biology and economics, but also other methods that have historically only been adopted in one of the subjects. In some cases, problems in one discipline have direct parallels in another. Applying insights already developed in economics could advance research in biology, and vice versa.

Here, I review three notions shared by biology and economics. First, I consider why maximising agents are studied and how their use in models is justified in both disciplines. Then, I study the different levels at which analogies of agency are used as conceptual tools, and where the use of these tools is valid. Finally, I treat different notions of the environment and how agents interact within it. These building blocks of modelling in both biology and economics will allow practitioners to better understand and draw conceptual parallels in each other's research.

1.2.1 Maximisation

Many problems in economics study decisions made by agents and their outcomes. A decision-making problem of this kind requires a set of alternatives from which to choose. The decision maker is then able to rank the alternatives in order of preference or choose among them. At this point, it is a natural step for economists to simply assume without further justification that individuals will always choose the most preferred option. Hence, maximisation in economic decision-making problems is a natural assumption.

In biology, the maximisation problem is more complex. The notion that life manifests function predates Darwin's (1859) theory of evolution by natural selection. Darwin's ideas were influenced by natural theologians. The most influential of these is William Paley, who observed design in the natural world and thus assumed a designer (Paley 1802). However, function and design do not necessarily imply that maximisation is achieved. Paley himself noted that even a broken watch still manifests evidence of design. Nonetheless, design in the natural world does imply goal-directedness, or teleology, and thus some maximand. That is, an organism is designed to fill some purpose. It can be described as striving to maximise, even if it does not achieve this goal.

Darwin's great insight was to become aware that the appearance of design does not imply a designer. It merely requires a selective process based on the differential survival and reproduction of individuals that are better adapted to function in their environment. Whilst bacteria, for instance, are not striving to do anything, natural selection will lead them to manifest features that appear designed to help them strive to increase their survival and reproduction.

Whilst the notion of design, and thus a maximand, in biology predates Darwin's first publication of *On the origin of species*, the earliest statement notion of maximisation as an outcome of natural selection came subsequently. This statement, whilst devoid of notions of design and goal-directedness, comes from Herbert Spencer's (1864) coining of the term "survival of the fittest" in his *Principles of Biology*, where he writes:

> *And by the continual destruction of the individuals that are the least capable of maintaining their equilibria in presence of this new incident force, there must eventually be arrived at an altered type completely in equilibrium with the altered conditions.*

Darwin adopted the term "survival of the fittest" in his fifth edition of *On the origin of species* (1869). Incidentally, Herbert Spencer's *Principles of Biology* was the earliest attempt to draw parallels between economics and Darwin's theory of evolution by natural selection.

Fisher (1930), the architect of the modern synthesis between Darwin and Mendel's ideas, set out the first formal notion of an improving process in biology. He derived the Fundamental Theorem of Natural Selection, which shows that:

> *The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time.*

Fisher seldom commented on the theorem making this statement obscure, but the first accepted interpretations suggest that it means natural selection causes an increase in the mean reproductive success of individuals in a population at a rate equal to the variance in fitness in that population (Price 1972, Ewens 1989). This interpretation is counter-intuitive because the aggregate reproductive success of a population must be approximately constant over time otherwise it would either go extinct or overrun the world (Frank 2011). The solution is that the 'environment', in which Fisher includes all gene frequencies, social interactions, and the physical environment must deteriorate at a rate equal to the increase in fitness for a given organism (Frank & Slatkin 1992). At the very least, this allowed Fisher to isolate an invariant quantity that increases under the action of natural selection except when no genetic variability in fitness remains in the population.

However, this does not provide a proof that natural selection actually maximises any quantity. In fact, subsequent work in population genetics, the analysis of gene frequency changes in theoretical populations, has repeatedly found cases where natural selection does not maximise mean fitness in populations (Ewens 2004). This has been shown both in single locus cases where genetic architecture can prevent optimal phenotypes from being expressed in populations, and more famously in multi-locus cases (Moran 1964, Karlin 1975).

Despite these theoretical reservations, the idea that life could only be understood if individuals were treated as purposeful agents was continuously present in biology, for example as argued in Russell's (1916) book *Form and Function*. This perspective enshrined the concept of a maximand, whether or not it was actually reached. The idea that maxima are achieved by natural selection received support from empirical scientists, particularly Lack who provided evidence that Starling clutch sizes maximise the number of viable offspring (1948).

This body of work grew into the assumption that individuals look and behave as if they were designed to maximise fitness, which remains the dominant paradigm in behavioural ecology. This idea was famously encapsulated as one of Tinbergen's (1963) 'four questions' in biology, adaptation. That is, the study of how an organism's trait helps it survive and reproduce. This question remains the only scientific route to ultimate explanations for why we observe the natural world in its present form and is thus critical in behavioural ecology (e.g Davies et al. 2012). Prediction in evolutionary biology has always been based on solving models for evolutionary optima (Parker & Maynard Smith 1990). Whilst some authors have criticised a dogmatic attachment to the assumption that organisms can be viewed as maximising agents (Gould & Lewontin 1979), the overwhelming success and tractability of explanations and predictions based on this approach ensure that it remains the most widely used. The success of this adaptationist approach is most evident in sex allocation theory (West 2009).

More recently, Grafen's (1999, 2000, 2002, 2006a, 2006b) Formal Darwinism Project has attempted to provide a firmer theoretical basis for the idea of natural selection as a maximising process. The key objective of the project is to link dynamic systems measuring changes in gene frequencies to formal optimisation programmes (Grafen

2014). These programmes consist of an instrument under the control of an optimiser, who chooses its value from a feasible set of options, and whose objective is to solve the programme by maximising the value of some function of the instrument. In his series of papers, Grafen shows that the expected change in gene frequencies is zero and no alternative phenotype can invade the population when all members of the population solve the optimisation programme, even when complications such as uncertainty and social interactions are included.

However, some philosophers of biology continue to criticise the Formal Darwinism Project and the adaptationist approach as a whole (Orzack 2014, Sarkar 2014). Unfortunately, the incontrovertible space created by the Formal Darwinism Project remains small because the arguments presented are technical and remain obscure to even eminent population geneticists (Ewens 2014, Lehmann & Rousset 2014). More mathematically rigorous arguments have been presented recently, but they cover only a subset of the cases required for general acceptance of a maximisation principle in biology (Batty et al. 2013).

Nonetheless, Darwin's verbal argument, the success of adaptationism in empirical and theoretical study, and steps towards formalisation of the maximisation approach should lead researchers to assume optimality as a good first approximation, at least. In certain cases, population genetic approaches may be required to understand the complexity of a system, but these are so intractable and specific that they are unlikely to allow great progress in behavioural ecology.

1.2.2 The Agent

Both economics and evolutionary biology recognise the world as being comprised of agents that represent decision-making units. Modelling in both disciplines studies the problems faced by these individuals units and attempts to isolate strategies by which they can interact with the world.

The Individual

Maximisation problems are often presented and solved for individuals. Indeed, the field of microeconomics aims to model economic activity by studying the choices made by individual economic agents pursuing their own self-interest. This approach supposes that individuals are autonomous agents, and therefore stems from the same individualist philosophy that provides the intellectual basis for institutions that enshrine the rights of individuals to pursue their own self-interest in many societies (Hobbes 1651, Kant 1785/1983, Mill 1859). Hence, the study of maximising economic agents runs alongside the development of institutions that allow them to behave in that way.

The study of the interests of the individual, rather than those of the state or social group, also has a practical foundation for economists studying how to enrich a society. In *The Wealth of Nations*, Adam Smith (1776) wrote that:

> *The annual revenue of every society is always precisely equal to the exchangeable value of the whole annual produce of its industry, or rather is precisely the same thing with that exchangeable value. As every individual, therefore, endeavours as much he can both to employ his capital in the support of domestic industry, and so to direct that*

> *industry that its produce may be of the greatest value; every individual necessarily labours to render the annual revenue of the society as great as he can.*

Whilst Smith was making the narrower case that the creation of trading monopolies creates distortions that impoverish societies, his insight that the pursuit of self-interest could promote efficient outcomes inspired future economic research. Lerner (1934) eventually demonstrated that when a group of maximising individuals is at a competitive equilibrium, it is impossible to make an individual better off without making another worse off. This is the first fundamental theorem of welfare economics. These foundations have made studying economic problems from the perspective of individual agents a natural approach. In biology, the status of the individual requires additional justification and I explore this below.

The Individual as Maximising Agent

Darwinism presents the individual organism as the unit on which natural selection acts. The individual organism occupies this privileged position because natural selection acts by selecting amongst individuals that carry heritable variation in reproductive fitness (Lewontin 1970). Indeed, natural selection can only act on phenotypes, which are by definition features of individual organisms (Johanssen 1911). Natural selection has an effect on gene frequencies, but cannot see through features of individual organisms and act directly on gene frequencies (Mayr 1963, Sober & Lewontin 1982).

From this perspective, it is natural to take the individual organism as our maximising agent. However, it is less obvious what that individual organism's maximand will be.

The maximand must both be a target of natural selection and be under the control of the individual agent (West & Gardner 2013). The first condition means that if a phenotype is positively associated with the maximand, then genes underlying that phenotype must increase in frequency. The second condition is critical because if an individual organism is not the causal agent for a phenotype, natural selection on that organism has no impact on the apparent design manifested through that phenotype. Inclusive fitness is alone in fulfilling these criteria. It is the offspring of the focal individual caused by the traits of that focal individual, added to the offspring of others caused by the traits of the focal individual weighted by genetic relatedness of the offspring of these others to the focal individual (Hamilton 1964). Whilst inclusive fitness is only one of many different ways of carving up the action of natural selection (Frank 1998), it has special status as the quantity that individuals subject to natural selection should appear designed to maximise (West & Gardner 2013).

Organismality

I have presented a view of natural selection as leading to inclusive fitness maximising individual organisms, but I have provided no clear definition of what an organism is. Ultimately, this is critical because it is at the level of the organism that behavioural ecologists should expect to observe apparent design.

Queller & Strassman (2009) simply argue that the organism is that which manifests apparent design in nature, which may be a logical definition but suffers the drawback of being circular. They then go on to describe unity of purpose as critical in allowing the evolution of apparent design, which requires high levels of cooperation and low levels of conflict between the component parts of the organism. Gardner & Grafen (2009) develop a more formal approach for understanding when collections of individual organisms can be considered maximising agents in their own right, as superorganisms. They offer concrete mechanisms, clonality and repression of competition, which cause the unity of purpose required for organismality.

Whilst helpful in understanding which biological entities we expect to manifest apparent design, these authors also highlight that most entities that we consider organisms will not manifest perfect unity of purpose. Instead, we can place biological entities on a plane with greater organismality when cooperation increases and conflict decreases amongst the constituent parts (West & Kiers 2009).

The Extended Phenotype

Many organisms appear to bear traits that clearly play no part in helping to maximise their own inclusive fitness. For example, an ant that ingests the brain fluke *Dicrocoelium dendriticum* climbs up a blade of grass where it is more likely to be eaten by a sheep (Moore 2002). Clearly, the ant is walking up the blade of grass, but it is not the causal agent for this action. Indeed, the true agent, the fluke, manipulates the ant. The walking, therefore, is an extended phenotype of the fluke and a manifestation of apparent design in that organism (Dawkins 1982).

The Phenotypic Gambit

If individuals can be treated as maximising agents, then any trait carried by that individual can be treated as if controlled by a single haploid locus. This perspective is known as the phenotypic gambit and greatly aids the study of evolutionary biology (Grafen 1984). In particular, the phenotypic gambit allows theoreticians to apply predictions widely rather than to a particular system, and it allows comparative studies to investigate results across multiple species rather than be limited by the need to treat all genetic architectures separately (Grafen 2014).

However, the phenotypic gambit is not literally true and genetic architecture has the potential to constrain evolution. A clear case of this is the relationship between sickle cell anaemia and malaria, where sub-optimal phenotypes persist because only heterozygotes both gain resistance to malaria and do not suffer from sickle cell anaemia (Grafen 1984). Despite this and other counterexamples, researchers persist with the phenotypic gambit because of its extraordinary predictive success, for example in sex allocation (West 2009). In addition, as the underlying genetics of many traits is elucidated, researchers are beginning to test the validity of the phenotypic gambit (Hadfield et al. 2007, Bull & Wang 2010, Springer et al. 2011). Whilst this work is ongoing, early results suggest that the gambit is a useful approximation (Cheverud 1988, Roff 1995, Réale & Festa-Bianchet 2000). A reason for this may be that the genetic architecture itself is evolving and thus allows a full exploration of phenotypic space until an optimum is achieved (Eshel & Feldman 1984, Hammerstein 1996).

The Gene

The view of individuals as maximising agents has also been challenged because individuals do not actually replicate themselves, so it is difficult to view them as the fundamental unit on which natural selection acts. Individuals do not increase or decrease in frequency in populations. On this basis, authors have argued that genes are the fundamental maximising agents in biology (Williams 1996, 1992; Dawkins 1976, 1982).

This view has been substantiated by Gardner and Welch's (2011) demonstration that, like individuals, genes are favoured to maximise their inclusive fitness. However, these authors also state that only adaptations controlled by a single gene can be called gene-level adaptations, and thus that a view based on adaptations at the level of the organism is more general. Nonetheless, when we use the phenotypic gambit, we assume that a single gene controls any phenotype (Bourke 2014). Thus, thinking in terms of individual level maximisation can immediately be translated to gene level maximisation. In addition, Dawkins (1976) argued that genes do not need to control entire phenotypes but only differences between phenotypes to allow gene-level adaptation as a useful metaphor. This makes gene level maximisation potentially even more robust.

Overall, available evidence seems to favour both gene and organism-level maximisation approaches, but the organism-level perspective has the major advantages of being the level at which we can observe natural selection acting and that adaptations can most often be unambiguously attributed to a single individual. At the same time, certain organisms display maladaptations that result from intra-genomic conflict. An example is cytoplasmic male sterility, which stems from differences between the fitness interests of mitochondrial genes and nuclear genes, as the mitochondria are only transmitted through females (Burt & Trivers 2006, Bourke 2011). Only maximisation at the gene level allows us to understand the conflict and correctly predict the maintenance of this organism level maladaptation. Keeping the gene-level perspective alongside the organism-level view allows evolutionary biologists to understand situations where intra-genomic conflict means that otherwise agential individuals lose their organismality.

Higher-level agents

Sometimes, the individual organism does not represent an independent decision-making unit in either biology or economics. This could be because the agent's strategy is tied to that of a larger group, or it could be because the agent is not capable of interacting directly with the environment. Below, I discuss how biology and economics treat these cases.

Major Transitions

The individual organisms that I have discussed until this point are often multicellular and are descended from unicellular life forms. Previously, these unicellular organisms were the level at which design was manifested in nature. Now, the individual cells can only replicate as part of the multicellular whole, and a major transition in organismality has occurred (Maynard Smith & Szathmáry 1995). These major transitions only occur when conflict within the new organism is negligible, such that it will act as a single maximising agent. It is these transitions that allow us to move from the gene to the organism-level perspective, and that also allow us to describe eusocial colonies as individuals (Bourke 2011).

Some authors have argued that adaptations can also arise for the good of a social group, and that social evolution should take these into account (Wilson & Wilson 2007). However, group-level adaptations can only arise once within-group conflict is negligible (Gardner & Grafen 2009). That is, only once the social group has undergone a major transition and is itself an individual.

Households, Firms, Governments, and Central Banks

Economic models assume agents above the level of the individual. This assumption is made without formal justification and it is possible that these higher-level agents do not have emergent properties that cannot be explained as an amalgamation of individual level choices. However, the objective in economic models is to create a minimal conceptual framework that allows predictions about economies (Mas-Collell et al. 1995). Thus, economists treat the internal functioning of higher-level agents such as households, firms, governments, and central banks as a 'black box' and use this abstraction to treat them as agents. This approach is not unlike the phenotypic gambit used by biologists.

This approach allows economists to develop general models of economies that incorporate all of these different types of agents. The most modern and sophisticated of these are known as dynamic stochastic general equilibrium (DSGE) models (Smets & Wouters 2003, Galí 2008). DSGE models are specified by: (i) preferences, functions that each agent in the economy is assumed to maximise; (ii) technology, the means by which agents generate outputs that may be consumed or sold; and (iii) the institutional framework, the set of rules governing economic interactions. The models are then used to predict the state of the economy as a whole, including its response to various shocks such as technological developments or changes to the oil price.

Considering higher-level agents allows economists to provide tractable models of entire economies, and it has the added benefit of framing the internal processes that explain deviations from maximisation at the level of these higher-level agents. An example is the field of intra-household bargaining, which studies negotiations between members of a household and helps explain how decisions are made when they impact the household as a whole (Sen 1990, Lundberg & Pollak 1993, Shelton & John 1996, Bina 1997).

More generally, principal-agent theory considers all problems where certain individuals are able to take action on behalf of others (Grossman & Hart 1983, Rogerson 1985). This is particularly important in the management of firms because the principals (shareholders) employ agents (management) to make operational decisions. The agents are expected to act in their own self-interest, so the objective of principals is to align the incentives of agents with their own. The shareholders of a firm can achieve this by designing contracts for management (Holmstron 1979, Milgrom & Roberts 1992). Principal-agent theory also applies more broadly than the management of firms. Governments regulating industries so as to maximise social welfare face similar problems (Baron & Myerson 1982).

Representative Agents versus Heterogeneous Agents

In many problems in economics and biology, all individuals face the same maximisation problem and the only variation between them is in the strategy they adopt. In this case, there is strategic equivalence between them and solving the maximisation problem for a single representative agent gives the solution for all (Grafen 2006a). However, in biology it is unclear when a representative agent actually exists. A solution does exist in economics, where a representative agent exists if there is a fictional individual whose maximisation problem when facing society's entire budget set would yield the economy's aggregate demand function (Mas-Colell et al. 1995). Every agent in a problem of this type will make the same choice given the same set of options.

Whilst it is difficult in practice to determine whether problems require the inclusion of heterogeneous agents, many biological models incorporate variation in state amongst individuals (McNamara & Houston 1996). In addition, the importance of incorporating class structure such as age into models has long been recognised (Fisher 1930). Incorporating heterogeneity has allowed researchers to predict a much more complete set of outcomes than assuming a single representative agent in every model.

Agent-Based Modelling

Both in economics and biology, agent-based modelling is an approach to understanding complex systems that consists of describing the system as made up of interacting agents. Individuals are given an internal state, which could consist of their attributes, assets, or information, and a set of rules that govern their behaviour. The models also specify a mechanism for changing the system over time. This could be differential survival and reproduction, growth of successful agents, or learning (Holland & Miller 1991, Bonabeau 2002). This permits either analytical tools or computer simulation to study the outcome of these processes on the state of the system over time. A classic example is the Axelrod's tournament that simulated agents interacting in an iterated Prisoner's Dilemma and remains influential as an explanation for cooperation (Axelrod 1984).

Particularly in economics, researchers have advocated greater use of agent-based modelling (Farmer & Foley 2009). Agent-based models are able to specify simple rules at the level of agents, but this may lead to highly complex features emerging in the system simulated (Arthur et al. 1997). In particular, rules that depart from rationality may be better able to predict panics and economic crashes than other approaches (Helbing et al. 2000). However, one key drawback is that there is no firm theoretical framework for which rules are more or less valid, so agent-based models can be constructed to predict almost anything.

1.2.3 The Environment

Agents solve maximisation problems in the environment, which consists of the factors that influence the outcomes of the strategies they adopt. Here, I consider two types of component that make up the environment: those that have agency and those that do not.

The environmental factors that do not have agency are those that are deemed not to be acting so as to solve their own maximisation programmes for the purposes of the problem that a biologist or economist is solving. For example, an individual agent can dam a river and produce a lake. The lake changes the environment, and thus the maximisation problem, of the agent but should not be ascribed agency (Odling-Smee et al. 2003). It simply reacts mechanically and may provide a beaver with a larger area over which it can escape predators or impose costs on an electricity company that compensates individuals for flooded homes.

In addition, other factors would normally be ascribed agency but modellers may assume that they do not change their strategy in response to the choices of the focal maximising agent, or that natural selection acts more slowly on these factors such that their response is held constant as the focal maximising agent evolves. For example, a symbiont's host may have a constant sanctioning rule while the symbiont evolves (West et al. 2002b). Similarly, courts may apply existing law even as new products are developed that change the market (Subramanian 1995). These types of environmental factors greatly simplify the maximisation problems.

Social Partners

The final environmental factor that a focal individual must consider in its maximisation problem is other agents. These may be other identical agents or otherwise agents that differ in some fundamental feature and therefore solve a different maximisation problem. The solutions these other agents find affect the optimal strategy for a focal individual and vice versa, thus complicating the search for optima.

Game Theory

Game theory studies situations where the payoffs of adopting a particular strategy depend on the strategies employed by others (von Neumann & Morgenstern 1944). This field allowed interactive decision-making problems to be analysed, particularly after the introduction of the Nash equilibrium (Nash 1951). The Nash equilibrium is a game theoretical solution, as it is a strategy that cannot be outcompeted by any other option given the strategy adopted by the social partner.

Game theory was immediately adopted in economics to analyse bargaining and strategic behaviour (Nash 1950, Schelling 1960), and was also considered a useful tool in biology (Lewontin 1961). However, the Nash equilibrium is not a stable solution to an evolutionary problem because alternative strategies might perform equally well and enter populations by drift. Maynard Smith and Price (1973) introduced the concept of the evolutionarily stable strategy, a rule that cannot be invaded by any alternative, and this solution concept allowed the widespread adoption of game theory in evolutionary biology.

Taylor-Frank

For continuous traits when phenotypes of different individuals are correlated to each other, Taylor and Frank (1996) developed an approach using maximisation methods from calculus. The change in reproductive fitness of a focal individual due to its own strategy (dw/dx) is the sum of the effect that its own strategy has on its own phenotype (dy/dx) weighted by the partial effect that its own phenotype has on its own fitness ($\partial w/\partial y$), and the effect that its own strategy has on social partner phenotype (dz/dx) weighted by the partial effect that its own phenotype has on its own fitness ($\partial w/\partial z$). We know that the inclusive fitness effect of an individual's change in strategy on its reproductive fitness is $\Delta_{IF}=\partial w/\partial y + (dz/dx)/(dy/dx)\ \partial w/\partial z$. Here, (dz/dx)/(dy/dx) is relatedness between a focal individual and its social partner, that is the regression coefficient of the strategy of the social partner on the strategy of the focal individual (Hamilton 1964). At equilibrium, the average strategy of representative agents is equal to the strategy of the focal individual, so this approach allows us to easily solve social maximisation problems. In economics, there is typically no relationship between individual and social partner strategy, so the regression coefficient can be assumed to be zero.

Multi-variable maximisation problems

In both biology and economics, certain maximisation problems involve two independent coevolving variables. For example, an economy might consist of individuals allocating labour to buy goods and firms hiring labour to produce goods (Walras 1874). Similarly, flowers and hummingbirds may both evolve to better exploit their mutualistic partners (Brown & Kodric-Brown 1979). This means that the solution for maximisation problems of one variable is presented in terms of the other. This leaves a system of simultaneous equations that is solved to yield solutions for each variable purely in terms of model parameters.

The Market

Sometimes, a social maximisation problem involves the exchange of goods or services. That is, a focal individual will be prepared to pay a cost to receive limiting factors in its maximisation problem. The focal individual will be prepared to transfer away other goods or services so long as it values the ones it loses less than what it receives. If transfers are feasible, there is a potential market. However, if the potential gains from trade are small, it is possible that they will be outweighed by the costs of transfer, transaction costs, and opportunities for mutually beneficial trade may not be taken advantage of (Coase 1937).

Two-individual trade

Markets consisting of only two individuals can offer significant gains from trade, but a priori there is no mechanism for partitioning these gains between the two individuals. If the two individuals cannot agree on a partition, the gains go unrealized. Indeed, individuals can be favoured to adopt intransigent strategies but will bear costs if they encounter others doing the same (Muthoo 1999). In addition, a negotiation process may be time consuming and this may impose costs on the two individuals, although one of the most important results in bargaining theory, the Nash Bargaining Solution, predicts that an agreement will be struck immediately due to these costs (Nash 1950).

Even when agreement is reached, enforcement may be problematic. In economics, the ability to enter into agreements is most often assumed. However, in biology cooperative interactions are vulnerable to cheating (Ghoul et al. 2014). Cheated individuals may respond by punishing so as to either avoid further costs or modify the behaviour of their social partners in the future (Clutton-Brock & Parker 1995, Gardner & West 2004).

Markets with competition

When markets have more than two participants, competitive forces help ensure that gains from trade are realized and predict which individuals accrue gains. In economics, the benchmark case is the perfectly competitive market. This requires four conditions: (i) no participant can impact the market price of the product because they have small market share; (ii) all participants sell an identical product; (iii) buyers have perfect information about the prices at which the product is sold by each participant and can switch; and (iv) individuals can freely enter the market as either buyers or sellers. Under perfect competition, all potential gains from trade are achieved. In economics, currency markets are increasingly nearing perfect competition. In biology, pollination mutualisms have many individuals filling each role (pollinators and pollinated) and the mobile polinators can easily switch partners if insufficient nectar is provided. This means that pollination systems may also also approach perfect competition (Selten & Shmida 1991).

Sellers of a good or service that control a significant proportion of its total supply are common cases in biology and are well studied in economics. For example, vervets and sooty mangabeys exchanging grooming for access to infants can only interact with the members of their troop (Fruteau et al. 2011). Similarly, the upfront costs of building a power plant ensure that new competitors seldom enter the energy market (Tirole 1988). The key feature of markets where individuals have control over supply is that they can increase the price at which it is sold. They do this by decreasing supply. There is less of that good or service, so the individuals that value it more increase their bids and all quantity supplied is sold at a higher price. Therefore, individuals with control over quantity supplied have a trade-off between quantity sold and price obtained. The resolution is always that they supply somewhat less than the quantity that maximises aggregate utility or fitness gains for the population.

1.2.4 Conclusion

I have demonstrated the close parallels between modelling in economics in biology, so it should come as no surprise that direct analogies between economics and biological models are easily found. For example, the trade-off between building a nest and laying eggs in birds is no different to the trade-off between acquiring capital and labour for companies.

Today, the most common application of biological principles in economics is in behavioural finance. Here, economists attempt to use biologically informed principles to predict the behavioural rules employed by agents in economic settings. This could allow governments to design mechanisms to ensure that choices made by individual agents come closer to maximising social utility (Thaler & Sunstein 2009). However, this field simply involves studying evolved preferences in order to explain departures from rationality as assumed in economic models. Another promising avenue involves studying markets where not all goods find buyers, for example those with varying quality of goods (Stiglitz 1987). Traditional economic models have assumed that demand and supply equalize over time (the invisible hand), but biologists have great experience studying cases where they do not (Hammerstein & Hagen 2005). For example, not all sperm produced fertilises an egg.

More applications of economic theory exist in biology, where economic language has long been used to shed light on features of biological systems such as the mating market or pollination mutualisms (Selten & Shmida 1991, Noe & Hammerstein 1994). The value of partner choice in stabilising cooperative interactions has made the use of market concepts self-evident, although directly applying models that incorporate biologically realistic assumptions has proven more difficult. More recently, results principal-agent theory has been applied to consider how evolved mechanisms may optimally control social partners whose idiosyncratic characteristics a host cannot easily predict (Archetti et al. 2011).

I hope that the parallels that I have drawn between economics and biology will help future researchers looking to cross the barrier between the fields to understand the similarities and differences between the conceptual frameworks used in each field. In addition, I hope to have provided some insight on the applicability of methods used in one field to challenges in the other.

1.3 Thesis Summary

This thesis contains five research projects, Chapters 2-6. The projects are models of coevolving social traits, all of which are applicable to studying mutualistic cooperation. Each model attempts to shed theoretical light on specific mechanisms that may be important in maintaining or disrupting mutualistic cooperation. Each chapter contains its own detailed introduction. Here, I provide an overview of the subjects covered.

Some authors have suggested that many cooperative interactions resemble markets and can be studied using economic concepts (Noë & Hammerstein 1994, 1995). A key study system for this hypothesis has been the plant-mycorrhizal symbiosis (Werner et al. 2014). In this mutualism, mycorrhizal fungi rely entirely on plants to supply them with carbon. In exchange, the fungi transfer phosphorus and other minerals to their plant partners. Both plants and mycorrhizal fungi are able to discriminate amongst their social partners, preferentially rewarding those who transfer more resources (Kiers et al. 2011). In Chapter 2, I study the rewarding schemes we should expect plants and mycorrhizal fungi to adopt. Then, I adapt a model of trade under comparative advantage to reflect the biological detail of the plant-mycorrhizal symbiosis (Ricard 1817). This model yields insights on the maintenance of mutualistic trade, the evolution of specialisation, and the effects of changing ecological conditions on agricultural yields.

In addition to cooperating with their mutualistic partners, recent evidence suggests that some individual may actively impair certain traits in their partners, restricting their ability to function outside of the symbiosis (Li et al. 2008, Heil et al. 2014). This could make these partners more reliant on mutualistic trade, to the benefit of the restricting individual. However, the theoretical plausibility of this hypothesis remains unclear, as the hypothesised benefits of restriction may not outweigh any costs associated with the impairing trait. In Chapter 3, I modify the model developed in Chapter 2 to incorporate a trait that allows mycorrhizal fungi to restrict the phosphorus acquisition of their plant partners. I explore the conditions under which this trait can be favoured by natural selection, and consider the trait's impact on mutualistic cooperation and the fitness of each partner.

Evolutionary theory predicts that cooperation is more readily favoured under high relatedness (Hamilton 1964). Models of mutualistic systems have also predicted that more related individuals will cooperate more with their mutualistic partners (Frank

1996). However, partner choice relies on a diverse set of partners (low relatedness) and may also be an important mechanism in maintaining cooperation (Noë & Hammerstein 1994, 1995). Indeed, my work in Chapters 2 and 3 suggests that a larger number of independent partners help to maintain cooperativeness in a biological market. This suggests that relatedness might disfavour cooperativeness in the mycorrhizal symbiosis, but some evidence suggests that fungal cooperativeness increases as fungal relatedness increases (Roger et al. 2013). I explore this apparent paradox in Chapter 4. I modify the biological market model from Chapter 2 to explicitly incorporate relatedness and I make plant carbon fixing potential depend on fungal cooperativeness. This allows me to study the effects of relatedness, dependence of resource acquisition on symbiont cooperativeness, and generalism versus specialisation in a biological market.

Whilst cooperation between species is ubiquitous and explained by a number of well-understood mechanisms, it is much more difficult to see how altruism between species could be favoured by natural selection. That is, could an individual be favoured to bear a lifetime reproductive cost in order to increase the lifetime reproductive success of members of another species? Frank (1994) suggested that this might be possible, but did not provide an explicit model. In Chapter 5, I perform a population genetic analysis of a trait whose bearer indiscriminately pays a fecundity cost and increases the fecundity of a member of a member of the other species. I derive conditions under which this trait can be favoured. I then perform an inclusive fitness analysis of this trait in order to determine whether or not it should be classified as altruism between species (Queller 1992).

Chapters 2-5 all consider interactions where the cooperativeness of individuals in at least one species is genetically determined. That is, these individuals cannot respond to the actions of their social partners. However, many social interactions involve individuals observing and responding to each other's actions, and evolutionary theory is enriched by taken this process into account (McNamara 2013). Negotiation games give us a framework to analyse these dynamic interactions (McNamara et al. 1999). However, research by Taylor & Day (2004) suggests that negotiation games suffer from a major drawback because they typically do not yield firm predictions. This result is puzzling because other work on negotiation games has predicted unique evolutionarily stable strategies (McNamara et al. 2003, Johnstone & Hinde 2006, Johnstone 2011). In Chapter 6, I reconcile these apparently contradictory results by studying the conditions under which negotiation games do and do not predict a unique outcome.

2

A biological market analysis of the plant-mycorrhizal symbiosis

2.1 Abstract

It has been argued that cooperative behaviour in the plant-mycorrhizal mutualism resembles trade in a market economy and can be understood using economic tools. Here, we assess the validity of this "biological market" analogy by investigating whether a market mechanism – that is, competition between partners over the price at which they provide goods – could be the outcome of natural selection. Then, we consider the conditions under which this market mechanism is sufficient to maintain mutualistic trade. We find that: (i) as in a market, individuals are favoured to divide resources among trading partners in direct relation to the relative amount of resources received, termed linear proportional discrimination; (ii) mutualistic trade is more likely to be favoured when individuals are able to trade with more partners of either species, and when there is a greater relative difference between the species in their ability to directly acquire different resources; (iii) if trade is favoured, then either one or both species is favoured to give up acquiring one resource directly, and vice versa. We then formulate testable predictions as to how environmental changes and co-evolved responses of plants and mycorrhizal fungi will influence plant fitness (crop yields) in agricultural ecosystems.

2.2 Introduction

Mutualistic cooperation between species poses a problem for evolutionary theory (Sachs et al. 2004, Foster & Wenseleers 2006, Leigh 2010). The problem is that – all else being equal – cheats who reduce their investment in a cooperative trait, whilst enjoying the benefits of others' investment, will be favoured by natural selection (West et al. 2007a, Ghoul et al. 2014). Consequently, natural selection will act to disfavour costly cooperation. Within a species, genetic relatedness between social partners may result in kin selection that directly favours selflessness (Hamilton 1964), whereas the emergence and stability of cooperation between species requires additional mechanisms (Foster & Wenseleers 2006, but see Frank 1994, Wyatt et al. 2013).

A number of empirical studies have shown that mutualistic cooperation can be stabilised when one of the partners exerts choice or control over the other (Agrawal & Karban 1997, Korb & Aanen 2003, Edwards et al. 2006, Johnstone & Bshary 2008, McFall-Ngai 2008). That is, members of the controlled species either irreversibly commit to their mutualistic partner or cannot choose at all, and the controlling partner employs some mechanism to enforce or select for cooperation (Noë 1990, Bull & Rice 1991, Pellmyr & Huth 1994, West & Herre 1994, West et al. 2002a, West et al. 2002b, Kiers et al. 2003, Frean & Abraham 2004, Goto et al. 2010, Jander & Herre 2010, Archetti et al. 2011). For example, legume species invest fewer resources into root nodules containing rhizobia that fix less nitrogen (Kiers et al. 2003; Simms et al. 2006; Oono et al. 2009, 2011; Regus et al. 2014).

In contrast, in the mutualism formed between plants and mycorrhizal fungi, neither partner wields total power to choose or control members of the other species. Here, every individual may interact with multiple partners simultaneously: multiple mycorrhizal fungi can colonise a single plant host, and each of these fungal individuals can potentially interact with multiple plant hosts (Selosse et al. 2006, Kiers & Denison 2008). Empirical work has shown that plants supply more carbohydrates to fungal partners that provide more phosphorus, and vice versa (Hammer et al. 2011; Kiers et al. 2011; Fellbaum et al. 2012, in press). Biological market theory has emerged as a tool to study how cooperation can be stabilised in many-to-many interactions (Noë et al. 1991; Noë 1992; Noë & Hammerstein 1994, 1995; Werner et al. 2014), having originally been applied to systems where control is wielded by a single partner class (Shmida & Cohen 1989, Shmida & Dafni 1989, Selten & Shmida 1991, Peleg & Shmida 1992, Peleg et al. 1992). The strength of biological market theory is to make networks of two-way trading connections tractable by treating them as if partners were trading goods within a central marketplace (Noe & Hammerstein 1994).

However, the validity of this biological market approach in analysing many-to-many interactions has yet to be formally evaluated. First, previous theory assumes the reward functions used by at least one class of partner (Schwartz & Hoeksema 1998; Hoeksema & Schwartz 2001, 2003; Kummel & Salant 2006). The question of which rewarding schemes natural selection will lead to has not been addressed. Natural selection could easily lead to consistent pricing across partners, or it could instead lead to discriminatory pricing, where different individuals face a different reward function. Second, previous theoretical models have assumed that mutually beneficial trade is made, rather than investigating when trade would be evolutionarily stable (Schwartz & Hoeksema 1998; Hoeksema & Schwartz 2001, 2003; Grman et al. 2012). There are many situations where trade or cooperation would be mutually beneficial but is not favoured by natural selection, as famously illustrated by the Prisoner's Dilemma. Third, previous biological market models have assumed that markets comprise either very few or else infinitely many traders (Schwartz & Hoeksema 1998; Hoeksema & Schwartz 2001, 2003; Akçay & Roughgarden 2007; de Mazancourt & Schwartz 2010; Akçay & Simms 2011; Grman et al. 2012). Incorporating the more realistic assumption of finite markets with a variable number of participants may lead to single individuals exerting partial control over the overall supply of a good – termed "bargaining power" (Johnson et al. 2012). This could lead to the collapse of trade (Baldwin 1948, Rieber 1982).

Here, we assess the validity of the biological market analogy, developing a market model based on current knowledge of the mycorrhizal symbiosis. We derive the conditions under which individuals receive the same market exchange rate for their goods and under which trade is maintained. When these conditions are satisfied, we apply an economic model where individuals compete to supply goods and services in biological settings. We use our market model to explore the selective forces behind specialisation in mutualisms. Finally, we consider the specific application of our model to the mycorrhizal symbiosis and the implications for agricultural scenarios. Specifically, we examine the consequences of: (i) variation in the number of trading partners of each species; (ii) the addition of phosphorus fertilisers; and (iii) rising CO_2 levels.

2.3 Model & Analyses

We develop a model for the cooperative exchange of two resources between two species. We phrase our model in terms of the plant-mycorrhizal mutualism in which carbon from the host is exchanged for phosphorus from the fungus. Here, we consider only exchange of these two resources, although in reality the fungal partner can provide other nutrients, such as nitrogen. While we examine cases of particular relevance to that interaction, our aim is to keep our overall model general so that it can be applied to other mutualisms. Consequently, in the general formulation of our model we allow mycorrhizal fungi to acquire carbon directly, even though in the arbuscular mycorrhizal (AM) symbiosis, the fungal partner is an obligate biotroph that is completely dependent on its host for carbon (Parniske 2008). Our approach allows us to explore the reasons natural selection has favoured reliance on host-derived carbon. To explain why mycorrhizal fungi do not acquire carbon directly, we must work out the fitness consequences for hypothetical fungi that can directly obtain carbon and show that natural selection will have eliminated them. This approach of considering a wider range of possibilities leads to a better understanding of the phenomena actually observed (Eddington 1928).

2.3.1 Direct Resource Acquisition

We consider a finite population of plants and mycorrhizal fungi that require carbon and phosphorus for growth and suppose that each individual in a species is identical except for strategy. We assume that there is a linear trade-off between the resources invested into carbon and phosphorus acquisition, although other trade-offs would yield qualitatively identical solutions so long as individuals are always relatively more efficient at acquiring one good than those in the other species (Ricardo 1817, Hoeksema & Schwarz 2003). We assume that they acquire a proportion x of the maximum amount of carbon that they can acquire and a proportion $1-x$ of the maximum amount of phosphorus. These maximum amounts are C_p and P_p for plants, and C_m and P_m for mycorrhizal fungi (in practice, $C_m=0$ for mycorrhizal fungi). In principle, increased growth in mutualism could mean that these maximum amounts increase. We neglect such effects because the primary purpose of our model is to investigate the influence of partner discrimination in mutualisms. Hence, plants acquire x_pC_p units of carbon and $(1-x_p)P_p$ units of phosphorus, whilst mycorrhizal fungi acquire x_mC_m units of carbon and $(1-x_m)P_m$ units of phosphorus. The maximum amount of a resource that an individual can acquire depends on two factors – the availability of that resource in the environment and the inherent ability of individuals of that species to acquire it. For biological realism, we also give mycorrhizal fungi a small initial endowment of carbon, I. This reflects the trace amounts of carbon that fungal spores require to develop, as well as their ability to maintain at least some carbon independence from trade with specific host plants, for example by drawing down from common mycorrhizal networks (Giovannetti et al. 2004; Sbrana et al. 2011). Nonetheless, it is clear that this amount must be small as mycorrhizal fungi grow poorly except in symbiosis.

2.3.2 Mutualistic Trade

In addition to acquiring carbon and phosphorus directly, we allow plants and mycorrhizal fungi to engage in mutualistic trade. Each plant has n_m mycorrhizal fungi as trading partners and each fungus has n_p plants. Adding or removing a trading partner means increasing or decreasing the number of trading links between individuals, so it measures the connectedness of the mutualistic system. Thus, it both changes the number of genotypes and the number of resources in the trading interaction. Plants transfer a proportion q_p of their directly acquired carbon to mycorrhizal partners and the fungi transfer a proportion q_m of their directly acquired phosphorus to plants.

What strategy for sharing resources between trading partners does natural selection favour? In principle, an individual could transfer all traded resources to one partner, could share equally between all partners, or could use any intermediate strategy. To determine the optimal sharing strategy across all partners, we only need to work out the relative amounts transferred to any pair of partners. This works because it allows us to consider the amount allocated to any given partner versus any other. With this information, we can calculate the ratios allocated between a sequence of as many partners as a focal individual has (a:b:c:d:e:f:etc). A plant is favoured to allocate a proportion f_{p1} of an amount of carbon C_t to fungus m_1 and a proportion $1-f_{p1}$ of the amount C_t to m_2, so as to maximise phosphorus received in return. The phosphorus received from each fungus is a proportion, f_{m1} or f_{m2}, of the phosphorus that each fungus trades, P_{t1} and P_{t2} respectively. The proportions f_{m1} and f_{m2} are functions of the focal plant's ($f_{p1}C_t$ or $(1-f_{p1})C_t$) and all other plants' (C_{re1} or C_{re2}) carbon allocation to that fungus. The focal plant maximises its phosphorus from trade when the equation $P_r = f_{m1}(f_{p1}C_t, C_{\mathrm{re1}})P_{t1} + f_{m2}((1-f_{p1})C_t, C_{\mathrm{re2}})P_{t2}$ is maximised. In the Appendix we show that:

> **Result 1** – Individuals are favoured to use a rule that allocates resources among partners of the other species in direct proportion to the relative amount of benefits they receive from each partner, when others do likewise. Specifically, a linear "proportional discrimination" (Tang-Martinez 2001) allocation can be an evolutionarily stable strategy in trading models (ESS, Maynard Smith & Price 1973, Riechert & Hammerstein 1983).

To illustrate, we find that in populations using linear proportional discrimination, if a plant receives two thirds of the benefits it acquires through trade from one mycorrhizal fungus and one third from another, it sends two thirds of the total carbon it allocates for trade to the former and one third to the latter. No other strategy arising in such a population can invade. Plants that either allocate all carbon to one partner or split carbon equally between all partners would have a lower fitness and hence be eliminated by natural selection.

Linear proportional discrimination leads to individuals that receive the same exchange rate for resources or services traded in many mutualistic contexts, including our model (see Appendix for details). We still need to show that quantities traded in our model can be non-zero. We do this by showing that when members of both species are simultaneously maximising their fitness, their evolved strategy includes sending resources to members of the other species. Henceforth, we assume that all individuals adopt a linear proportional discrimination rule.

Table 2.1 | Parameters and evolved strategies used in the analysis.

Symbol:	**Definition:**
$C_{\mathrm{p/m}}$:	Quantity of carbon available for an individual plant/mycorrhizal fungus to acquire
C_{t}:	Quantity of carbon traded by an individual plant
C_{re}:	Quantity of phosphorus received in trade by an individual mycorrhizal fungus, excluding what it receives from the focal plant
I:	Initial carbon endowment of mycorrhizal fungi
$P_{\mathrm{p/m}}$:	Quantity of phosphorus available for an individual plant/mycorrhizal fungus to acquire
P_{r}:	Quantity of phosphorus received in trade by an individual plant
P_{t}:	Quantity of phosphorus traded by an individual mycorrhizal fungus
$n_{\mathrm{p/m}}$:	The number of heterospecific trading partners available to each plant/mycorrhizal fungus
a:	Exponent that mediates the marginal effect of additional carbon or phosphorus on plant fitness
b:	Exponent that mediates the marginal effect of additional carbon and phosphorus on mycorrhizal fungus fitness
$x_{\mathrm{p/m}}$:	Proportion of resources that plants/mycorrhizal fungi allocate to acquiring carbon. They allocate the remainder of their resources to acquiring phosphorus. $'$ denotes the average across the population
$q_{\mathrm{p/m}}$:	Proportion of carbon/phosphorus that plants/mycorrhizal fungi allocate to trade. $'$ denotes the average across the population

2.3.3 Evolution of Resource Acquisition and Transfer

After acquisition and trading of resources, each individual has a final amount of carbon (C_{f}) and phosphorus (P_{f}). These amounts jointly determine fitness. We choose fitness functions so that: (i) an individual's fitness is zero unless they possess both resources; (ii) increasing the level of either resource gives diminishing marginal fitness returns, such that both are limiting in the neighbourhood of individuals' evolved strategies (Haig & Westoby 1988, Rosenheim et al. 2010); (iii) there are constant returns to scale, so that a change in fitness due to different trading dynamics can be measured against a consistent baseline as resource availability changes.

Specifically, we assume that plant fitness is given by $w_{\text{p}}=C_{\text{fp}}{}^{a}P_{\text{fp}}{}^{1-a}$, and mycorrhizal fitness is given by $w_{\text{m}}=C_{\text{fm}}{}^{b}P_{\text{fm}}{}^{1-b}$, where the exponents $0<a<1$ and $0<b<1$ mediate the marginal fitness effects of additional resources. These functions are commonly used to satisfy the above requirements in the economics literature and are termed “Cobb-Douglas functions” (Cobb & Douglas 1928).

We now re-write these fitness functions, replacing the final amounts of carbon and phosphorus (C_{f} and P_{f}) with explicit expressions for the amounts acquired and traded for (see Table 2.1 for a list of parameters and evolved strategies used in the analysis). We consider a focal plant with a strategy pair (x_{p}, q_{p}), which may not be the ESS, in a nearly uniform population in each species with proportions of carbon acquired clustered around x'_{p} and x'_{m}, and allocations to trade clustered around q'_{p} and q'_{m}.

The plant acquires an amount $x_{\text{p}}C_{\text{p}}$ of carbon and retains a fraction $1-q_{\text{p}}$ of this, so that it has a final quantity of carbon given by $C_{\text{fp}}=x_{\text{p}}C_{\text{p}}(1-q_{\text{p}})$. The plant also acquires an amount of phosphorus $(1-x_{\text{p}})P_{\text{p}}$ directly and receives an amount of phosphorus $P_{\text{r}} = P_{\text{t}}n_{\text{m}}s_{\text{p}}$ via trade, where P_{t} is the quantity of phosphorus each mycorrhizal fungus trades, n_{m} is the total number of mycorrhizal fungi hosted by the plant and s_{p} is the share of the traded phosphorus the focal plant acquires (see Appendix for a derivation of s_{p} in terms of model parameters and strategies). Mycorrhizal fungi each acquire, on average, a quantity $(1-x'_{\text{m}})P_{\text{m}}$ of phosphorus and allocate a proportion q'_{m} of it to trade. Hence, the average quantity of phosphorus allocated to trade by each fungus is $P_{\text{t}}=(1-x'_{\text{m}})P_{\text{m}}q'_{\text{m}}$. This means that the total quantity of phosphorus the focal plant trades for is $P_{\text{r}}=(1-x'_{\text{m}})P_{\text{m}}q'_{\text{m}}n_{\text{m}}s_{\text{p}}$, assuming that no resources are lost due to transaction costs. The final quantity of phosphorus available to plants is the sum of the quantity they take up from the soil and the quantity they acquire via trade, so $P_{\mathrm{fp}}=(1-x_{\mathrm{p}})P_{\mathrm{p}}+(1-x'_{\mathrm{m}})P_{\mathrm{m}}q'_{\mathrm{m}}n_{\mathrm{m}}s_{\mathrm{p}}$. Now, we replace C_{fp} and P_{fp} in the focal plant's fitness function with the equations in this paragraph to yield

$$w_{\mathrm{p}} = (x_{\mathrm{p}}C_{\mathrm{p}}(1-q_{\mathrm{p}}))^{a}((1-x_{\mathrm{p}})P_{\mathrm{p}} + n_{\mathrm{m}}(1-x'_{\mathrm{m}})P_{\mathrm{m}}q'_{\mathrm{m}}s_{\mathrm{p}})^{(1-a)}\,. \tag{1a}$$

Similarly, a focal mycorrhizal fungus' fitness is

$$w_{\mathrm{m}} = (I + x_{\mathrm{m}}C_{\mathrm{m}} + n_{\mathrm{p}}x'_{\mathrm{p}}C_{\mathrm{p}}q'_{\mathrm{p}}s_{\mathrm{m}})^{b}((1-x_{\mathrm{m}})P_{\mathrm{m}}(1-q_{\mathrm{m}}))^{(1-b)}\,. \tag{1b}$$

We then study the evolution of the four variables that determine resource acquisition (x_{p} and x_{m}) and transfer (q_{p} and q_{m}). We have already assumed that individuals share the resources they allocate to trade by linear proportional discrimination, now we seek to predict how what resource mix they acquire directly and the quantities they allocate to trade. We find the ESSs (x_{p}*, q_{p}*) for plants and (x_{m}*, q_{m}*) for fungal partners. The ESS for plants determines that for mycorrhizal fungi and vice-versa, so we denote pairs of co-evolutionary ESSs as (x_{p}*, q_{p}*, x_{m}*, q_{m}*) (Riechert & Hammerstein 1983). Four ESS scenarios are possible: (i) there is no mutualistic trade ($q_{\mathrm{p}}=q_{\mathrm{m}}=0$); (ii) plants acquire only carbon directly ($x_{\mathrm{p}}=1$) and mycorrhizal fungi acquire only phosphorus directly ($x_{\mathrm{m}}=0$); (iii) plants acquire only carbon directly ($x_{\mathrm{p}}=1$), but mycorrhizal fungi acquire both phosphorus and carbon directly ($0<x_{\mathrm{m}}<1$); (iv) plants acquire both phosphorus and carbon directly ($0<x_{\mathrm{p}}<1$), but mycorrhizal fungi acquire only phosphorus directly ($x_{\mathrm{m}}=0$) (see Appendix for details). Scenario (iii) cannot occur in nature, but as discussed above it is essential to consider the scenario in order to explain why it does not occur.

We use our model and the ESSs it yields to explore three questions. First, when is mutualistic trade evolutionarily stable? Second, when is one of the partners favoured to acquire only one resource, and hence rely completely on the other species for the other resource? Third, what are the consequences for agricultural yields due to changes in partner numbers (n_p and n_m), atmospheric carbon concentrations (C_p and C_m), and phosphorus fertiliser availability (P_p and P_m)?

2.3.4 Under what conditions do individuals engage in mutualistic trade?

Carbon and phosphorus are excludable goods. That is, only their owners can benefit from them. Hence, the obstacle to cooperative trade is not a free-rider problem (Hardin 1968). Instead, cooperative trade occurs as long as individuals in both species can earn a sufficient return from participating. We find a pair of co-evolutionary ESSs with trade (q_p, $q_\mathrm{m}>0$) when

$$\frac{C_\mathrm{p}P_\mathrm{m}}{P_\mathrm{p}C_\mathrm{m}} > \frac{n_\mathrm{p}n_\mathrm{m}}{(n_\mathrm{p}-1)(n_\mathrm{m}-1)} . \tag{2}$$

This result shows that a market analogy is valid, as natural selection can both maintain trade and lead to all individuals receiving the same market exchange rate for their goods in our model. The result also shows that we should only expect trade when ecological parameters satisfy the conditions in inequality (2), even though mutually beneficial trade is possible under all parameter values in our model.

> **Result 2** - Mutualistic trade is promoted when individuals in both species are less efficient at acquiring the resource that they can acquire by trade (P_p or C_m decreases) or are more efficient at acquiring the resource that they cannot acquire by trade (C_p or P_m increases) (Figure 2.1). These changes increase the benefit of acquiring resources by trade.

Result 2 is in line with previous predictions that mutual dependence increases the likelihood of mutualistic cooperation (Foster & Wenseleers 2006; Leigh 2010) and trade (Cordella & Gabszewicz 1997).

> **Result 3** - Mutualistic trade is promoted when the number of potential competitors in each species (n_p or n_m) increases (Figure 2.1). The increase in mycorrhizal partner numbers decreases a single individual's control over total phosphorus traded (i.e. its bargaining power). With this increase, a focal mycorrhizal fungus benefits less from manipulating the total amount of phosphorus in the market to increase its value (Cordella & Gabszewicz 1998). Instead, it benefits relatively more from competing intensely for carbon by trading phosphorus, thus promoting trade.

To illustrate Result 3, consider the scenario where n mycorrizal fungi provide an equal amount of phosphorus to a plant. Each fungus therefore gets a fraction $1/n$ of the traded carbon. Now suppose that one mycorrhizal fungus doubles its supply of phosphorus to the plant, thus receiving $2/(n+1)$ of the traded carbon in return. The

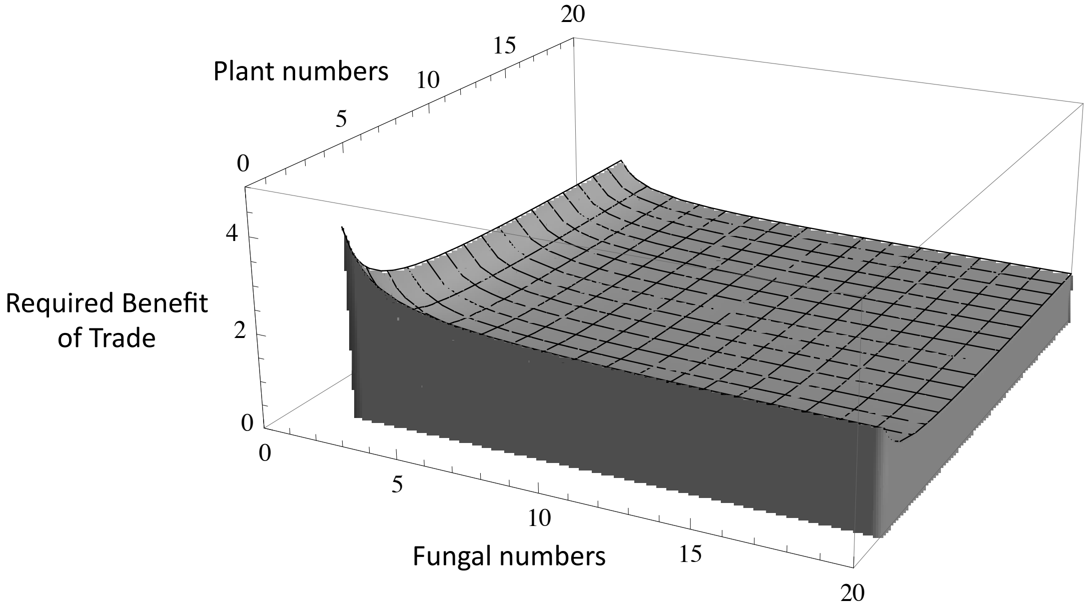
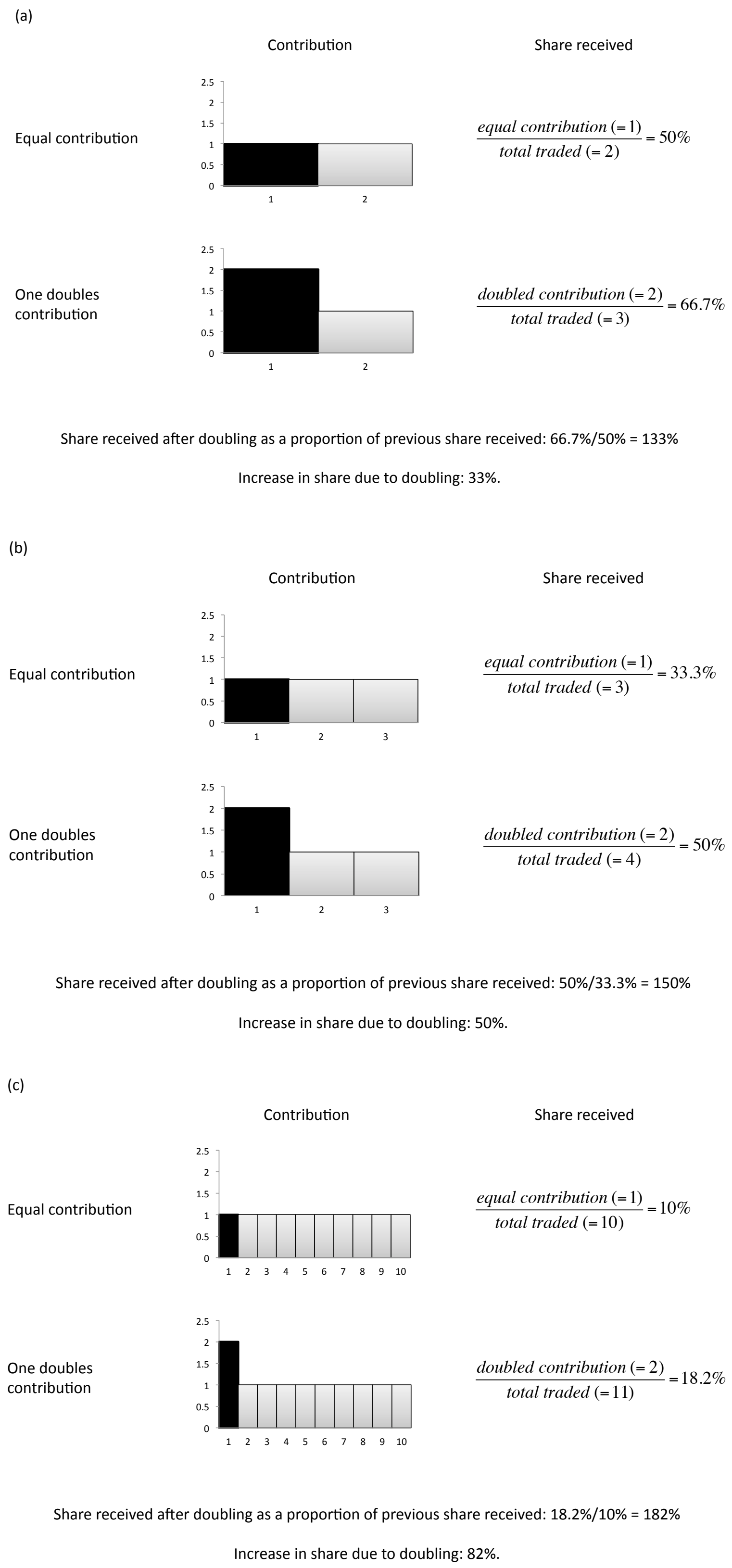


Figure 2.1 | Condition for the stability of mutualistic trade. Above the threshold surface, $C_{\mathrm{p}}P_{\mathrm{m}}/P_{\mathrm{p}}C_{\mathrm{m}} = n_{\mathrm{p}}n_{\mathrm{m}}/((n_{\mathrm{p}} - 1)(n_{\mathrm{m}} - 1))$, the benefit of specialisation and trade is large enough that individuals benefit from maintaining resource transfer. This condition becomes easier to satisfy as the number of individuals in each species, n_{p} or n_{m}, increases.

carbon returned to that fungus is increased by a factor $2n/(n + 1)$, which increases with larger n (Figure 2.2). A similar result has already been derived in the economics literature (Cordella & Gabscewicz 1997). However, it runs counter to widespread thinking in biology that cooperation is more likely to be outcompeted by selfishness as the number of social partners increases (Frank 1994).

> **Result 4** - The absence of trade is always evolutionarily stable, except when at least one species can acquire only one resource without trading (C_{p}, P_{p}, C_{m}, or P_{m}=0). In general, if individuals in one of the species are not trading, it does not pay for members of the other species to engage in mutualistic trade. However, if individuals in one species cannot acquire one resource by other means, they must trade to survive. This illustrates that biological cooperation is easier to maintain



(a)

$$\frac{equal\ contribution\ (=1)}{total\ traded\ (=2)} = 50\%$$

$$\frac{doubled\ contribution\ (=2)}{total\ traded\ (=3)} = 66.7\%$$

Share received after doubling as a proportion of previous share received: 66.7%/50% = 133%

Increase in share due to doubling: 33%.

(b)

$$\frac{equal\ contribution\ (=1)}{total\ traded\ (=3)} = 33.3\%$$

$$\frac{doubled\ contribution\ (=2)}{total\ traded\ (=4)} = 50\%$$

Share received after doubling as a proportion of previous share received: 50%/33.3% = 150%

Increase in share due to doubling: 50%.

(c)

$$\frac{equal\ contribution\ (=1)}{total\ traded\ (=10)} = 10\%$$

$$\frac{doubled\ contribution\ (=2)}{total\ traded\ (=11)} = 18.2\%$$

Share received after doubling as a proportion of previous share received: 18.2%/10% = 182%

Increase in share due to doubling: 82%.

Figure 2.2 | Mutualistic trade and the number of trading partners. The proportional increase in resources returned to the black individual for doubling its contribution increases with the number of same species competitors, as illustrated by an increase from two (a), to three (b), to ten (c).

than to initiate, as has been shown elsewhere (Axelrod & Hamilton 1981).

2.3.5 When does selection favour specialisation?

We now explore the conditions that favour specialisation. Here, we use specialisation to mean when individuals of a species acquire only one resource, and rely on trade for the other.

> **Result 5** - Whenever trade is favoured, either one or both species are favoured to stop acquiring one resource directly, and only acquire it through trade (x_{p}=1 or x_{m}=0 at each pair of trading ESSs). The reverse also holds. Whenever individuals in one species are favoured to adopt a strategy where they forsake acquiring one resource directly, trade is favoured.

We find that when trade is favoured, plants are favoured to acquire carbon, but not phosphorus, when

$$P_{\mathrm{p}} \leq \frac{bC_{\mathrm{p}}(n_{\mathrm{p}}-1)(n_{\mathrm{p}}-1+a)(n_{\mathrm{m}}-1)n_{\mathrm{m}}P_{\mathrm{m}}}{n_{\mathrm{p}}((1-a)C_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}}n_{\mathrm{m}}+I(1-b)(n_{\mathrm{p}}-1+a)n_{\mathrm{m}}^{2}-(1-a)bC_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}})} \qquad (3a)$$

(Figure 2.3). When trade is favoured, mycorrhizal fungi are favoured to acquire phosphorus, but not carbon, when

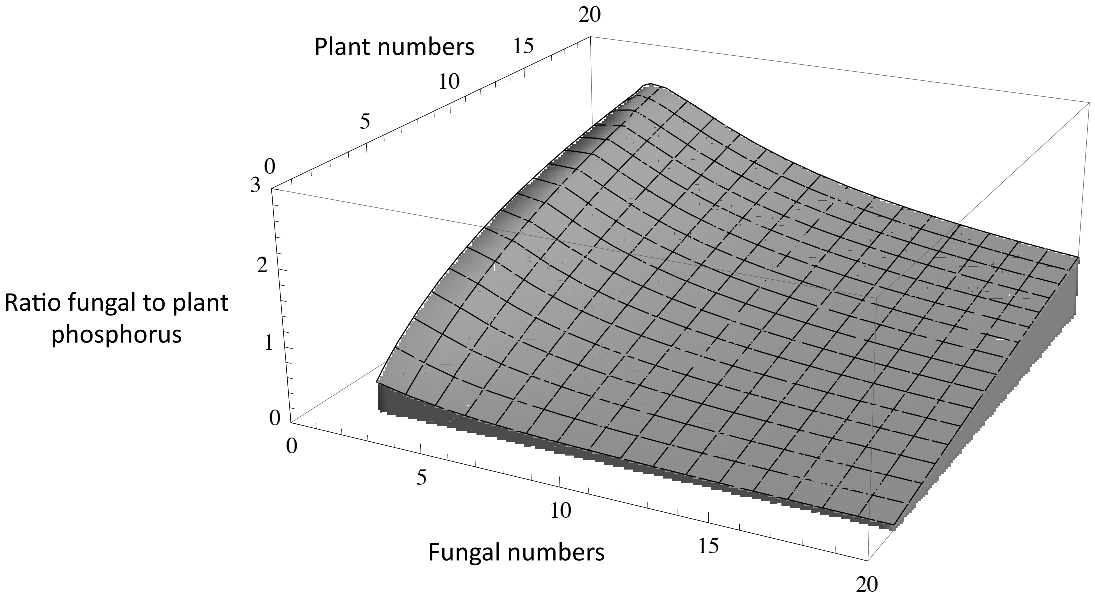


Figure 2.3 | Specialisation and Partner Numbers. Above the surface, condition (3a) is satisfied. Plants acquire only carbon directly. Below it, plants acquire both resources directly. This surface is the critical ratio of fungal phosphorus to plant phosphorus, above which plants are favoured to rely completely on mycorrhizal fungi for phosphorus (In graph, a=0.6, b=0.4, C_p=1, I=0.1).

$$C_p \geq \frac{(bC_m - I(1-b))(n_p - 1 + a)n_m^2}{(1-a)(n_p - 1)n_p(n_m - b)}. \qquad (3b)$$

Result 6 - Specialisation is more favoured as individuals become less efficient at acquiring the resource they trade for (P_p, C_m, and/or I are small relative to P_m and/or C_p). These changes increase the marginal benefit of acquiring more of the resource that they cannot acquire through trade.

Result 7 - Specialisation is more favoured when individuals interact with fewer members of the other species, or when individuals of the other species interact with more trading partners. For example, decreasing the number of plants (n_p) or increasing the number of mycorrhizal fungi (n_m) increases the total quantity of phosphorus relative to the total quantity of carbon in the market. This increases the scarcity, and therefore value, of the carbon. This favours plants that invest relatively more in carbon acquisition, whether for their own use or to benefit from its increased value in trade.

These results demonstrate why mycorrhizal fungi are, in general, not favoured to acquire carbon directly. Once the fungus is engaged in a stable mutualistic relationship where it is a specialised partner, it gains no fitness benefits from the ability to acquire carbon directly. Consequently, mycorrhizal fungi are likely to lose any adaptations related to direct (non-host) carbon acquisition. The results in this section capture one of the central predictions of trade under comparative advantage: at least one class of trader will specialise completely, and individuals will be more likely to specialise the greater their relative disadvantage in acquiring one resource (Ricardo 1817). We highlight the generality of this principle, as it has also been recovered in other models where individuals are able to acquire two resources (Hoeksema & Schwartz 2003, Grman et al. 2012).

2.3.6 Agricultural Consequences

We now explore three scenarios with relevance to agriculture, although artificial selection may impose a different fitness maximand than individual yield. However, we feel it is instructive to use individual yield as a null hypothesis for the maximand achieved by artificial selection and see whether our predictions prove useful in agricultural contexts. We consider how co-evolutionary changes combine to determine variation in agricultural yields (i.e. plant fitness, f_p) and mycorrhizal cooperativeness (which we define as the proportion of their phosphorus that they send to plants, q_m) in response to: (i) changes in the number of mutualistic partners; (ii) the application of phosphorus fertilisers (higher P_m and/or P_p); (iii) an increase in atmospheric carbon (which is never available to mycorrhizal fungi, C_m=0).

Partner Numbers

When host plants are grown as agricultural crops, this can alter plant density in a way that alters the number of available trading partners for each individual plant and mycorrhizal fungus. We do not consider the costs of searching for mutualistic partners or setting up a trading link. The inclusion of search costs in models of sexual selection has led to the evolution of qualitatively different partner choice strategies (Janetos 1980; Halliday 1983; Parker 1983; Real 1990, 1991). However, this does not mean that our model is equivalent to a model where they are assumed to be zero. Our inclusion of a limited number of mutualistic partners per individual acknowledges that there are both costs and benefits to acquiring additional partners, although a full treatment of the factors that will lead to more or fewer partners is beyond the scope of our model. We also note that partner selection is likely to be less important in mutualisms like the plant-mycorrhizal symbiosis than in sexual selection. This is because, in the plant-mycorrhizal symbiosis, individuals maintain multiple partners at the same time and retain the ability to preferentially reward better partners even after they have started cooperating. In addition, it may be difficult for mycorrhizal or plants to assess each other's value as a partner prior to the start of a trading interaction, except when there are major incompatibilities. It is possible that the best strategy is simply to initiate a trading interaction with all compatible nearby partners and then preferentially reward those that transfer the most resources. In addition, costs to finding partners or setting up trading links may be important in the evolutionary origin of a de novo mutualism, but need not be if the mutualism arises from a pre-existing association between plants and fungi. Moreover, we are not considering the origin of mutualism but its maintenance and elaboration, and the costs of setting up a trading link are likely negligible relative to the quantity of resources flowing through the network (Mikkelsen et al. 2008).

> **Result 8** - An increase in the number of fungal partners per plant (n_m) increases both the cooperativeness of each mycorrhizal fungus (q_m) and the fitness of each plant (f_p). This is because the same plant carbon becomes shared between more fungal partners, increasing the marginal benefit of additional carbon for each mycorrhizal fungus. They are favoured to transfer more phosphorus to compete for this carbon, thus increasing plant fitness. When plants acquire both resources before trade (condition 4a is not satisfied), the increase in fitness is slow because plants compete for phosphorus by increasing their investment in carbon acquisition and transferring that carbon to the fungal partner. When plants acquire only carbon directly, they cannot acquire any more of it to compete for fungal phosphorus. Therefore, plant fitness begins to increase rapidly, but at a diminishing rate (Figure 2.4).

The increase in plant fitness caused by an increase in fungal numbers follows easily from the consequences of market supply and demand. These forces have been verbally analysed in biological settings by Noë and Hammerstein (1994), but ours is the first model to quantify this effect. There are two factors in our model that increase plant fitness. First, an increase in fungal numbers increases phosphorus availability in the system. Second, even holding aggregate phosphorus availability constant, an increase in the number of individuals makes each individual fungus more cooperative. Grman et al. (2012) identify a similar trend that increased fungal biomass will lead to increased plant fitness because phosphorus becomes more readily available, but their model only considers one trader of each type, so the added impact on plant fitness of increased per capita fungal cooperativeness is not captured. The predicted increase in fungal cooperativeness is also novel in the economic literature. Previous work suggests that less phosphorus may be supplied per fungus due to falling phosphorus prices because suppliers, in this case mycorrhizal fungi, increase in number (Amir & Lambson 2000).

> **Result 9** - An increase in the number of plant partners per mycorrhizal fungus (n_{p}) has a small positive effect on fungal cooperativeness, proportional to the size of the fungal carbon endowment (I). The impact on cooperativeness is small because two effects oppose. (i) The quantity of carbon that each mycorrhizal fungus receives, given the amount of phosphorus it sends, increases. This effect selects for more cooperative mycorrhizal fungi as trading away phosphorus yields a greater carbon return. (ii) Each mycorrhizal fungus receives more plant carbon, so the marginal value of an additional unit is lower, thus decreasing the quantity of phosphorus it trades. Overall, plant fitness decreases because more plants compete for a quantity of phosphorus

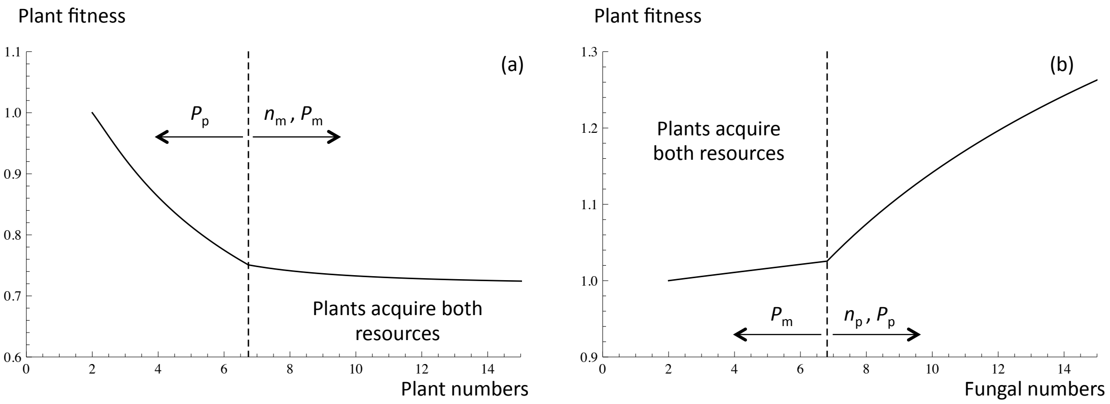


Figure 2.4 | Effect of number of partners on plant fitness. (a) Plant fitness decreases with the number of plants. When plants acquire both resources directly (left of dashed line), the rate of fitness decrease slows dramatically as plants are no longer reliant on mycorrhizal fungi for phosphorus. (In graph, n_p=10, C_p=1, P_p=0.5, P_m=1, a=0.7, b=0.3, I=0.1). (b) Plant fitness increases with the number of mycorrhizal partners, n_m. When plants acquire only carbon directly (right of dashed line), fitness increases more rapidly as plants can no longer compete with each other by increasing the resources they allocate to acquiring carbon directly. (In graph, n_m=5, C_p=1, P_p=0.5, P_m=1, a=0.7, b=0.3, I=0.1).

that increases at a slow rate. This results in less phosphorus per individual plant. When there are few plants, the decrease in fitness is rapid. However, the plants become increasingly self-reliant for phosphorus when their numbers increase (condition 4a is not satisfied). Hence, further decreases in plant fitness are small (Figure 2.4).

While the loss in fitness per plant with an increase in plant numbers follows directly from supply and demand predictions, the increase in fungal cooperativeness is again a novel and unexpected result.

Results 8 and 9 predict opposite effects on plant fitness because, all else being equal, having more competitors is bad for a focal individual’s fitness. In contrast, having more trading partners competing against each other is good for the focal individual’s fitness. Overall, extending plant-mycorrhizal networks (adding both plant and fungal partners) can have conflicting effects on agricultural yields: plants lose fitness when mycorrhizal fungi make connections with more plant partners, but gain fitness as they make connections with more fungal partners (Figure 2.4, Weremijewicz & Janos 2013). In addition, our model highlights potential for conflict over network size and composition as mycorrhizal fungi can benefit from increases in the number of both mycorrhizal fungi and plants, leading to different fitness optima in the two species (Figure 2.5).

Phosphorus Fertiliser Availability

An increase in phosphorus fertiliser availability will increase the amount of phosphorus available to plants (P_p), the amount of phosphorus available to mycorrhizal fungi (P_m), or both. In practice, scenarios where phosphorus availability increases to each plant (but not to each mycorrhizal fungus) are likely only when the quantity of mycorrhizal fungi increases as well, thus forcing the fungi to compete amongst each other for the increased phosphorus. However, our model can tease apart the separate effects of increase in phosphorus available to plants and mycorrhizal fungi. The effect of a simultaneous increase in both is a combination of the two separate effects that can be determined through empirical parametrisation of our model.

> **Result 10** – An increase in phosphorus available exclusively to plants decreases fungal cooperativeness, whereas an increase in phosphorus availability to mycorrhizal fungi increases their cooperativeness.
> Again, these effects will be small, proportional to the fungi's initial

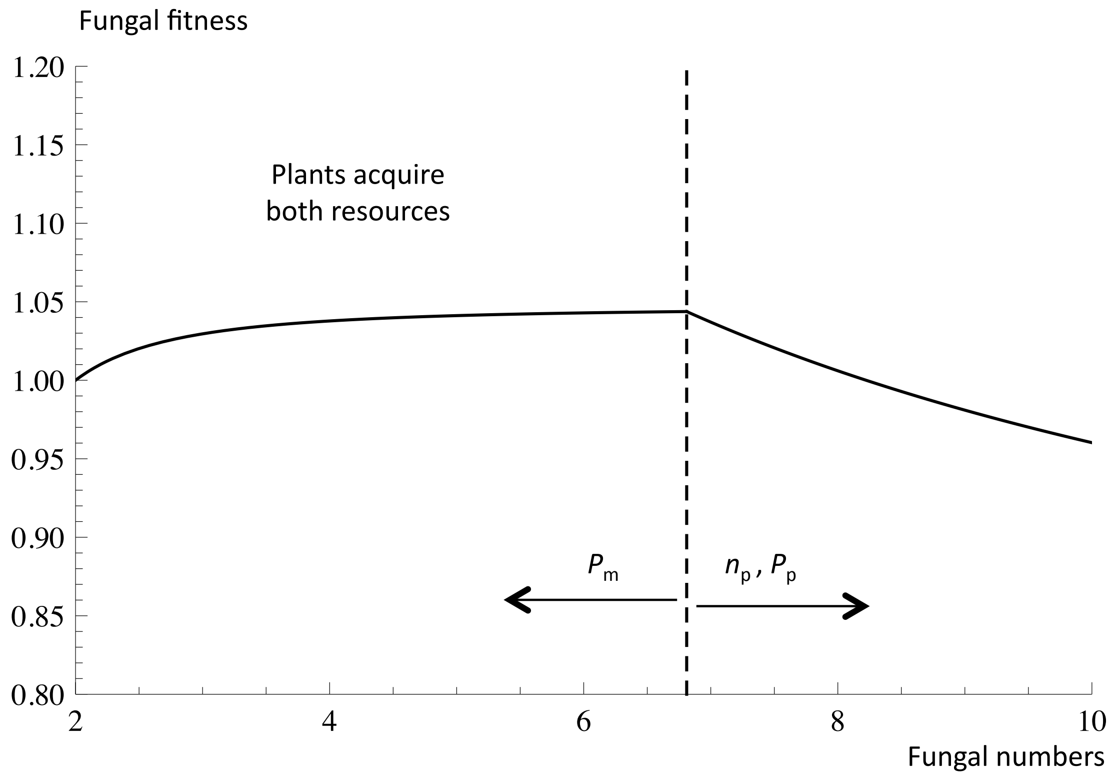


Figure 2.5 | Effect of mycorrhizal numbers on mycorrhizal fitness. When there are few mycorrhizal fungi, their fitness increases as with their numbers. This occurs because they can induce plants to acquire more carbon and less phosphorus directly, thus lowering the phosphorus price of carbon. However, once plants acquire only carbon directly (right of dashed line), mycorrhizal fungi lose fitness as their numbers increase. (In graph, n_p=10, C_p=1, P_p=0.5, P_m=1, a=0.7, b=0.3, I=0.1).

carbon endowment I, because two effects oppose: (i) if additional phosphorus is available, it is relatively less valuable in trade than if consumed by the mycorrhizal fungi. This selects mycorrhizal fungi to transfer less phosphorus; (ii) the increased levels of phosphorus increase the marginal benefit of a unit of carbon, so mycorrhizal fungi are selected to transfer more phosphorus in exchange for this carbon.

Result 11 – Increases in phosphorus availability, whether to plants or mycorrhizal fungi, increase plant fitness. However, this effect is threshold dependent. When plants acquire only carbon directly, they do

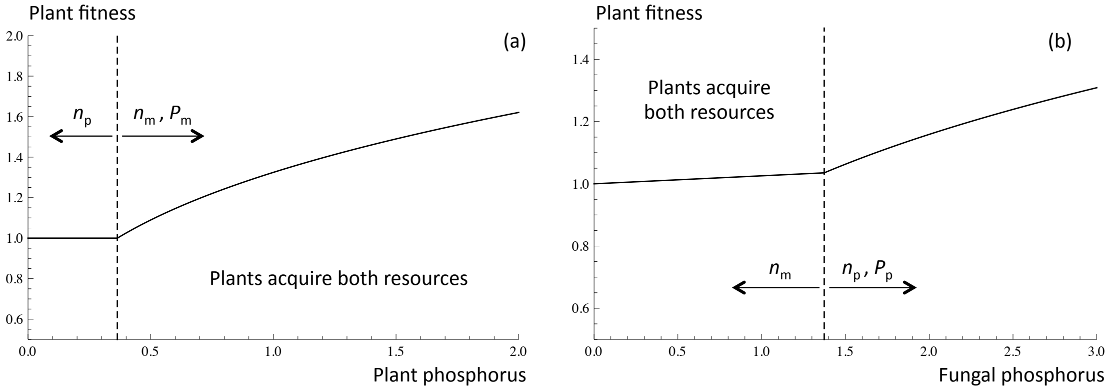


Figure 2.6 | Effect of phosphorus availability on plant fitness. (a) Plants only benefit from an increase in phosphorus they can acquire directly once they start acquiring it (right of dashed line). (In graph, n_p=10, n_m=5, C_p=1, P_m=1, a=0.7, b=0.3, I=0.1). (b) Plant fitness always increases with the quantity of phosphorus available to mycorrhizal fungi. Fitness increases much more rapidly once plants acquire only carbon directly (right of dashed line, condition (6a) is satisfied) and therefore cannot compete with each other for phosphorus by acquiring more carbon directly. (In graph, n_p=10, n_m=5, C_p=1, P_p=0.5, a=0.7, b=0.3, I=0.1).

not benefit from an increase in the phosphorus directly available to them (P_p), as they do not use this source. Plants benefit from an increase in either phosphorus source when they acquire both resources directly, as is most biologically realistic (Figure 2.6). However, in this scenario, they benefit very little from an increase in phosphorus available to mycorrhizal fungi (P_m). They compete for this additional phosphorus by acquiring more carbon directly and transferring it to the fungal partner. Plants benefit more from an increase in phosphorus available to mycorrhizal fungi when they are fully reliant on mycorrhizal phosphorus (Figure 2.6).

Result 10 analyses how strategies change with changes in phosphorus availability. Here, our model differs significantly from the model of Grman et al. (2012). Their model predicts a significantly less cooperative mutualist at high phosphorus availability to fungi because their single mycorrhizal fungus exploits monopoly power. In our model that allows multiple fungal individuals, as is most likely in the natural world, competition prevents this outcome. Result 11 analyses changes in plant fitness with phosphorus availability and highlights the same expected threshold dependencies found previously (Grman et al. 2012).

While the plants gain fitness even when additional phosphorus is not available to them except through trade, mycorrhizal fungi lose fitness when plants can acquire more phosphorus directly. This is because plants become less reliant on them.

> **Result 12** – When phosphorus availability to plants, P_p, reaches sufficiently high levels, trade between plants and mycorrhizal fungi ceases. However, plant fitness does not suffer once this happens. When phosphorus is so easily available to plants, it is cheaper for the plants to acquire it directly than to acquire it through trade.

Hoeksema and Schwarz (2003) provide a more comprehensive analysis of conditions when mutualistic trade is not beneficial, although our model extends this by also showing when mutually beneficial trade fails to evolve due to public goods dilemmas. This outcome has already been shown in the economics literature (Bacchiega 2013).

Atmospheric Carbon Concentrations

How will rising CO_2 levels influence trade between plants and their mycorrhizal fungi?

> **Result 13** - Rising CO_2 concentrations increase plant yield because plants are able to acquire more carbon directly (*C* increases). In addition, rising CO_2 levels increase fungal cooperativeness, although the effect will again be proportion to the fungal carbon endowment *I*, and hence small, because two effects oppose: (i) mycorrhizal fungi are selected to transfer more phosphorus because plants can transfer more carbon in return; (ii) more carbon is available, which decreases its marginal value, and selects for mycorrhizal fungi to transfer less phosphorus.

Result 13 predicts diminishing marginal fitness returns for an increase in the availability of a limiting resource. This is the default prediction in both economics and biology.

2.4 Discussion

Our work builds on previous research in biological market theory and its predictions. We demonstrate the validity of the market analogy and extend predictions on specialisation and trade in mutualisms. We then use the biological market framework to make predictions about the agricultural consequences of ecological change.

2.4.1 Biological Markets

The plant-mycorrhizal mutualism consists of two-way trading connections between individuals. We have shown that this system can lead to the equivalent outcome as a central marketplace to which all individuals must bring the goods they trade. Specifically, we found that natural selection can both lead to all individuals receiving the same market exchange rate for their goods and maintain trade. We derived our results using pre-existing frameworks in the economics literature used for analysing trade, termed "non-cooperative trading games" (see Appendix). Within species interactions were analysed using frameworks for competition between suppliers of a particular good, where these suppliers must compete by adjusting quantities they bring to markets. This competitive structure is termed "Cournot competition" (Cournot 1838, see Appendix).

Our results depend on linear proportional discrimination the strategy used for sharing resources. This is not a problem in economics, where it is typically assumed that individuals receive goods in proportion to the amount of money they pay, but it was not obvious that natural selection could lead to the same outcome. Linear proportional discrimination is evolutionarily stable when two conditions are satisfied: (i) responses to changes in the price at which resources are available are equally strong in any individual in a species and (ii) individuals may vary, but the ratio of benefits traded (C or P allocated to trade) to benefits received (C or P received through trade) is the same for any individual in each species (see Appendix). The ratio of exchange need not be 1:1 for the resources, but it must remain consistent across trades in that particular population. The optimal foraging theory literature on Ideal Free

Distributions suggests that these two conditions are likely to often be met, especially whenever individuals differ only in their competitive ability to acquire resources and are free to engage with whatever mutualistic partners they choose or whenever individuals acquiring more resources grow faster (Whitham 1980, Harper 1982, Sutherland & Parker 1985, Parker & Sutherland 1986, Houston & McNamara 1988, Sutherland et al. 1988, Inman 1990, Kacelnik et al. 1992, Krivan 1997). Whilst plants and arbuscular mycorrhizal fungi have been shown to allocate more carbon resources to individuals offering more phosphorus in return (Bücking & Shachar-Hill 2005, Bever et al. 2009, Kiers et al. 2011), it is not known if they actually use a linear proportional discrimination rule. One confounding factor is that while plants trade only carbon with fungal partners, the fungal partners can trade additional resources, such as nitrogen and trace elements (Tanaka and Yano 2005; Chen et al. 2003). How this asymmetry in the diversity of goods offered by the two species affects proportional discrimination is unknown. Tracking and quantifying the exchange of multiple resources in mycorrhizal networks remains empirically difficult.

We have also shown that trade can only be maintained by linear proportional discrimination when individuals are exposed to enough potential competitors of the same species (inequality (2)). As the number of competitors goes up, this increases competition for the resources provided by the mutualistic partner, and hence favours transferring more resources to the other species to earn a greater share of trade. It also increases the total amount of resources available to members of the mutualistic species, thus favouring these individuals to transfer more resources in return. If there are too few competitors, then a decrease in resources transferred can always be favoured, and trade can even collapse altogether (Figure 2.1). Empirical work in the mycorrhizal symbiosis suggests that individuals most often trade in large networks of partners (Giovannetti et al. 2004; Montesinos-Navarro et al. 2012), and so discriminating between individuals (and allocating resources accordingly) is likely to be a useful mechanism for maintaining cooperation (Figure 2.2). The exact physiology of how this discrimination could take place is the focus of on-going work. It has been shown, for example, that an increase in host plant carbon can trigger the uptake of nutrients, such as nitrogen, by the fungal partner (Fellbaum et al. 2012). Vice-versa, fungal partners can discriminate among adjacent roots differing in carbon resources (Bücking & Shachar-Hill 2005; Kiers et al. 2011), even allocating more nutrients to plants grown under sun rather than shade conditions (Fellbaum et al. in press). However, such examples of fair-trade are not always the norm (e.g. Merckx and Bidartondo 2008, Walder et al. 2012).

2.4.2 Trade and Specialisation

A link between trade and specialisation has long been recognised in economics (Ricardo 1817), and the tendency for specialisation to drive trade has been explored in the biological market literature (Schwartz and Hoeksema 1998, Hoeksema & Schwartz 2001, Grman et al. 2012). Indeed, mutualisms tend to evolve more easily when species are highly specialised on a partner, as the benefits of trade are greater (Poisot et al. 2011). In our model, we recover and extend these results, suggesting that trade and specialisation will go hand in hand: specialisation evolves when mutualistic trade is present, and vice versa. In biological settings, it was unclear whether or not trade would drive specialisation. Mycorrhizal fungi could have potentially benefited from retaining the ability to acquire carbon directly (rather than being dependent on the host), thus retaining bargaining power with plants (Bergmüller et al. 2007). However, physiological evidence suggests that whilst mycorrhizal fungi have not lost all of their saprophytic abilities, they do not possess the key genes to obtain carbon directly (e.g. genes to degrade plant cell walls, Tisserant et al. 2014). Instead, they have clearly evolved a dependence on host plant carbon, only expressing their full genetic potential when in symbiosis (Corradi & Bonfante 2012). An explanation suggested by our model is that mycorrhizal fungi compete most fiercely with other mycorrhizal fungi for plant carbon. As a result, only adaptations that will help them acquire more of the host carbon can be favoured by natural selection even if these adaptations entail greater dependence on the host. The fungal spores that fail to complete their life cycle when they do not have plant partners may be an indication of how strong the selective pressure to be a strong competitor in trade can be. The feedback loop between trade and specialisation may help explain how the mycorrhizal symbiosis and other mutualisms evolve from facultative to obligate (Aanen & Hoekstra 2007).

2.4.3 Ecological Change and Agricultural Consequences

We have found that the impact of the number of social partners on plant fitness (and thus potentially crop yields) is threshold dependent (Figure 2.4). Initially, increasing the number of mycorrhizal fungi per plant has only a small beneficial effect on plant fitness. However, once plants start relying entirely on trade for phosphorus, plant fitness increases rapidly, even though mycorrhizal cooperativeness increases at a diminishing rate throughout. In contrast, as plant number per fungal partner rises, plant fitness falls rapidly but then levels off, even though mycorrhizal cooperativeness remains constant. Therefore our model suggests that large networks are likely to be better for plants, as the variety of suppliers mean that plants can rely on mycorrhizae for phosphorus and enjoy the fitness gains associated with specialising on acquiring carbon.

The benefits of an increase in phosphorus availability are similarly threshold dependent (Figure 2.6). When plants do not acquire phosphorus from the soil, only an increase in phosphorus available to mycorrhizal fungi (P_m) increases plant fitness. On the other hand, when plants acquire both carbon and phosphorus directly, only an increase in phosphorus available directly to plants (P_p) significantly increases plant fitness. We also predict that mycorrhizal fungi lose fitness when plants can acquire more phosphorus directly, as plants become less reliant on them. This effect has the potential to select for mycorrhizal fungi that prevent, whether partially or completely, plants from acquiring phosphorus directly. There is some evidence that mycorrhizal fungi have evolved ways to suppress the direct nutrient uptake pathway of their host plants. The apparent deactivation of the direct pathway in plants colonised by mycorrhizal fungi is hypothesised to be a result of down-regulation of the plant phosphorus transporters in root epidermis and root hairs (Smith et al. 2011). While our model shows that changing phosphorus conditions do not necessarily have a major effect on cooperativeness (i.e. the proportion of fungal phosphorus allocated to trade), it does suggest that there is room for the fungal partner to evolve greater control of soil resources.

Predicting the effects of increasing atmospheric CO_2 concentration on crop yields is difficult, and remains a hotly debated topic (Jaggard et al. 2010). While carbon becomes more readily available to plants, the increase in fitness directly attributable to increased carbon is likely to show diminishing returns, as other resources become more limiting. Our model suggests that this benefit is enhanced by interactions with mutualists. Mycorrhizal fungi will be competing for a larger pool of plant carbon, which encourages them to transfer more phosphorus, although this will be moderated by the increasingly limiting role of phosphorus throughout the system. Consistent with these predictions, long-term studies, such as the free air CO_2 enrichment (FACE) experiment in Switzerland suggest that increasing CO_2 can drive strong selection pressures in mycorrhizal fungi (Staddon et al. 2004). Within 8 years, fungal isolates (e.g. *Glomus* sp.) from plots treated with elevated CO_2 improved the nitrogen nutrition of their host plants significantly more than those in plots treated with ambient CO_2 (Gamper et al. 2005). As predicted in our model, the mycorrhizal fungi became more cooperative. These experiments demonstrate the potential for harnessing evolved mutualistic strategies in order to increase crop yields. An improved understanding of the co-evolutionary dynamics, with a particular emphasis on identifying thresholds beyond which plant growth increases rapidly, is a key part of a "Darwinian Agricultural" strategy to increase crop yields in a more sustainable manner (Denison et al. 2003, Denison 2013).

2.5 Appendix

2.5.1 Linear proportional discrimination

Here we derive the conditions under which linear proportional discrimination is an evolutionarily stable strategy (Riechert & Hammerstein 1983). The games for plants and mycorrhizal fungi are identical, so we only derive the conditions for plants. We consider rules for allocating resources between members of any pair of arbitrarily labelled fungal trading partners, m_1 and m_2. We suppose a strategy set consisting of functions $f(P_{\mathrm{r1}}[f_{\mathrm{t-1}}], P_{\mathrm{r2}}[1-f_{\mathrm{t-1}}])$ that return a real number $f_t \in [0,1]$, where $P_{\mathrm{r1}}[f_{\mathrm{t-1}}]$ and $P_{\mathrm{r2}}[1\text{-}f_{\mathrm{t-1}}]$ are the amounts of phosphorus that a focal plant receives from mycorrhizal fungi m_1 and m_2 respectively. We also require that a function in the strategy set yield an iterative solution where $f(P_{\mathrm{r1}}[f_\infty], P_{\mathrm{r2}}[1-f_\infty]) = f_\infty$, using $f_{\mathrm{t-1}}$=0.5 as the initial condition. We define the payoff function of the evolutionary game as $P_{\mathrm{r}} = P_{\mathrm{r1}}[f_\infty] + P_{\mathrm{r2}}[1-f_\infty]$.

Now, we test whether or not linear proportional discrimination is an ESS in plants, assuming mycorrhizal fungi also adopt that strategy. If it is, then it is an ESS in mycorrhizal fungi, assuming plants also adopt that strategy. Hence, it is a co-evolutionary ESS (Riechert & Hammerstein 1983). The linear proportional discrimination strategy is the function

$$f(P_{\mathrm{r1}}[f_{\mathrm{t-1}}], P_{\mathrm{r2}}[1-f_{\mathrm{t-1}}]) = \frac{P_{\mathrm{r1}}[f_{\mathrm{t-1}}]}{P_{\mathrm{r1}}[f_{\mathrm{t-1}}] + P_{\mathrm{r2}}[1-f_{\mathrm{t-1}}]} \tag{4}$$

Now, we work out the iterative solution when all individuals use linear proportional discrimination for the focal plant, f_∞^*. At this solution, the focal plant shares an amount of carbon allocated for trade, C_{t}, between the two mycorrhizal fungi, giving a proportion $C_{\mathrm{t}}f_\infty^*$ and a proportion $C_{\mathrm{t}}(1\text{-}f_\infty^*)$ of that amount to m_1 and m_2 respectively. These mycorrhizal fungi also receive total amounts of carbon $C_{\mathrm{re1}}[f_\infty^*]$ and $C_{\mathrm{re2}}[1\text{-}f_\infty^*]$ respectively from all of their other plant trading partners (i.e. not including the focal plant). These amounts depend on the carbon provided by the focal plant to a given mycorrhizal fungus, the strategies of other plants impact the payoff function of a focal plant through these amounts in our ESS analysis. In this case, we consider the consequences of assuming that all other plants use linear proportional discrimination. When a focal plant provides more carbon, phosphorus from that fungus becomes more expensive and other plants allocate more carbon to alternative sources. The fungi use the amounts of carbon received to allocate the quantities of phosphorus they allocate to trade, $P_{\mathrm{t}1}$ and $P_{\mathrm{t}2}$ between their trading partners. At the iterative solution, f_∞^* satisfies

$$\frac{P_{\mathrm{t}1}}{C_{\mathrm{t}} f_\infty^* + C_{\mathrm{re}1}[f_\infty^*]} = \frac{P_{\mathrm{t}2}}{C_{\mathrm{t}}(1-f_\infty^*) + C_{\mathrm{re}2}[1-f_\infty^*]} \tag{5}$$

if both fungal partners receive carbon, $f_\infty^* \neq 0$ or 1. Intuitively, this means that when all individuals use linear proportional discrimination, phosphorus is acquired at the same price from all trading partners that receive carbon. For a plant to find a strategy better than proportional discrimination, it must be able to acquire more phosphorus by allocating more carbon to one mycorrhizal fungus and less to another. However, by allocating more carbon to a fungus, the plant increases the price of phosphorus from that fungus. Therefore, it is allocating more carbon to acquire phosphorus at the higher price. This means that the plant will only gain overall if the supply decrease it causes in the other mycorrhizal fungus sufficiently decreases the price of phosphorus from that fungus. The smaller quantity it acquires at the new lower price must be cheap enough that it compensates for the increased cost of acquiring a larger quantity at a higher price.

The payoff to a plant using any strategy in the strategy set is

$$P_{\mathrm{r}} = \frac{C_{\mathrm{t}} f_{\infty}}{C_{\mathrm{t}} f_{\infty} + C_{\mathrm{re1}}[f_{\infty}]} P_{\mathrm{t1}} + \frac{C_{\mathrm{t}}(1 - f_{\infty})}{C_{\mathrm{t}}(1 - f_{\infty}) + C_{\mathrm{re1}}[1 - f_{\infty}]} P_{\mathrm{t2}} . \tag{6}$$

We now calculate the iterative solution f_∞ that maximises P_{r} when all mycorrhizal fungi use linear proportional discrimination. We calculate $\partial P_{\mathrm{r}}/\partial f_\infty$ and $\partial^2 P_{\mathrm{r}}/\partial {f_\infty}^2$ and evaluate these derivatives at the value of f_∞^* determined by linear proportional discrimination (equation (5)). We then assume that the instantaneous change in carbon supplied to a mycorrhizal fungus by all other plants due to a change in the price at which phosphorus can be acquired is equally strong in both fungi m_1 and m_2 (we term this change "market compensation" and can express our assumption mathematically as $\partial C_{\mathrm{re1}}/\partial f_\infty \mid_{f_\infty = f_\infty^*} = -\partial C_{\mathrm{re2}}/\partial f_\infty \mid_{f_\infty = f_\infty^*}$). Any strategy adopted by all other plants leads to equal market compensation if all individuals are connected into a trading network that is identical from each individual's perspective, which we assume in our model. We then simplify $\partial P_{\mathrm{r}}/\partial f_\infty \mid_{f_\infty = f_\infty^*}$ and find that phosphorus received is maximised using proportional discrimination if

$$\frac{C_{\mathrm{re1}}[f_\infty^*]}{P_{\mathrm{t1}}} = \frac{C_{\mathrm{re2}}[1 - f_\infty^*]}{P_{\mathrm{t2}}} . \tag{7}$$

That is, no strategy in the strategy set can return more phosphorus to the focal plant than linear proportional discrimination when equation (7) is satisfied. The payoff function P_{r} is maximised. Finally, we consider strategies that would behave identically to linear proportional discrimination when played against a population of identical plants and identical mycorrhizal fungi all using linear proportional discrimination, such as $f(P_{\mathrm{r1}}[f_{\mathrm{t-1}}], P_{\mathrm{r2}}[1 - f_{\mathrm{t-1}}]) = 1/2$. We assume that small variation in resources allocated to trade amongst individuals differentiate between these other strategies and linear proportional discrimination in our model. As linear proportional discrimination is always the optimal strategy when equation (7) is satisfied, this last assumption makes it the unique best response and thus an ESS.

Whilst these assumptions are restrictive, the assumptions that individuals are in the same position in trading networks, that individuals receive more resources when they have more available to trade, and that there is some variation in resource availability to individuals are reasonable approximations to biological reality. It suggests that linear proportional discrimination, which leads to resources being acquired at equal prices, is likely to be difficult to invade in many mutualistic trading systems.

2.5.2 Conditions for existence of trading ESS and equilibrium allocations

We take plant fitness from equation (1a), and substitute model parameters and evolved strategies for the proportion of traded phosphorus acquired by the focal plant, s_{p}, which is equal to the share of total traded carbon that the plant acquires which we now write down in terms of model parameters. The numerator of s_{p} is the total amount of carbon that the focal plant provides in trade which is the proportion of acquired carbon that the focal plant allocates to trade, $C_{\mathrm{t}}=x_{\mathrm{p}}C_{\mathrm{p}}q_{\mathrm{p}}$. The denominator of s_{p} is the total amount of carbon traded by all competing plants, including the focal individual. There are n_{p}-1 competitors, and the average amount of carbon each trades is the average proportion of the average total amount of carbon that each plant acquires, $x_{\mathrm{p}}' C_{\mathrm{p}} q_{\mathrm{p}}'$. We add this across all of the competitors and add the amount of carbon provided by the focal individual, so the denominator is $((n_{\mathrm{p}} - 1)x_{\mathrm{p}}{}' C_{\mathrm{p}} q'_{\mathrm{p}} + x_{\mathrm{p}} C_{\mathrm{p}} q_{\mathrm{p}})$. Hence, the proportion of total traded phosphorus that the plant acquires is s_{p}=$(x_{\mathrm{p}} C_{\mathrm{p}} q_{\mathrm{p}})/((n_{\mathrm{p}} - 1)x_{\mathrm{p}}{}' C_{\mathrm{p}} q'_{\mathrm{p}} + x_{\mathrm{p}} C_{\mathrm{p}} q_{\mathrm{p}})$. This means that equation (1a) is now entirely expressed in terms of model parameters and evolved strategies. The same approach allows us to express equation (1b) in the same way.

We now calculate the fixed points with respect to allocation to direct carbon acquisition and trade, $\partial w_{\mathrm{p}}/\partial x_{\mathrm{p}} = \partial w_{\mathrm{p}}/\partial q_{\mathrm{p}} = 0$. At an ESS, any focal plant receives population mean fitness to first order, so we take its strategy to be the population average ($q_{\mathrm{p}} = q'_{\mathrm{p}}$, $x_{\mathrm{p}} = x'_{\mathrm{p}}$). Substituting, we find that at a fixed point

$$q'_{\mathrm{p}} = \frac{(1-a)q'_{\mathrm{m}}(1-x'_{\mathrm{m}})(n_{\mathrm{p}}-1)n_{\mathrm{m}}P_{\mathrm{m}}}{a(1-x'_{\mathrm{p}})n_{\mathrm{p}}^2P_{\mathrm{p}} + q'_{\mathrm{m}}(1-x'_{\mathrm{m}})(n_{\mathrm{p}}-1+a)n_{\mathrm{m}}P_{\mathrm{m}}} \tag{8a}$$

$$x'_{\mathrm{p}} = a + \frac{q'_{\mathrm{m}}(1-x'_{\mathrm{m}})(n_{\mathrm{p}}-1+a)n_{\mathrm{m}}P_{\mathrm{m}}}{n_{\mathrm{p}}^2P_{\mathrm{p}}}\,. \tag{8b}$$

Similarly, we find that the fixed-point values of trade and direct carbon acquisition for mycorrhizal fungi are

$$q'_{\mathrm{m}} = \frac{bC_{\mathrm{p}}x'_{\mathrm{p}}q'_{\mathrm{p}}n_{\mathrm{p}}(n_{\mathrm{m}}-1)}{(n_{\mathrm{m}}-b)C_{\mathrm{p}}x'_{\mathrm{p}}q'_{\mathrm{p}}n_{\mathrm{p}} + (1-b)(I + C_{\mathrm{m}}x'_{\mathrm{m}})n_{\mathrm{m}}^2} \tag{8c}$$

$$x'_{\mathrm{m}} = \frac{bC_{\mathrm{p}}x'_{\mathrm{p}}q'_{\mathrm{p}}n_{\mathrm{p}} - (C_{\mathrm{p}}x'_{\mathrm{p}}q'_{\mathrm{p}}n_{\mathrm{p}} + In_{\mathrm{m}})n_{\mathrm{m}} + b(I + C_{\mathrm{m}})n_{\mathrm{m}}^2}{C_{\mathrm{m}}n_{\mathrm{m}}^2}\,. \tag{8d}$$

We find that there is a unique solution that satisfies 8a-d

$$(x'_{\mathrm{p}}, q'_{\mathrm{p}}, x'_{\mathrm{m}}, q'_{\mathrm{m}}) = \left(a, 0, b - \frac{I(1-b)}{C_{\mathrm{m}}}, 0 \right). \tag{9}$$

Any mutant in either species that uses a different strategy to the one specified in (9) has lower fitness as long as individuals in both species can acquire both resources directly, hence (9) defines a co-evolutionary ESS when C_{p}, C_{m}, P_{p}, and P_{m} are positive.

In addition, plants and mycorrhizal fungi are constrained to allocations to direct carbon acquisition and trade between 0 and 1. We look for other pairs of ESSs that are constrained maxima on this boundary. We eliminate $x'_{\mathrm{p}} = 0$ and $q'_{\mathrm{p}} = 1$ as this would leave plants without carbon, and $x'_{\mathrm{m}} = 1$ and $q'_{\mathrm{m}} = 1$ as this would leave mycorrhizal fungi without phosphorus. We first set $x'_{\mathrm{p}} = 1$ and work out the evolved best response values for the other variables if all other individuals use the same strategy:

$$(x'_{\mathrm{p}}, q'_{\mathrm{p}}, x'_{\mathrm{m}}, q'_{\mathrm{m}}) = \left(\begin{array}{c} 1, \dfrac{(1-a)(n_{\mathrm{p}}-1)}{n_{\mathrm{p}}-1+a}, \\ \dfrac{(bC_{\mathrm{m}} - (1-b)I)(n_{\mathrm{p}}-1+a)n_{\mathrm{m}}^2 - (1-a)C_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}}(n_{\mathrm{m}}-b)}{C_{\mathrm{m}}(n_{\mathrm{p}}-1+a)n_{\mathrm{m}}^2}, \quad . \\ \dfrac{(1-a)C_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}}(n_{\mathrm{m}}-1)}{(1-b)(I+C_{\mathrm{m}})(n_{\mathrm{p}}-1+a)n_{\mathrm{m}}^2 + (1-a)C_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}}(n_{\mathrm{m}}-b)} \end{array} \right) \tag{10}$$

We verify whether fitness at $x_{\mathrm{p}} = 1$ is greater than at $x_{\mathrm{p}} < 1$, given the corresponding values of q'_{p}, x'_{m}, and q'_{m}:

$$\frac{\partial w_{\mathrm{p}}}{\partial x_{\mathrm{p}}}\Big|_{x'_{\mathrm{p}}=1} > 0 \Leftrightarrow \frac{C_{\mathrm{p}}P_{\mathrm{m}}}{P_{\mathrm{p}}C_{\mathrm{m}}} > \frac{n_{\mathrm{p}}n_{\mathrm{m}}}{(n_{\mathrm{p}}-1)(n_{\mathrm{m}}-1)}. \tag{11}$$

In the parameter region from (11), the best response values in (10) are feasible (and (10) is thus a co-evolutionary ESS) if the inverse of condition (3b) in the main text is satisfied:

$$C_{\mathrm{p}} \leq \frac{(bC_{\mathrm{m}} - I(1-b))(n_{\mathrm{p}}-1+a)n_{\mathrm{m}}^2}{(1-a)(n_{\mathrm{p}}-1)n_{\mathrm{p}}(n_{\mathrm{m}}-b)}. \tag{12}$$

We can also set $x'_{\mathrm{m}} = 0$ and find a pair of ESSs by the same method with

$$(x'_{\mathrm{p}}, q'_{\mathrm{p}}, x'_{\mathrm{m}}, q'_{\mathrm{m}}) = \left(\frac{e}{C_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}}^2(n_{\mathrm{m}}-b)P_{\mathrm{p}}}, \frac{(n_{\mathrm{p}}-1)n_{\mathrm{m}}(bC_{\mathrm{p}}(n_{\mathrm{p}}-1)(n_{\mathrm{m}}-1)P_{\mathrm{m}} - I(1-b)n_{\mathrm{p}}n_{\mathrm{m}}P_{\mathrm{p}})}{e}, 0, \frac{(n_{\mathrm{p}}n_{\mathrm{m}} - n_{\mathrm{p}} - n_{\mathrm{m}} + 1)P_{\mathrm{m}}C_{\mathrm{p}}b - I(1-b)n_{\mathrm{p}}n_{\mathrm{m}}P_{\mathrm{p}}}{C_{\mathrm{p}}(n_{\mathrm{p}}-1)(n_{\mathrm{m}}-b)P_{\mathrm{m}}} \right) \tag{13}$$

where expression $e = n_{\mathrm{p}}\big(a(n_{\mathrm{m}}-b)C_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}} - I(1-b)(n_{\mathrm{p}}-1+a)n_{\mathrm{m}}^2\big)P_{\mathrm{p}}$ $+bC_{\mathrm{p}}(n_{\mathrm{p}}-1)(n_{\mathrm{p}}-1+a)(n_{\mathrm{m}}-1)n_{\mathrm{m}}P_{\mathrm{m}}$.

Fitness is also maximised at $x_{\mathrm{m}} = 0$ in the parameter region defined by (11), given the best response values in (13). These are feasible when the inverse of condition (3a) in the main text is satisfied:

$$P_{\mathrm{p}} \geq \frac{bC_{\mathrm{p}}(n_{\mathrm{p}}-1)(n_{\mathrm{p}}-1+a)(n_{\mathrm{m}}-1)n_{\mathrm{m}}P_{\mathrm{m}}}{n_{\mathrm{p}}((1-a)C_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}}n_{\mathrm{m}}+I(1-b)(n_{\mathrm{p}}-1+a)n_{\mathrm{m}}^2-(1-a)bC_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}})}. \qquad (14)$$

Finally, we set $x'_{\mathrm{p}} = 1$ and $x'_{\mathrm{m}} = 0$. We find that

$$(x'_{\mathrm{p}}, q'_{\mathrm{p}}, x'_{\mathrm{m}}, q'_{\mathrm{m}}) = \left(\begin{array}{c} 1, \dfrac{(1-a)(n_{\mathrm{p}}-1)}{n_{\mathrm{p}}-1+a}, 0, \\ \dfrac{(1-a)bC_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}}(n_{\mathrm{m}}-1)}{(1-a)C_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}}(n_{\mathrm{m}}-b)+I(1-b)(n_{\mathrm{p}}-1+a)n_{\mathrm{m}}^2} \end{array} \right). \qquad (15)$$

These strategies are a co-evolutionary ESS when neither inequality (12) nor inequality (14) is satisfied.

2.5.3 Economic Background and Future Avenues

Here, we draw parallels between our model and existing work in economics. In this section, we retain language used in economics. Although we derive our model from a biological perspective, similar models of trade have been derived and analysed in economics. We present this work for two audiences. First, biologists may be interested in the precise market structure that we suggest the mycorrhizal symbiosis resembles, and from which branches of economics further insight may be drawn. Second, we hope that economists studying models applicable to biology will be motivated to resolving outstanding questions.

Our model assumes a very simple production set for both plants and mycorrhizal fungi, where individuals in each species can acquire both carbon and phosphorus.

Each individual makes a production decision based on the combination of carbon and phosphorus that maximises its fitness after trade. The problem is exactly that faced by individuals in the most fundamental two-country, two-commodity models of trade under comparative advantage (Smith 1776, Ricardo 1817). Extensions of our model for more complex resource acquisition trade-offs, more individual types, or more traded goods are possible using Heckscher-Ohlin-Samuelson theory (Ohlin 1933). In particularly, Dornbusch et al. (1977, 1980) generalised the study of trade under comparative advantage for arbitrarily many goods, while Jones (1961) and Shiozawa (1977) provided models that incorporate both many trader types and many goods.

Within each species, we assume that individuals compete by setting the quantity of resources that they transfer to their mutualistic partners. We also assume that setting the quantity of resources sent is a one-shot simultaneous move game. This form of competition corresponds exactly to the Cournot model (Cournot 1838). This model considers a fixed number of firms competing to maximise their profits, without colluding, by choosing the quantity they supply to the market. Cournot competition differs from other market frameworks by assuming that firms do not compete by setting the price at which they are willing to supply (Bertrand 1883). This is an unrealistic assumption in many economic settings, but seems appropriate for biological agents. In addition, Cournot competition assumes that firms are not free to enter or exit the marketplace at will (Dunne et al. 2009). Again, this is seldom true in economic settings, but may better reflect biological problems where individuals may defend local resources such as food, access to mates or mutualistic partners. More complicated economic models incorporate partial barriers to entering a market (Spence 1977, Dixit 1980). These can be costly to maintain or overcome, and their study may give further insight into whether biological predictions change when the assumption of a fixed set of partners is lifted. Finally, the Cournot framework does not allow firms to change their quantity supplied in response to the actions of their competitors. This implies that our model assumes that quantities allocated to trade are genetically fixed. Sophisticated techniques are available in the literature on economic games and allow us to consider alternative models where individuals can adjust quantities supplied over time (Fudenberg & Tirole 1992, Osborne & Rubinstein 1994).

We then assume that all individuals in one species receive the same price for the resources they allocate to trade. This means that our model can be classified as a non-cooperative trading game. These were developed as tools to study two-sided trading interactions (Shubik 1972, Shapley 1977, Shapley & Shubik 1977). However, the models we referenced in the previous sentence share the assumption that individuals must bring all of their goods to the market, even if it means buying some of them back. Dubey and Shubik (1978) provided a model more appropriate for biological interactions, where individuals need only provide a part of their resource endowment for trade. We adopt this formulation in our model. These models of non-cooperative trade may be applied to consider more complexity in mutualistic interactions, as they have been extended to study the trade of a large number of resources. Further developments also consider additional trader types (Dubey & Shapley 1994).

Our model incorporates more recent advances in the study of non-cooperative trade. In particular, our model considers how the use of market power due to being one of a limited number of participants in a market affects trade (Gabszewicz & Vial 1972, Cordella & Gabszewicz 1997, Cordella & Gabszewicz 1998, Bacchiega 2012). Some of the results in our model have direct analogues in this pre-existing work. These include Result 2-7, where the conditions under which trade evolves are considered and the links between specialisation and trade are established. However, our inclusion of a more realistic Cobb-Douglas function to determine fitness is entirely novel, modifies the conditions under which particular outcomes arise, and show that previous predictions hold in more plausible settings (Cobb & Douglas 1928).

3

Restricting mutualistic partners to enforce trade reliance

3.1 Abstract

Mutualisms are cooperative interactions between individuals of different species, often involving the trade of resources. Here, we suggest that otherwise cooperative mutualists might be able to gain a benefit from actively impairing their partners' ability to obtain resources directly, restricting their ability to function without a particular mutualistic species. We show that: (i) impairment can be favoured when impairing individuals receive more favourable terms of trade; (ii) restriction can lead to cooperation being maintained in conditions where cooperative behaviour would otherwise collapse; and (iii) being restricted can lead to either an increase or decrease in a plant's fitness. We discuss the applicability of this scenario to mutualisms such as those between plants and mycorrhizal fungi. These results identify a novel conflict in mutualisms, but also demonstrate how this conflict can help maintain cooperation.

3.2 Introduction

Mutualistic interactions are central to the survival and/or reproduction of most species on earth. They provide essential ecosystem services such as pollination and seed dispersal, as well as constituting critical components of global carbon and nutrient cycles (Bronstein et al. 2004, Tylianakis et al. 2008). Mutualistic cooperation usually involves the different species trading either services or resources. For example: mycorrhizal fungi supply their host plants with phosphorous and other nutrients in exchange for host carbon; ants defend trees in exchange for food and housing; and flowering plants provide insects and birds with food in exchange for pollination services (Parniske 2008, Heil et al. 2009, Potts et al. 2010).

Whilst these mutualisms are based on cooperative trade, there is an underlying tension because each partner is favoured to maximise its benefit from the interaction, leading to conflict and exploitation (van Baalen & Jansen 2001). In the extreme, non-cooperative cheats, who gain benefits from the cooperation of others without paying the cost of cooperation themselves, can even lead to the collapse of mutualisms (Ghoul et al. 2014). But, can conflict ever lead to increased cooperation in mutualisms? We suggest that mutualists can be selected to pay costs in order to impair the resource acquisition pathways of their partners, so as to promote resource trade. Consequently, conflict over where resources are acquired from can favour increased cooperation. However, the theoretical plausibility of this hypothesis remains unclear, as active impairment could incur costs to both partners, which could outweigh any benefits of increased trade.

We examine this hypothesis theoretically, by modelling the interaction between two species. Our aim is to examine if and why individuals would be favoured to impair the resource acquisition ability of their mutualistic partners, with whom they are also cooperating. Whilst we examine a relatively general model, we phrase it in terms of the interaction between plants and mycorrhizal fungi to provide biological grounding. We consider a costly trait that enables mycorrhizal fungi to restrict (decrease) the ability of their plant partners to directly take up phosphorus from the soil (Smith et al. 2011). We first examine whether and how such a trait could be favoured in mycorrhizal fungi. We then examine the consequences of restriction, for both the stability of the mutualism and the fitness of their restricted plant partners.

3.3 Results

We consider the coevolution of strategies in both mycorrhizal fungi and plants. We assume a finite population where each plant and mycorrhizal fungus has n_f and n_p social partners of the other species respectively (we assume $n_p>1$ to allow partner discrimination) and that all individuals in a species are identical except for strategy. Both mycorrhizal fungi and plants require phosphorous and carbon for growth. Each mycorrhizal fungus has an initial supply of one unit of carbon and acquires a quantity P_f of phosphorus from the soil. The mycorrhizal fungus may decrease its plant partners' access to phosphorus by a restricting trait (r), and this also directly reduces the fungus' fitness to a fraction $(1-r)$ of what it would be in the absence of restriction. We assume that plants face a linear trade-off between the acquisition of carbon versus phosphorus, such that a plant that invests a proportion x of its acquisition effort into carbon acquisition obtains an amount xC_p of carbon and $(1-x)(1-\bar{r})^e P_p$ of phosphorus, where C_p and P_p are the maximum availabilities of carbon and phosphorus respectively, $\bar{r}$ is the average restriction strategy of its fungal partners, and $e > 0$ modulates the cost effectiveness of the restricting trait.

We assume that plants and mycorrhizal fungi can discriminate amongst trading partners, as has been empirically demonstrated in this and other mutualisms (Bever et al. 2009, Kiers et al. 2011, Biedermann & Kaltenpoth 2014, Hojo et al. 2014). Plants transfer a proportion q_{p} of their carbon to mycorrhizal fungi, while mycorrhizal fungi transfer a proportion q_{f} of their phosphorous to plants. Fungal strategy is fixed over the course of the interaction, and hence its dynamics are over evolutionary timescales, but the plant's allocation to trade and resource acquisition is dynamic over behavioural timescales, and it is the strategy underlying how it trades in response to partner cooperation that evolves. The evolution of restriction requires a model that takes into account phenotypic plasticity in plants, rather than just assuming a genetically fixed strategy. In many other models, strategies are assumed to only change over evolutionary timescales (reviewed in McNamara 2013). Taking phenotypic plasticity in plants into account adds biological realism, and a model that incorporates the possibility for phenotypic plasticity in mycorrhizal fungi would be a further improvement. We assume that all individuals use a linear proportional discrimination rule to divide resources amongst their partners, which means rewarding better trading partners by transferring more resources in proportion to the ratio in which they are received. Wyatt et al. (2014) have shown that this can be an evolutionarily stable strategy (ESS) in trading mutualisms with the characteristics presented in this model (Maynard Smith & Price 1973, Riechert & Hammerstein 1983).

We assume fitness functions $w_{\mathrm{p}}=C_{\mathrm{tp}}{}^{a}P_{\mathrm{tp}}{}^{1-a}$ for plants and $w_{\mathrm{f}}=C_{\mathrm{tf}}{}^{b}P_{\mathrm{tf}}{}^{1-b}(1-r)$ for mycorrhizal fungi, where C_{tp}, P_{tp}, C_{tf}, and P_{tf} are the total amounts of carbon and phosphorus acquired (after trade), and where $0<a<1$ and $0<b<1$ mediate the effects of carbon and phosphorus on fitness. These fitness functions mean that both resources are limiting in the neighbourhood of individuals' evolved strategies (Haig & Westoby 1988, Rosenheim et al. 2010). Explicit expressions for the total amounts of carbon and phosphorus acquired in terms of evolved strategies and model parameters are given in the Supplementary Information.

3.3.1 Does it ever pay to restrict a partner's access to resources?

It is well established in economics and the biological markets literature that traders can obtain an advantage from gaining greater control over resource supply (Noë et al. 1991, Noë & Hammerstein 1994, Noë & Hammerstein 1995). This is because resource control can lead to increased dependence and hence more favourable terms of trade. We find that an analogous effect occurs in our model. Specifically, mycorrhizal fungi are favoured to restrict their plant partners' direct access to phosphorus (i.e. $r>0$) when two conditions are satisfied: (i) phosphorus restriction by the fungus is sufficiently cost effective; (ii) plants would otherwise obtain an appreciable amount of phosphorous directly from the soil.

Restriction is cost effective when $e>n_f/b$ (condition (i), above). Increasing the cost effectiveness (e) makes this condition less stringent, and hence promotes restriction, whilst increasing the number of mycorrhizal fungi per plant (n_f) or decreasing the importance of carbon for mycorrhizal fitness (b) makes restriction less likely. In our model, restriction acts as a public good because it lowers the cost of carbon for all the fungi trading with a restricted plant, but it is only favoured when the direct fitness effect of restricting is positive. However, even when restriction is favoured, this public good will be produced below the socially optimal level for mycorrhizal fungi.

Restriction is only favoured if plants would otherwise obtain an appreciable amount of phosphorous directly from the soil (condition (ii), above). If plant phosphorus acquisition is minimal relative to fungal phosphorus acquisition ($n_p x P_p << n_f P_f$), mycorrhizal fungi remain in effective control of supply and thus have no incentive to restrict plant phosphorus access. Appreciable plant phosphorus acquisition requires both sufficient carbon and sufficient phosphorus availability for plants. First, carbon must be sufficiently available that plants are favoured not to put all their resources into acquiring carbon, and so are favoured to put some resources into obtaining phosphorous directly. This occurs when $C_p > (n_p - 1 + a) n_f^2 / (1 - a)(n_p - 1) n_p (be - n_f)$. Second, plants must be efficient at obtaining phosphorus directly from the soil, which is when $P_p > C_p (n_p - 1)(be - n_f) P_f / n_p ((1 - b)e + n_f)$.

If conditions (i) and (ii) are both satisfied, then mycorrhizal fungi are favoured to restrict plants’ access to phosphorus. By doing this, they make phosphorous more valuable to plants, and are then able to get more carbon in exchange for the phosphorous that they trade. Our model therefore predicts that mycorrhizal fungi can be favoured to provide a public good, restriction. Other fungi can benefit from a higher phosphorus price even if they do not contribute to restriction. However, critically, restriction is not a global public good as the benefits are only available to those fungi that interact with a restricted plant (Kaul et al. 1999). This means that if competition between offspring is global in a large population of mycorrhizal fungi, the effect that restricting has in increasing the fitness of some local competitors is immaterial. Evidence suggests that long-distance dispersal occurs in mycorrhizal fungi, although its role in fitness has not been elucidated (Allen et al. 1989, Reddell et al. 1997, Frank et al. 2006). If dispersal is largely local, mycorrhizal fungi interacting with the same plant are likely to be relatives. Therefore, the cost of providing a public good to a competitor may be offset by the fact that this competitor is a relative. In the case of an infinite island model, these effects exactly cancel (Taylor 1992a).

A formal analysis of possible scales of competition in mycorrhizal fungi and their impact on the provision of public goods is beyond the scope of this model. However, the mere fact that a good is public does not mean that natural selection cannot favour its provision. If the benefit to an individual of providing a public good is large enough, then the good can be provided irrespective of its beneficial effect on others unless they are negatively related. Free-rider problems can even diminish as the number of agents benefiting from the public good increases (Bliss & Nalebuff 1984).

3.3.2 What is the effect of restriction on the stability of mutualistic trade?

Theory suggests that hosts are under strong selection pressure to avoid cooperating with less-beneficial symbionts. Therefore, we might expect a breakdown in cooperation under phosphorus restriction. Our model, however, yields the opposite result: allowing mycorrhizal fungi to restrict the direct phosphorus uptake pathway in plants allows cooperation to be maintained under conditions where it otherwise would not be.

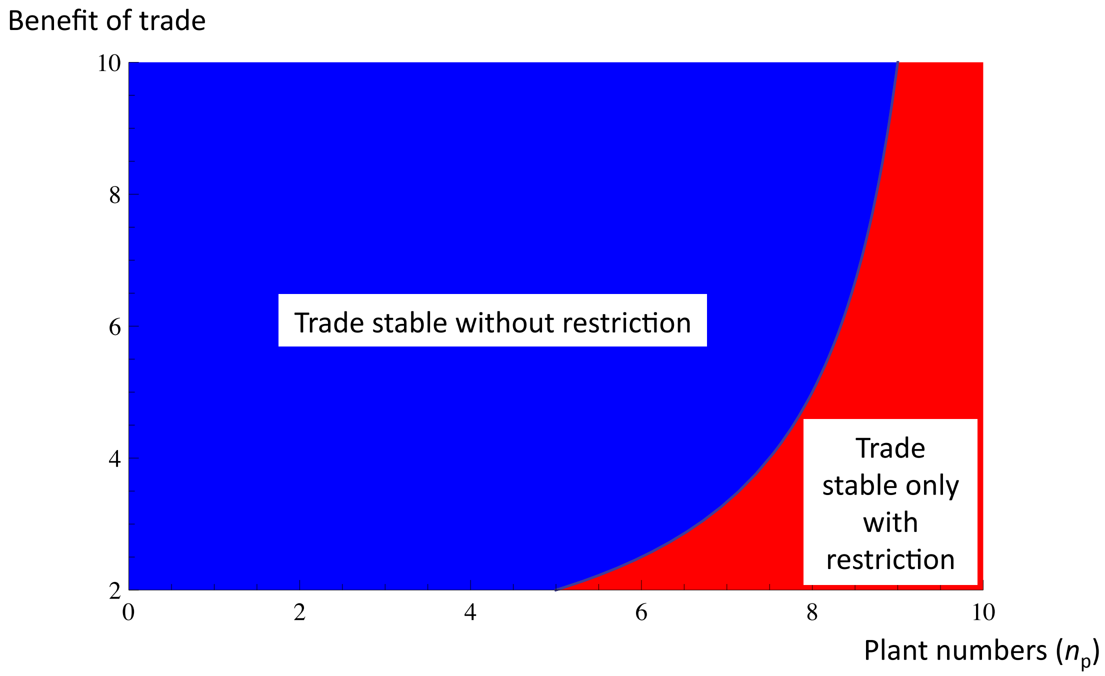


Figure 3.1 | The effect of phosphorus restriction on the stability of mutualistic trade. In the blue region, mutualistic trade is favoured with or without fungal phosphorus restriction. In the red region, mutualistic trade is only favoured when we allow fungal phosphorus restriction. Restriction favours trade when it would otherwise collapse because the benefit is too low.

If we do not allow fungi the option of restricting, we find that trade collapses when the quantity of phosphorus available to plants increases beyond the threshold $P_p > C_p P_f b(n_p-1)/(1-b)n_p$. That is, the benefits of trade are too low (Figure 3.1). As more phosphorous becomes available, plants will decrease carbon supply to their fungal partners, because they do not need to trade with the fungi to obtain phosphorous. This decreases the total carbon traded, driving the mycorrhizal fungi to transfer less phosphorus in return, thus decreasing the phosphorus incentive for plants to engage in trade. Ultimately, trade collapses altogether.

However, we find that restriction can maintain trade at any level of resource availability, by maintaining the plants' dependence on mycorrhizal trade (Figure 3.1). Mycorrhizal fungi receive a higher price for their phosphorus through their control of

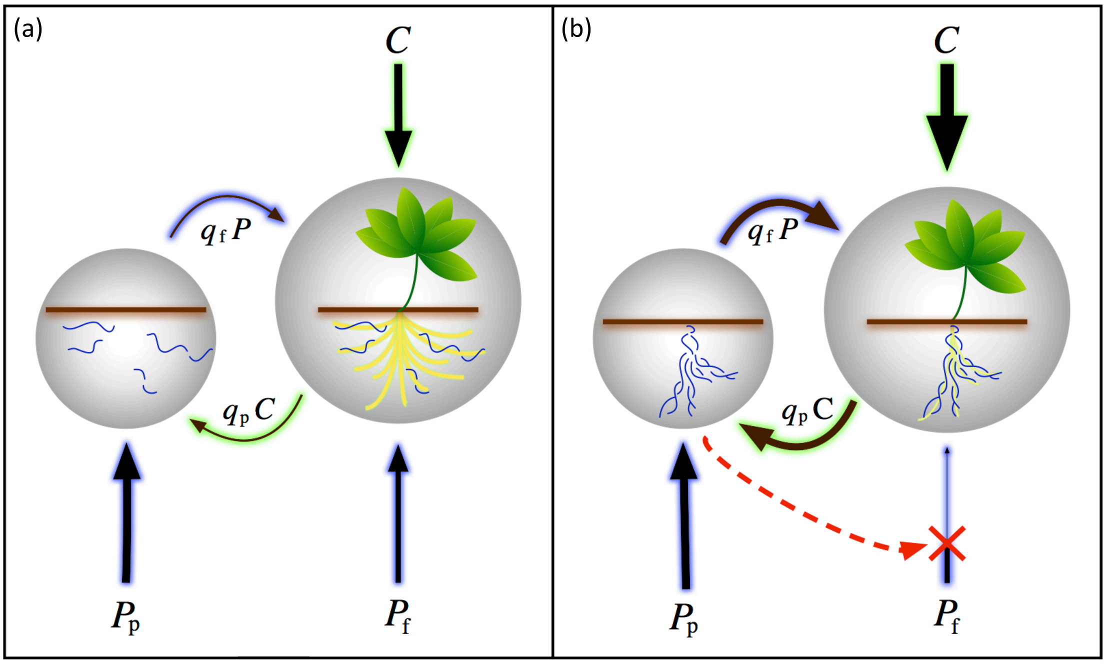


Figure 3.2 | The effect of phosphorus restriction on the mutualistic system. (a) Plants acquire phosphorus and carbon, whilst mycorrhizal fungi acquire phosphorus. Plants trade carbon to mycorrhizal fungi in exchange for phosphorus. (b) Mycorrhizal fungi restrict the ability of plants to acquire phosphorus (red cross). This restriction makes plants reliant on fungal phosphorus, so plants invest more into acquiring carbon directly and trade more carbon to compete for phosporous. The increased flows of carbon in trade favour mycorrhizal fungi that transfer more phosphorus.

the phosphorus supply, which favours them to supply larger quantities of phosphorus (Figure 3.2). This increased propensity to trade phosphorus maintains cooperation. The increased stability of mutualisms when each partner has greater control over one resource has already been recognised (Wyatt et al. 2014, Franklin et al. 2014) – our result provides a novel mechanism by which this control can be achieved.

3.3.3 How does restriction affect plant fitness?

Restriction could potentially have positive or negative consequences for plant fitness. Restriction reduces phosphorus availability, so the first order effect of impairing the resource acquisition pathway is to decrease plant fitness. However, phosphorus restriction also changes the terms of trade, which increases plant specialisation on carbon acquisition. This specialisation could increase the efficiency of the mutualistic system, as plants are relatively better at carbon acquisition, and so could potentially provide a fitness benefit to the plant.

Overall, we find that the influence of restriction on plant fitness depends on the amount of phosphorus available for direct uptake by plants (Figure 3.3). Although restriction usually decreases plant fitness, we find that in certain situations restriction can increase plant fitness. At low levels of phosphorus availability, restriction never evolves. At intermediate phosphorus availability, when there would be trade even without restriction, restriction increases plant fitness when $C_p<n_f(1-b)/(n_p-1)n_p$. This requires two biological conditions to be satisfied. First, there must be few plants relative to fungal strains (small n_p, large n_f), so that each plant has bargaining power over the terms of trade. Although plant numbers need to be small, they must be greater than one. Otherwise, discriminatory strategies are no longer available to mycorrhizal fungi.

The second condition required for restriction to increase plant fitness is that there are only small quantities of carbon potentially available for trade (small C_p), which combined with the phosphorous that plants can take up from the soil, means that both parties have relatively little to gain from trade. This gives plants an incentive to use their bargaining power, thus making trade even less attractive for fungi. Consequently, the fungi transfer even less phosphorus, further diminishing the available gains from trade. In contrast, restriction makes plants more dependent on fungi for phosphorus. This favours plants that increase carbon traded, which in turn

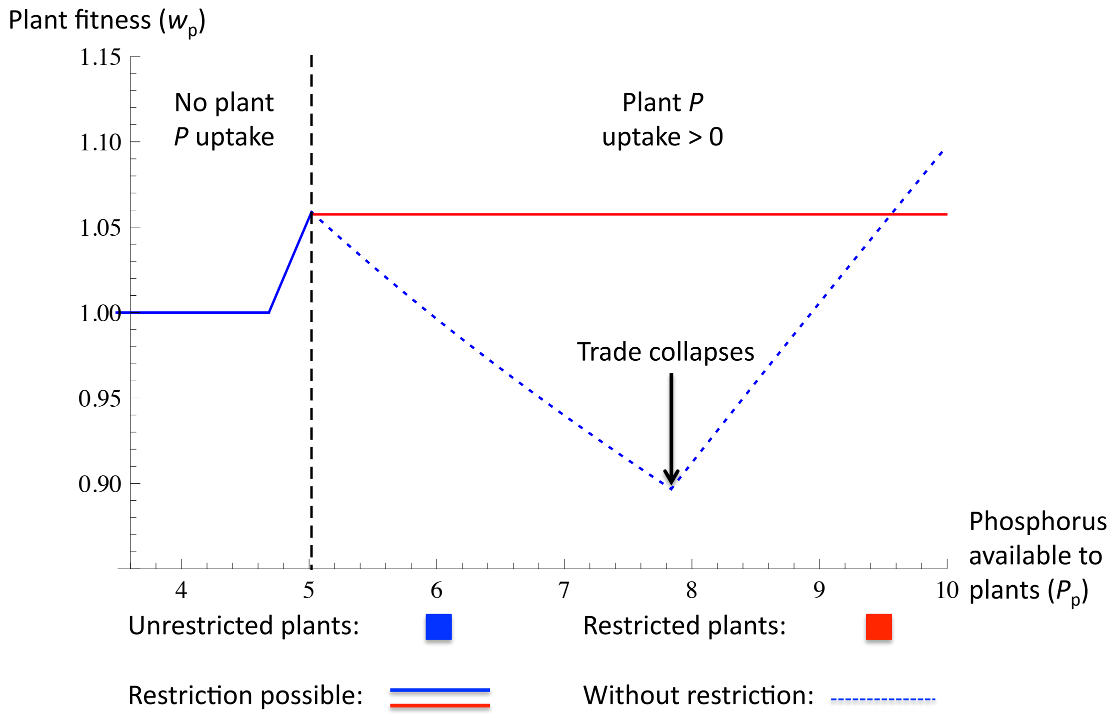


Figure 3.3 | Plant fitness with and without restriction. The impact of fungal restrictions on plant fitness changes with the phosphorus available for direct uptake by plants (P_p). When plants do not acquire any phosphorus, restrictions are not favoured and so have no impact (left of black dashed line). When restriction does not happen, phosphorus acquisition by competitor plants reduces carbon supply (downward sloping dotted line), and can mean that restricted plants would have higher fitness (as shown in graph). When restrictions are not possible, trade collapses and plant fitness recovers to exceed fitness without restriction as P_p increases (upward sloping dotted line). (In graph, $n_p=2$, $n_f=12$, $C_p=1.9$, $P_f=5.5$, $a=0.17$, $b=0.6$, $e=110$)

favours fungi that increase phosphorus transfer. This higher level of trading benefits all partners.

When sufficient phosphorus is available for trade to collapse in the absence of restriction (inequality (5) is satisfied), plant fitness increases with restriction when $P_p<(bC_pe(n_p-1)n_p+n_f(n_f-C_p(n_p-1)n_p))P_f/n_p^2((1-b)e+n_f)$. This increase in plant fitness despite resource losses due to restriction can occur for the same reasons as detailed above. However, at high levels of phosphorus availability to plants, it is increasingly difficult for mycorrhizal trade to compensate for the costs of restriction. At extremely high levels of phosphorus, trade with mycorrhizal fungi cannot compensate for restriction.

The result that plant fitness can increase with restriction relies on the decreased plant cooperativeness predicted when there are few competitors (Supplementary Information). This emphasises a key difference between mutualistic cooperation driven by market dynamics as in this model, rather than alignment of fitness interests. In general, a smaller number of competitors increases alignment of interests, and hence selects for cooperation. By contrast, in market systems a smaller number of partners means less competition to be the best mutualist, and hence less trade per individual and in the market as a whole.

Even though plants may sometimes benefit from restriction, plants are never selected to reduce their own direct phosphorus uptake because the cost of taking up less phosphorus would not be outweighed by increased phosphorus received in trade. The reason for this is that the phosphorus available in trade depends on the direct uptake of all plants that share a fungal partner, not just that of a single plant.

Is it ever beneficial for plants to cut connections with their fungal partners completely? Our model suggests that when phosphorus available for direct uptake by plants is present in very high concentrations, plants without any fungal mutualistic partners gain more phosphorus compared to plants that are colonised, but restricted, by fungal partners (Figure 3.4). In these circumstances, interacting with mycorrhizal fungi leads to a fitness cost not benefit, and so if plants can completely terminate their interaction with their fungal partners, then they would be selected to do so. A

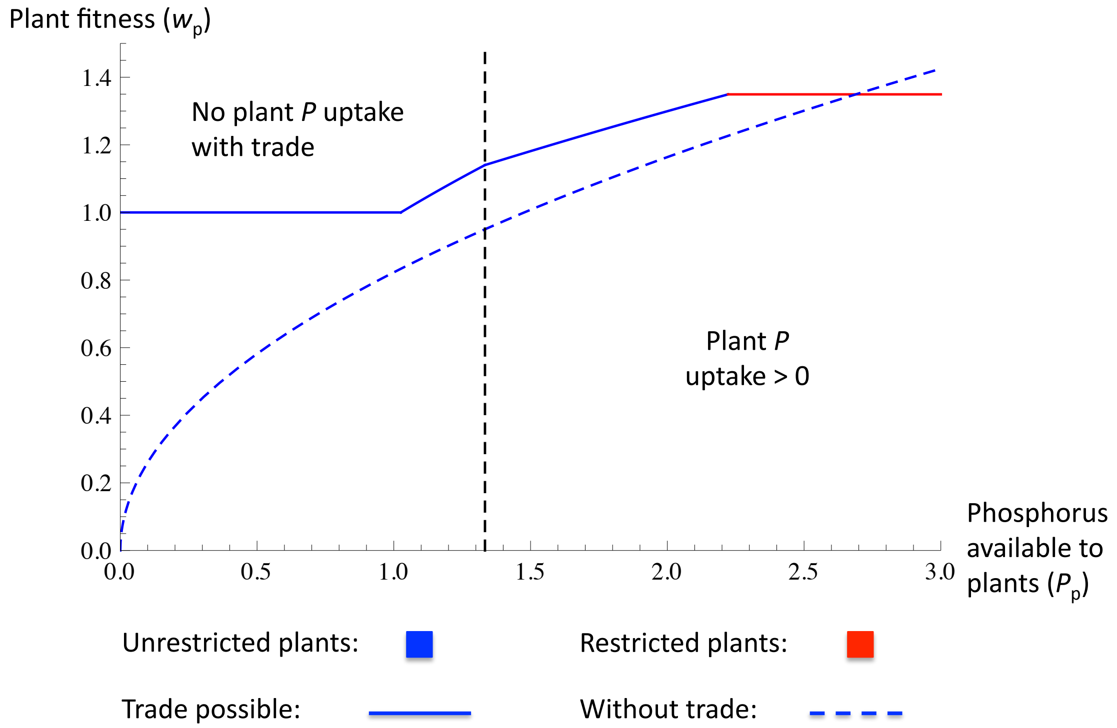


Figure 3.4 | Plant fitness with and without trade. The impact of trade on plant fitness changes with phosphorus available for direct uptake by plants (P_p). When plants do not directly acquire any phosphorus, trade increases plant fitness (left of black dashed line). When plants acquire phosphorus but mycorrhizal fungi are not favoured to restrict, trade also increase plant fitness (solid blue line right of dashed black line). When fungi begin to restrict, the restriction cancels out any beneficial effects of increases in P_p for plants (red line). Here, plants may be better off if they do not have trading partners. (In graph, n_p=3, n_f=3, C_p=5, P_f=2, a=0.5, b=0.5, e=12)

reduction in fungal colonisation is sometimes observed under very high nutrient conditions (Nagy et al. 2009, Balzergue et al. 2013). However, in some cases, plants might not be able to completely cut their interactions with their fungal partners, which can lead to a fitness cost of interacting with fungi, termed mycorrhizal depression (Figure 3.4; Smith et al. 2011, Smith & Smith 2013, Franklin et al. 2014).

3.3.4 Biological applications

There are a number of biological examples that suggest restriction mechanisms of the form predicted by our model. For example in some cases, mycorrhizal fungi appear to inhibit the plant's direct phosphorous uptake pathway via molecular suppression mechanisms (Li et al. 2008, Grace et al. 2009, Smith et al. 2009, Smith & Smith 2013). In the ant-acacia mutualism, Acacia trees have been shown to provide a protein food source that alters their mutualistic ants' digestion, limiting the extent to which these ant partners can use other food sources (Heil et al. 2014). In this cases, the mutualist is still providing a resource (protein), but it also manipulates its partner's future access to alternative sources. Our model suggests that restriction mechanisms could be widespread in trading mutualisms. More generally, we might also expect restriction within species when different classes of individual exchange benefits; for example, when a male harms a female in order to decrease her life expectancy and thus increase her immediate investment into reproduction with the harming male (Johnstone & Keller 2000, Morrow et al. 2003, Lessells 2005).

3.3.5 Conclusions

We have shown that individuals can be favoured to restrict the quantity of resources directly acquired by their mutualistic partners in order to make their own supply of those resources more valuable. Human history has repeatedly proved how devastatingly effective such strategies can be, as demonstrated by the eradication of spice-producing trees by the Dutch in the East Indies or England's embargo on textiles manufactured in its colonies (O'Brien et al. 1991, O'Rourke & Williamson

2002). Indeed, our model predicts that restriction is both most cost-effective and most damaging when the restricting partner becomes an effective monopolist. However, in mutualisms where restricting individuals compete with their peers for trade, restriction may lead to increased reliance on trade by both partner species, and consequently promote cooperation. This can even stabilise mutualisms in circumstances under which they would otherwise break down.

3.4 Supplementary Information

3.4.1 Conditions for the evolution of trade, plant specialisation, and restriction

We derive expressions for the total amounts of carbon and phosphorus acquired (C_{tp}, P_{tp}, C_{tf}, and P_{tf}) in terms of evolved variables and model parameters. To do so, we first consider a focal plant with a strategy pair (x, q_{p}), which may or may not be an ESS. This plant is in a nearly uniform population in each species with plant proportion of investment into carbon acquisition and allocations to trade clustered around $\bar{x}$ and $\bar{q}_{\text{p}}$ respectively, and where the fungal allocation to trade and investment in restriction are nearly uniform and clustered around $\bar{q}_{\text{f}}$ and $\bar{r}$ respectively. The focal plant acquires an amount xC_{p} of carbon and retains a fraction 1-q_{p} of this, so that it has a total quantity of carbon $C_{\text{tp}}=xC_{\text{p}}(1-q_{\text{p}})$.

The plant also acquires an amount of phosphorus $(1-\bar{r})(1-x)P_{\text{p}}$ directly and receives an amount of phosphorus $P_{\text{r}} = P_{\text{f}}\bar{q}_{\text{f}}n_{\text{f}}s_{\text{p}}$ via trade, where $P_{\text{f}}\bar{q}_{\text{f}}$ is the average quantity of phosphorus traded by each mycorrhizal fungus trades, n_{f} is the total number of mycorrhizal fungi hosted by the plant and s_{p} is the share of the traded phosphorus the focal plant acquires. By linear proportional discrimination, plants acquire traded phosphorus based on the relative amount each provides. Thus, the focal plant's share (s_p) is the proportion of total carbon transferred that the focal plant provides. This is the total quantity that the plant transfers ($xC_\mathrm{p}q_\mathrm{p}$), divided by the total quantity provided by all competitors including the focal plant ($((n_\mathrm{p}-1)\bar{x}C_\mathrm{p}\bar{q}_\mathrm{p}+xC_\mathrm{p}q_\mathrm{p})$. Hence, the proportion of total traded phosphorus that the plant acquires is $s_\mathrm{p}=(xq_\mathrm{p})/((n_\mathrm{p}-1)\bar{x}\bar{q}_\mathrm{p}+xq_\mathrm{p})$. The total quantity of phosphorus available to plants is the sum of the quantity they take up from the soil and the quantity they acquire via trade, so $P_\mathrm{tp}=(1-\bar{r})(1-x)P_\mathrm{p}+P_\mathrm{f}\bar{q}_\mathrm{f}n_\mathrm{f}(xq_\mathrm{p})/((n_\mathrm{p}-1)\bar{x}\bar{q}_\mathrm{p}+xq_\mathrm{p})$.

Making these substitutions into the plant's fitness function given in the main text yields

$$w_\mathrm{p}=(xC_\mathrm{p}(1-q_\mathrm{p}))^a\left((1-x_\mathrm{p})P_\mathrm{p}(1-\bar{r})^d+\frac{n_\mathrm{f}P_\mathrm{f}\bar{q}_\mathrm{f}xq_\mathrm{p}}{(n_\mathrm{p}-1)\bar{x}\bar{q}_\mathrm{p}+xq_\mathrm{p}}\right)^{1-a}. \tag{1a}$$

Similarly, the fitness function for a focal mycorrhizal fungus is

$$w_\mathrm{f}=\left(1+\frac{n_\mathrm{p}\bar{x}C_\mathrm{p}\bar{q}_\mathrm{p}q_\mathrm{f}}{(n_\mathrm{f}-1)\bar{q}_\mathrm{f}+q_\mathrm{f}}\right)^{1-b}(P_\mathrm{f}(1-q_\mathrm{f}))^b(1-r). \tag{1b}$$

We use equations (1a) and (1b) to calculate evolutionary maxima. Specifically, we calculate ESSs, strategies where deviations from population mean strategies leads to decreased fitness (mathematically: $\partial w_\mathrm{p}/\partial x\,|_{x=\bar{x},q_\mathrm{p}=\bar{q}_\mathrm{p}}=0$ and $\partial w_\mathrm{p}/\partial q_\mathrm{p}\,|_{x=\bar{x},q_\mathrm{p}=\bar{q}_\mathrm{p}}=0$ for plants, $\partial w_\mathrm{f}/\partial q_\mathrm{f}\,|_{q_\mathrm{f}=\bar{q}_\mathrm{f},r=\bar{r}}=0$ and $\partial w_\mathrm{f}/\partial r\,|_{q_\mathrm{f}=\bar{q}_\mathrm{f},r=\bar{r}}=$

0 for mycorrhizal fungi). The ESSs for plants depend on the strategies employed by fungi, and the ESSs for fungi depend on the strategies employed by plants (Riechert & Hammerstein 1983). Hence, we need to find the ESSs for plants given fungal strategy ($x^*|_{\bar{q}_\mathrm{f},\bar{r}}$ and $q_\mathrm{p}^*|_{\bar{q}_\mathrm{f},\bar{r}}$), and the ESSs for fungi given plant strategy ($q_\mathrm{f}^*|_{\bar{x},\bar{q}_\mathrm{p}}$ and $r^*|_{\bar{x},\bar{q}_\mathrm{p}}$). Then, we can solve these four resulting expressions to find coevolved ESSs in terms of model parameters only (x*, q_p*, q_f*, r*). We first calculate the equilibria of fitness for allocation to direct carbon uptake and trade in a focal plant, $\partial w_\mathrm{p}/\partial x_\mathrm{p} = \partial w_\mathrm{p}/\partial q_\mathrm{p} = 0$. At an ESS, any individual receives population mean fitness to first order, so we take the focal plant's strategy to be the population average ($x = \bar{x}$, $q_\mathrm{p} = \bar{q}_\mathrm{p}$). Substituting, we find that at equilibrium

$$\bar{x} = a + \frac{(n_\mathrm{p} - 1 + a)P_\mathrm{f}(q_\mathrm{f} + (n_\mathrm{f} - 1)\bar{q}_\mathrm{f}}{n_\mathrm{p}^2 P_\mathrm{p}(1 - \left(1 - \frac{\bar{r}(n_\mathrm{f}-1)+r}{n_\mathrm{f}}\right)} \tag{2a}$$

and

$$\bar{q}_\mathrm{p} = \frac{(1-a)(n_\mathrm{p} - 1)P_\mathrm{f}(q_\mathrm{f} + (n_\mathrm{f} - 1)\bar{q}_\mathrm{f}}{(n_\mathrm{p} - 1 + a)P_\mathrm{f}(q_\mathrm{f} + (n_\mathrm{f} - 1)\bar{q}_\mathrm{f}) - a(1-\bar{x})n_\mathrm{p}^2 P_\mathrm{p}\left(1 - \frac{\bar{r}(n_\mathrm{f}-1)+r}{n_\mathrm{f}}\right)^e} . \tag{2b}$$

We use the expressions for $\bar{x}$ and $\bar{q}_\mathrm{p}$ in equations (2a) and (2b) in the equation for fungal fitness (1b) and calculate the maxima with respect to allocation to trade and phosphorus restriction, $\partial w_\mathrm{f}/\partial q_\mathrm{f} = \partial w_\mathrm{f}/\partial r = 0$. Again, at an ESS, any individual receives population mean fitness to first order, so we take the focal fungus' strategy to be the population average ($q_\mathrm{f} = \bar{q}_\mathrm{f}$, $r = \bar{r}$). Substituting, we find that at a fixed point

$$\bar{q}_{\mathrm{f}} = \frac{n_{\mathrm{f}}}{(1-b)e + n_{\mathrm{f}}} \tag{3a}$$

and

$$\bar{r} = 1 - \left(\frac{C_{\mathrm{p}}(n_{\mathrm{p}}-1)(be-n_{\mathrm{f}})P_{\mathrm{f}}}{n_{\mathrm{p}}((1-b)e+n_{\mathrm{f}})P_{\mathrm{p}}} \right)^{\frac{1}{e}} . \tag{3b}$$

Using the expressions for $\bar{q}_{\mathrm{f}}$ and $\bar{r}$ from equations (3a) and (3b) in equations (2a) and (2b), we find plant strategy as a function of model parameters only

$$\bar{x} = a + \frac{(n_{\mathrm{p}}-1+a)n_{\mathrm{f}}^2}{C_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}}(be-n_{\mathrm{f}})} \tag{3c}$$

$$\bar{q}_{\mathrm{p}} = \frac{(n_{\mathrm{p}}-1)n_{\mathrm{f}}^2 P_{\mathrm{f}}}{(n_{\mathrm{p}}-1)n_{\mathrm{f}}^2 P_{\mathrm{f}} + aC_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}}(be-n_{\mathrm{f}})P_{\mathrm{f}}} \tag{3d}$$

Therefore, equations 3a-d specify a co-evolutionary ESS when each of $\bar{x}$, $\bar{q}_{\mathrm{p}}$, $\bar{q}_{\mathrm{f}}$, and $\bar{r}$ are between 0 and 1, as all values outside this range are not feasible strategies. The values of $\bar{q}_{\mathrm{p}}$ and $\bar{q}_{\mathrm{f}}$ specified by equations (3b) and (3c) are always between 0 and 1. The value of $\bar{r}$ specified by equation (3b) is between 0 and 1 if $e > n_{\mathrm{f}}/b$ and $P_{\mathrm{p}} > C_{\mathrm{p}}(n_{\mathrm{p}} - 1)(be - n_{\mathrm{f}})P_{\mathrm{f}}/n_{\mathrm{p}}((1-b)e + n_{\mathrm{f}})$, while the value of $\bar{x}_{\mathrm{p}}$ specified by equation (3d) is between 0 and 1 if $C_{\mathrm{p}} > (n_{\mathrm{p}} - 1 + a)n_{\mathrm{f}}^2/(1-a)\big(n_{\mathrm{p}} - 1\big)n_{\mathrm{p}}(be - n_{\mathrm{f}})$. Hence, when these three inequalities are satisfied, (3a-d) is a co-evolutionary ESS.

We look for other strategies that are constrained maxima. That is, strategies where any alternative with higher fitness is not feasible (allocations less than 0 or greater than 1). We eliminate $\bar{x} = 0$ and $\bar{q}_\mathrm{p} = 1$ as this would leave plants without carbon, and $\bar{r} = 1$ and $\bar{q}_\mathrm{f} = 1$ as this would leave mycorrhizal fungi with either zero fitness or no phosphorus. We first set $\bar{q}_\mathrm{f} = q_\mathrm{f} = 0$ and work out the evolved best response values for the other variables if all other individuals use the same strategy:

$$\left(\bar{x},\bar{q}_\mathrm{p},\bar{q}_\mathrm{f},\bar{r}\right)=\left(a,0,0,0\right). \tag{4}$$

We verify whether fitness at $q_\mathrm{f} = 0$ is greater than at $q_\mathrm{f} > 0$, given the corresponding values of $\bar{x}$, $\bar{q}_\mathrm{p}$, and $\bar{r}$:

$$\frac{\partial w_\mathrm{f}}{\partial q_\mathrm{f}}\Big|_{\bar{q}_\mathrm{f}=0}<0 \Leftrightarrow P_\mathrm{p}>\frac{C_\mathrm{p}(n_\mathrm{p}-1)bP_\mathrm{f}}{(1-b)n_\mathrm{p}}. \tag{5}$$

Hence, the strategies defined by (4) are a co-evolutionary ESS if the inequalities in (5) are satisfied. We then set $\bar{r} = r = 0$ and find the condition for a co-evolutionary ESS by the same method with:

$$\left(\bar{x},\bar{q}_\mathrm{p},\bar{q}_\mathrm{f},\bar{r}\right)=\left(\begin{array}{r} a+\dfrac{(n_\mathrm{p}-1+a)n_\mathrm{f}(bC_\mathrm{p}(n_\mathrm{p}-1)P_\mathrm{f}-(1-b)n_\mathrm{p}P_\mathrm{p})}{C_\mathrm{p}(n_\mathrm{p}-1)n_\mathrm{p}^2P_\mathrm{p}}, \\ \dfrac{(n_\mathrm{p}-1)n_\mathrm{f}(bC_\mathrm{p}(n_\mathrm{p}-1)P_\mathrm{f}-(1-b)n_\mathrm{p}P_\mathrm{p})}{n_\mathrm{p}(aC_\mathrm{p}(n_\mathrm{p}-1)n_\mathrm{p}-(1-b)(n_\mathrm{p}-1+a)n_\mathrm{f})P_\mathrm{p}+bC_\mathrm{p}(n_\mathrm{p}-1)(n_\mathrm{p}-1+a)n_\mathrm{f}P_\mathrm{f}}, \\ b+\dfrac{(1-b)n_\mathrm{p}P_\mathrm{p}}{C_\mathrm{p}(n_\mathrm{p}-1)P_\mathrm{f}},0 \end{array}\right). \tag{6}$$

We verify whether fitness at $r = 0$ is greater than at $r > 0$, given the corresponding values of $\bar{x}$, $\bar{q}_\mathrm{p}$, and $\bar{q}_\mathrm{f}$:

$$\frac{\partial w_\mathrm{p}}{\partial r}\Big|_{\bar{r}=0} < 0 \Leftrightarrow P_\mathrm{p} > \frac{C_\mathrm{p}(n_\mathrm{p}-1)(be-n_\mathrm{f})P_\mathrm{f}}{n_\mathrm{p}((1-b)e+n_\mathrm{f})} \tag{7}$$

In the parameter region from (7), the best response values in (6) are feasible (and (6) is thus a co-evolutionary ESS) if

$$C_\mathrm{p} > \frac{(n_\mathrm{p}-1+a)n_\mathrm{f}^2}{(1-a)(n_\mathrm{p}-1)n_\mathrm{p}(be-n_\mathrm{f})}. \tag{8}$$

Finally, we set $\bar{x} = x = 1$. In this case, the phenotype of plants may or may not respond to a small change in fungal strategy, depending on parameter values. We first suppose that it does not, so

$$(\bar{x},\bar{q}_\mathrm{p},\bar{q}_\mathrm{f},\bar{r}) = \left(1, \frac{(1-a)(n_\mathrm{p}-1)}{n_\mathrm{p}-1+a}, \frac{(1-a)bC_\mathrm{p}(n_\mathrm{p}-1)n_\mathrm{p}(n_\mathrm{f}-1)}{(n_\mathrm{f}-b)(1-a)C_\mathrm{p}(n_\mathrm{p}-1)n_\mathrm{p}+(1-b)(n_\mathrm{p}-1+a)n_\mathrm{f}^2}, 0\right). \tag{9}$$

Now, we verify whether fitness at $x < 1$ is indeed greater than at $x = 1$, given the corresponding values of $\bar{q}_\mathrm{p}$, $\bar{q}_\mathrm{f}$ and $\bar{r}$:

$$\frac{\partial w_{\mathrm{p}}}{\partial x}\Big|_{\bar{x}=1} > 0 \Leftrightarrow P_{\mathrm{p}} < \frac{bC_{\mathrm{p}}(n_{\mathrm{p}}-1)(n_{\mathrm{p}}-1+a)(n_{\mathrm{f}}-1)n_{\mathrm{f}}P_{\mathrm{f}}}{n_{\mathrm{p}}((n_{\mathrm{f}}-b)(1-a)bC_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}}+(1-b)(n_{\mathrm{p}}-1+a)n_{\mathrm{f}}^{2})}. \qquad (10)$$

Hence, plant phenotype does not deviate from $\bar{x} = 1$ when fungal strategy is at its optimum and (9) is thus a co-evolutionary ESS whenever parameter values satisfy inequality (10).

If instead the phenotype of plants responds to fungal strategy when $\bar{x} = x = 1$, fungal strategy is set so that $\bar{x}$ in (3d) is exactly 1:

$$\left(\bar{x},\bar{q}_{\mathrm{p}},\bar{q}_{\mathrm{f}},\bar{r}\right) = \left(1,\frac{(1-a)(n_{\mathrm{p}}-1)}{n_{\mathrm{p}}-1+a},\frac{(1-a)n_{\mathrm{p}}^{2}P_{\mathrm{p}}}{(n_{\mathrm{p}}-1+a)n_{\mathrm{f}}P_{\mathrm{f}}},0\right). \qquad (11)$$

We verify whether fitness at $q_{\mathrm{f}} = (1-a)n_{\mathrm{p}}^{2}P_{\mathrm{p}}/\left(n_{\mathrm{p}}-1+a\right)n_{\mathrm{f}}P_{\mathrm{f}}$ is a maximum, given the corresponding values of $\bar{q}_{\mathrm{p}}$, $\bar{q}_{\mathrm{f}}$ and $\bar{r}$:

$$\frac{\partial w_{\mathrm{f}}}{\partial q_{\mathrm{f}}}\Big|_{\bar{q}_{\mathrm{f}}} = 0 \Leftrightarrow P_{\mathrm{p}} < \frac{bC_{\mathrm{p}}(n_{\mathrm{p}}-1)(n_{\mathrm{p}}-1+a)n_{\mathrm{f}}P_{\mathrm{f}}}{n_{\mathrm{p}}((1-a)C_{\mathrm{p}}(n_{\mathrm{p}}-1)n_{\mathrm{p}}+(1-b)(n_{\mathrm{p}}-1+a)n_{\mathrm{f}}}. \qquad (12)$$

So, (11) is a co-evolutionary ESS whenever parameter values satisfy inequality (12), but not inequality (10). If inequality (10) is satisfied, plant phenotype would not deviate from $\bar{x} = 1$ with a change in fungal strategy.

4

Relatedness and dependence in a biological market

4.1 Abstract

Models of symbioses based on the idea of biological markets predict that cooperative exchange increases when individuals can choose amongst a diverse set of mutualistic partners. This is because the ability for individuals to interact preferentially with only their most cooperative partners incentivises their partners to cooperate rather than be rejected from social interactions. On the other hand, other bodies of theory, together with empirical observations, suggest that diversity among an individual's mutualistic partners may act to inhibit cooperation. This is because low diversity (which is equivalent to high relatedness) allows individuals to invest in their mutualistic partner even if the return benefits go to others, as they gain indirect fitness benefits. Here, we develop a biological-market model of the plant-mycorrhizal mutualism, in which plants trade carbon with their mycorrhizal partners in exchange for phosphorus, to investigate how these effects interact. We find that higher relatedness among a mycorrhizal fungus' plant partners leads to lower levels of carbon transfer to fungi because related plants are favoured to compete less with each other for fixed fungal resources. In contrast, higher relatedness among a plant's fungal partners need not lead to lower levels of phosphorus transfer to plants. This occurs because both

potential and actual plant carbon acquisition is dependent on mutualist resources, such that relatives cooperate to provide more resources to their plant partners. We also find that related individuals can elicit increased cooperation out of members of their partner species, and this allows us to consider the impact of relatedness and dependence on plant seed production. These results demonstrate how a biological market perspective can incorporate relatedness between social partners, and suggest that relatedness may complement partner choice in maintaining cooperativeness.

4.2 Introduction

The fitness of individuals in a mutualistic interaction depends on a fundamental trade-off. They can cooperate and help their mutualistic partners, or they can exploit the partnership by contributing little while still reaping the benefits (Frank 1996). In the extreme, symbionts may be favoured to provide no benefits to their partners, in which case the mutualism would collapse.

Two routes have been suggested to resolve this social dilemma and maintain mutualistic cooperation. First, partner choice, when a mutualist preferentially interacts with and rewards more cooperative symbionts, provides an incentive for each individual symbiont to be more cooperative (Noë et al. 1991, Noë & Hammerstein 1994, West et al. 2002b, Johnstone & Bshary 2008, Sachs et al. 2010). This mechanism only operates effectively when there is a diverse (low relatedness) set of symbionts among which the mutualist can choose. An example is cleaner fish mutualisms where clients can choose among cleaning stations, and thus do not return to cleaning stations where they have previously received poor service (Bshary &

Grutter 2005). The diversity need not be manifested in a large range of strategies. The only requirement is a large set of competing genotypes, even though they might be favoured to adopt similar strategies.

Second, high relatedness amongst symbionts sharing a mutualistic partner would mean that each individual profits from the reproduction of other related symbionts in the host. So long as aggregate level of benefits returned are dependent on symbiont cooperativeness, this would increase the incentive to invest in the mutualistic partner as the additional benefits accrue to relatives of the investing symbiont (Frank 1996, Aanen et al. 2009, File et al. 2012, Kaltenpoth et al. 2014). In many cases, this has led to the evolution of vertical transmission of mutualistic partners, as this results in a host that is colonised by related kin (Bright & Bulgheresi 2010).

However, these two effects will often work simultaneously in real-world systems. This means that the overall impact of relatedness in mediating mutualistic cooperation remains unclear (Frank 1997a, Foster & Kokko 2006, Weyl et al. 2010). Furthermore, the role of factors like generalism versus specialism (e.g. are specialists more likely to require a diverse set of partners) and dependence (e.g. does level of dependence affect whether a diverse set of partners is good or bad) on the effect of relatedness is unexplored. This conceptual gap means that an empirical understanding of the forces at work in each system must be developed independently. This prevents researchers from applying insights from other mutualisms to formulate hypotheses in their own systems.

We use a co-evolutionary approach to examine the overall consequences of the interactions between relatedness, generalism versus specialisation, and dependence in mediating cooperativeness in a mutualistic partnership. We develop a biological market model of the mutualistic trade of carbon and phosphorus between potentially generalist plants and obligately specialist mycorrhizal fungi that incorporates relatedness and a means for a focal fungus to benefits its relatives through increased cooperativeness. We frame our model in terms of the plant-mycorrhizal symbiosis for biological concreteness, but will discuss the more general relevance of our results.

4.3 Model and Analyses

We consider a population of plants and mycorrhizal fungi that require carbon and phosphorus for growth, where plants supply mycorrhizal fungi with carbon in exchange for phosphorus collected from the soil. We suppose that the amount of phosphorus available in the soil is fixed and the maximum amount of phosphorus that a focal plant can take up is P_p, while the maximum amount of phosphorus that a focal fungus can take up is P_f. We assume that plant carbon fixation is limited by leaf surface area. We equate leaf surface area to plant somatic growth, which is partially dependent on resources received from mycorrhizal fungi, and thus their average cooperativeness, $\bar{q}_f$. We suppose that total plant carbon fixation potential is $d\bar{q}_f+(1-d)$, where d captures the partial dependence of plant somatic growth on fungal resources and varies from 0 to 1. The dependence term d has no impact on the benefit that phosphorus provided by mycorrhizal fungi offers to plants except through changing their ability to acquire carbon without fungal cooperation. Mycorrhizal fungi cannot acquire any carbon except through mutualistic trade with plants.

We assume that a focal plant faces a linear trade-off between the resources invested into carbon and phosphorus acquisition, although other trade-offs would yield qualitatively identical solutions (Hoeksema & Shwartz 2003). Specifically, a focal plant fixes a proportion x of the maximum amount of carbon it can acquire and takes up a proportion 1-x of the maximum amount of phosphorus. This leaves the focal plant with a quantity $x(d\bar{q}_f+(1-d))$ and $(1-x)P_\mathrm{p}$ of phosphorus. Meanwhile, a focal mycorrhizal fungus acquires a quantity P_f of phosphorus only, some of which it will supply to plants in exchange for carbon.

This focal plant and mycorrhizal fungus grow in a finite trading population of other plants and mycorrhizal fungi, where all individuals in a species are assumed identical except for strategy. We define a focal individual's interacting group as: (i) itself; (ii) individuals in the other species that are trading partners of the focal individual; and (iii) individuals in the focal individual's species that compete for resources from the focal individual's trading partners. The focal plant trades away a proportion q_p of the carbon it acquires to mycorrhizal fungi in its interacting group (where we define $q_\mathrm{p}x$ as its cooperativeness), and is thus left with a total quantity of carbon $C_\mathrm{p}=(1-q_\mathrm{p})x(d\bar{q}_f+(1-d))$. In exchange, the focal mycorrhizal fungus trades away a proportion q_f of the phosphorus it takes up, and is left with a total quantity of phosphorus $P'_\mathrm{f}=(1-q_\mathrm{f})P_\mathrm{f}$. The average resource acquisition strategy of the other plants in the interacting group is $\bar{x}$, while the average proportion of carbon traded away is $\bar{q}_\mathrm{p}$. The average proportion of phosphorus traded away by mycorrhizal fungi in the interacting group is $\bar{q}_\mathrm{f}$. Fungal strategy is genetically determined, and hence its dynamics are over evolutionary timescales. However, the plant's allocation to trade and resource acquisition is dynamic over behavioural timescales, and it is the strategy underlying how it trades in response to partner cooperation that evolves. In many other models, strategies are assumed to only change over evolutionary timescales (reviewed in McNamara 2013). Taking phenotypic plasticity in plants into account adds biological realism, and a model that incorporates the possibility for phenotypic plasticity in mycorrhizal fungi would be a further improvement. We then define $C_{\Sigma p}$ as the total quantity of carbon potentially available to all plants in the interacting group, so the total quantity of carbon traded away by these plants is $\bar{q}_p \bar{x} C_{\Sigma p}(d\bar{q}_f+(1-d))$. Similarly, we define $P_{\Sigma f}$ as the total quantity of carbon available to all mycorrhizal fungi in an interacting group, so the total quantity of carbon traded away by all mycorrhizal fungi is $\bar{q}_f P_{\Sigma f}$.

We now assume that all individuals use a linear proportional discrimination rule to divide resources amongst their trading partners, which means rewarding better trading partners by transferring more resources in proportion to the ratio in which they are received. Wyatt et al. (2014) have shown that this can be an evolutionarily stable strategy in trading mutualisms with the characteristics presented in this model (ESS, Maynard Smith & Price 1973, Riechert & Hammerstein 1983). This means that the focal plant receives a share (s) of the total phosphorus available in trade, $\bar{q}_f P_{\Sigma f}$, equal to the proportion of total traded carbon that it transfers, $s_p = q_p x C_p / \bar{q}_p \bar{x} C_{\Sigma p}$. Similarly, the focal fungus receives a share $s_f = q_f P_f / \bar{q}_f P_{\Sigma f}$ of the total carbon traded by plants, $\bar{q}_p \bar{x} C_{\Sigma p}(d\bar{q}_f+(1-d))$. Therefore, putting together the amounts taken up and traded for, the focal plant acquires a total amount of phosphorus $P_p'=(1-x)P_p+ \bar{q}_f P_{\Sigma f} s_p$. The focal mycorrhizal fungus acquires a total amount of carbon $C_f=\bar{q}_p \bar{x} C_{\Sigma p}(d\bar{q}_f+(1-d))s_f$.

Using the above expressions for the total quantities of carbon and phosphorus acquired by plants and mycorrhizal fungi, we assume that plant seed production, which we equate to fitness, is $w_{\mathrm{p}}=\left(C_{\mathrm{p}}\right)^{a}\left(P_{\mathrm{p}}'\right)^{1-a}$ and that the fitness of mycorrhizal fungi is $w_{\mathrm{f}}=(C_{\mathrm{f}})^{b}(P_{\mathrm{f}}')^{1-b}$, where $0<a<1$ and $0<b<1$ mediate the effects of carbon and phosphorus on fitness. These fitness functions mean that both resources are limiting in the neighbourhood of individuals' evolved strategies (Haig & Westoby 1988, Rosenheim et al. 2010).

We then study the evolution of the three strategies: plant carbon acquisition, plant allocation to trade, and fungal allocation to trade (x, q_{p}, and q_{f} respectively). We find the co-evolutionary ESS for plants (x^*, q_{p}^*) and mycorrhizal fungi (q_{f}^*) (Riechert & Hammerstein 1983, Appendix for full expressions). We use Taylor & Frank's (1996) method to determine the equilibrium strategies when taking kin-selected effects into account. Relatedness must be greater than zero as the interacting group includes the focal individual.

We consider the effect of relatedness in both species on the cooperativeness of all interacting mutualistic partners. In addition, we analyse the impact of varying the dependence of plant somatic growth on a symbiotic source. Finally, we also predict conditions under which plant seed production is likely to be higher. This is an easily measurable output in experiments and therefore allows researchers to test the accuracy of our predictions in this mutualistic system.

4.4 Results

Cooperativeness towards individuals of the same species always increases as relatedness increases. However, how levels of cooperativeness towards mutualistic partners are mediated changes qualitatively with ecological conditions. Therefore, we focus on studying cooperativeness towards mutualistic partners. Wherever the term cooperativeness is used, it should be taken to mean towards mutualistic partners rather than towards members of the same species. There are three ecological scenarios where relatedness and dependence lead to very different effects: (i) when plants take up phosphorus directly from the soil, rather than relying on their symbiotic fungi; (ii) when mycorrhizal fungi give just enough phosphorus that plants do not take it up directly; and (iii) when there is no threat that plants will start taking up phosphorus from the soil as too little is available, but mycorrhizal fungi keep transferring phosphorus because they are competing for plant carbon (Figure 4.1 for a complete description of the effect of relatedness and dependence on cooperativeness in both species).

4.4.1 Plants take up phosphorus from the soil

When plants take up phosphorus from the soil, our model predicts that fungal cooperativeness (q_p*) increases as fungal relatedness (r_f) increases (Figures 4.2 & 4.3). Fungal cooperativeness approaches b as fungal relatedness approaches zero, and increases until it reaches a maximum of $2b/(1+b)$ when both fungal relatedness and plant dependence (d) are unity (full expression for fungal cooperativeness in Appendix).

	Plants take up phosphorus from the soil	Mycorrhizal fungi fill plants' phosphorus needs	Competition between fungi maintains phosphorus transfer
Plant relatedness increases	Plant coop. decreases, no effect on fungal coop.	Plant coop. decreases, fungal coop. increases	Plant coop. decreases, no effect on fungal coop.
Fungal relatedness increases	Plant and fungal coop. increase	No effect on plant or fungal coop.	No effect on plant coop., fungal coop decreases
Plant dependence increases	Plant and fungal coop. increase	No effect on plant or fungal coop.	No effect on plant coop., fungal coop increases

Figure 4.1 | The effect of relatedness and the plant growth dependence on fungal cooperativeness on plant and fungal cooperativeness. The effects of changing parameter values in our model depend on the ecological scenario. Only three scenarios qualitatively different scenarios are possible.

If dependence is zero, fungal cooperativeness remains at *b* irrespective of fungal relatedness (Figure 4.2). The fungi cannot increase plant somatic growth, and thus cannot affect the total carbon fixation potential of plants. However, more cooperative fungi do increase plant cooperativeness ($q_\mathrm{p}{}^*x^*$). This benefit to increased cooperation cancels with the increased cost of competing with relatives for plant carbon. If plant growth dependence increases, fungal cooperativeness also increases.

In contrast, plant cooperativeness decreases as plant relatedness (r_p) increases. Their maximum cooperativeness when plant relatedness approaches zero and their somatic growth is entirely dependent on mutualist resources is $bP_{\Sigma\mathrm{f}}(1 + r_\mathrm{f})/\big(C_{\Sigma\mathrm{p}}P_\mathrm{p}(1 + br_\mathrm{f})\big)$. When plant relatedness reaches unity, their cooperativeness approaches zero because a single genotype controls all carbon in the mutualistic system and fungi are willing to pay any price for even the smallest quantity of carbon (full expression for plant cooperativeness in Appendix).

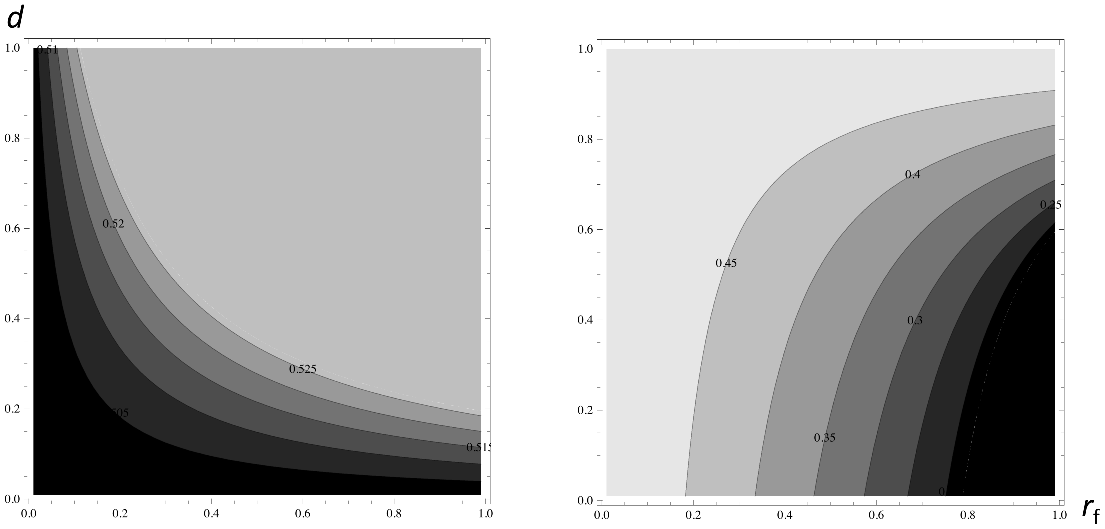


Figure 4.2 | Contour plot of the effect of fungal relatedness on fungal cooperativeness against plant growth dependence. Depending on environmental conditions, fungal cooperativeness either increases or decreases as fungal relatedness increases. (Left panel) At high levels of phosphorus availability to a focal plant, fungi become more cooperative as both fungal relatedness and dependence increase. This reaches a plateau when plants stop acquiring phosphorus from the soil. (In graph, $C_{\Sigma p}$=35/6, P_p=1.5, $P_{\Sigma f}$=16, r_p=0.5, a=0.35, b=0.5). (Right panel) At low levels of phosphorus availability to a focal plant, fungi becomes less cooperative as fungal relatedness increases but more cooperative as dependence increases. When relatedness is high and dependence is low, fungal cooperativeness reaches a lower plateau, as fungi are favoured to just fulfil plants' phosphorus needs. (In graph, $C_{\Sigma p}$=35/6, P_p=0.5, $P_{\Sigma f}$=16, r_p=0.5, a=0.35, b=0.5)

Under these conditions, growth dependence can either increase or decrease plant seed production (Figure 4.4). If plants are very dependent, an increase in dependence is more likely to make seed production increase because the additional trade at higher dependence is very valuable. On the other hand, if plants are not dependent, trade flows are smaller so their seed production is more likely to decrease with increased dependence.

These variables also impact the likelihood that plants act as generalists that acquire both carbon from the atmosphere and phosphorus from the soil. If we hold dependence at zero, we find that plants are generalists when

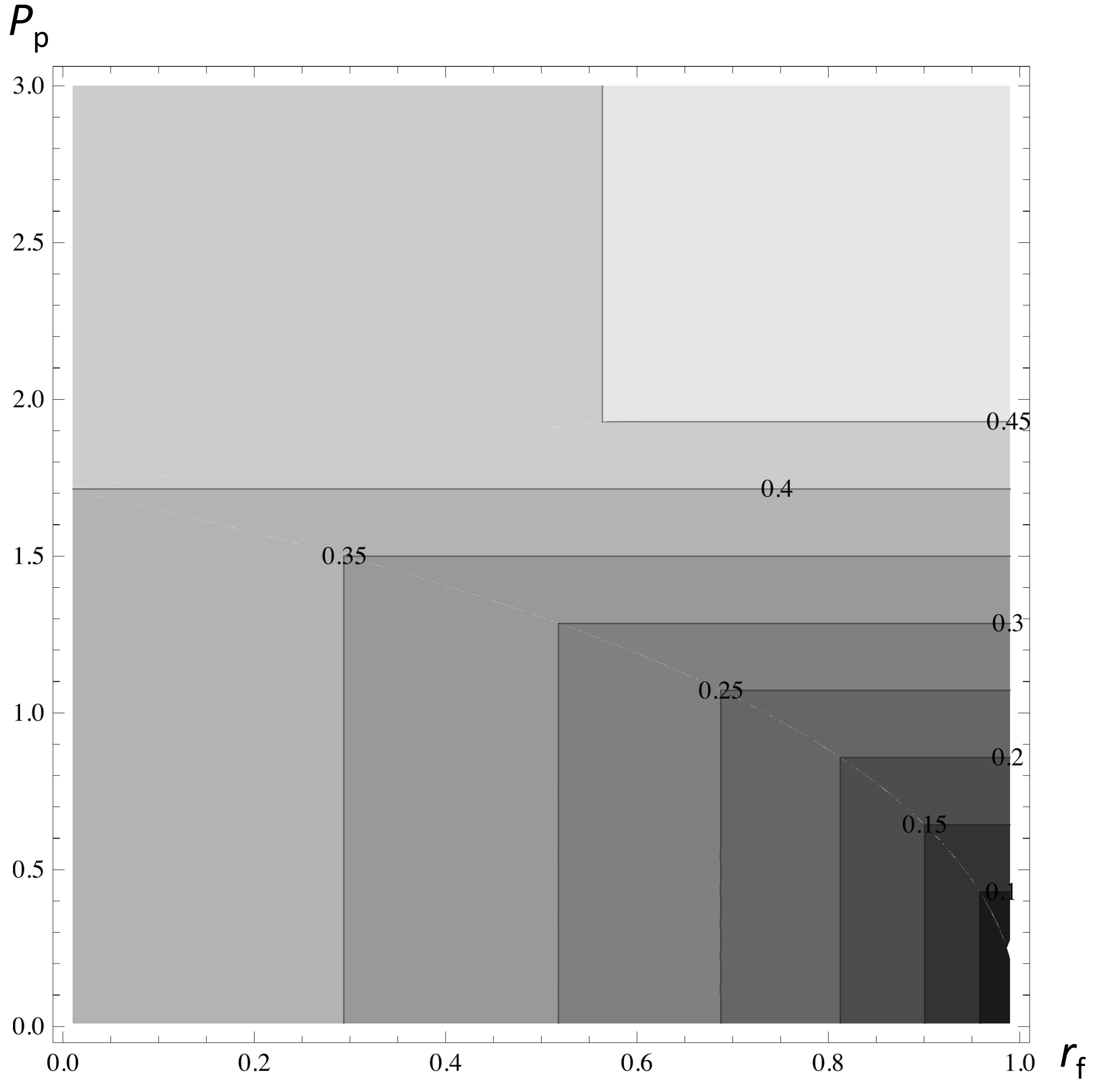


Figure 4.3 | Contour plot of the effect of fungal relatedness on fungal cooperativeness against phosphorus availability to a focal plant. At low levels of phosphorus availability to a focal plant, the plant is reliant on fungi for phosphorus. Related fungi are less cooperative because compete less for plant carbon. At high levels of phosphorus availability to a focal plant, related fungi cooperate to send more phosphorus to the focal plant. This ensures that it continues to acquire and transfer carbon. (In graph, $C_{\Sigma p}$=7, $P_{\Sigma f}$=20, d=0.6, r_p=0.5, a=0.5, b=0.4)

$P_p > b\mathrm{P}_{\Sigma f}(1-(1-a)r_p)/\left((1-a)C_{\Sigma p}\right)$ (Figure 4.3). Plants are more likely to be generalists when their relatedness is higher, as they will need to acquire less carbon for trade. On the other hand, plants are less likely to be generalists as their somatic growth dependences or as fungal relatedness increases. Either of these leads to fungi that provide more phosphorus and thus encourage plants to acquire more carbon from

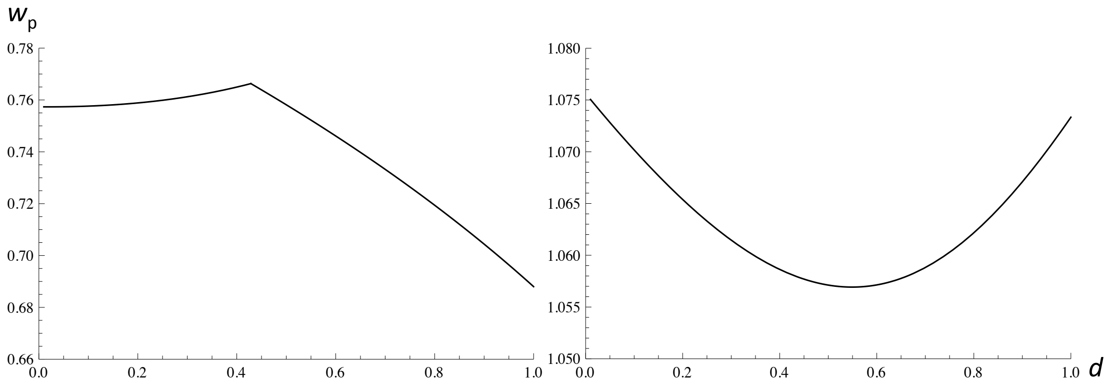


Figure 4.4 | The effect of plant growth dependence on plant fitness. Depending on environmental conditions and the existing level of dependence, an increase in plant growth dependence on fungal cooperativeness can either increase or decrease plant fitness. (Left panel) Here, little phosphorus is available to a focal plant. At low levels of dependence, greater dependence means that fungi must cooperate more to ensure carbon supply in trade. Hence, plant fitness increases. At high levels of dependence, plants acquire only carbon because it is scarce in the mutualistic system. As dependence increases, carbon becomes scarcer so fungi need to transfer less phosphorus to fulfil plants' needs. Thus, plant fitness falls. (In graph, $C_{\Sigma\mathrm{p}}=10$, $P_{\mathrm{p}}=0.4$, $P_{\Sigma\mathrm{f}}=20$, $r_{\mathrm{p}}=0.8$, $r_{\mathrm{f}}=0.8$, $a=0.2$, $b=0.4$). (Right panel) Here, more phosphorus is available to a focal plant. At low levels of dependence, greater dependence means that plants lose carbon, and this is not compensated by increases in fungal cooperativeness. Hence, plant fitness falls as dependence increases. At high levels of dependence, greater dependence incentivises plants to acquire phosphorus. Fungal cooperativeness increases rapidly both to increase carbon uptake and to ensure that plants acquire little phosphorus from the soil. Thus, plant fitness increases as dependence increases. (In graph, $C_{\Sigma\mathrm{p}}=10$, $P_{\mathrm{p}}=1.2$, $P_{\Sigma\mathrm{f}}=20$, $r_{\mathrm{p}}=0.8$, $r_{\mathrm{f}}=0.8$, $a=0.2$, $b=0.4$)

the atmosphere and rely on trade for phosphorus (full expression for condition of plant generalism in Appendix).

4.4.2 Mycorrhizal fungi fulfil plants' phosphorus needs

An alternative possibility is that plants are specialists that only acquire carbon directly because mycorrhizal fungi provide them with just enough phosphorus. If fungi provided any less, plants would begin to take up phosphorus from the soil. This does not mean that plants would not be better off with more phosphorus, merely that given the rate at which they can acquire phosphorus and carbon from the soil, they acquire only carbon.

In this case, fungal cooperativeness is $(1 - a)C_{\Sigma \mathrm{p}}P_{\mathrm{p}}/\big(P_{\Sigma \mathrm{f}}(1 - (1 - a)r_{\mathrm{p}})\big)$. Two forces maintain fungal phosphorus transfer. First, mycorrhizal fungi transfer phosphorus to compete for plant carbon. Second, mycorrhizal fungi transfer phosphorus because if they transferred any less, plants would start taking it up from the soil. The second force maintains phosphorus transfer above what competition amongst fungi would normally dictate. Hence, an increase or decrease in fungal relatedness, which mediates competition amongst fungi, has no impact on their cooperativeness.

Fungal cooperativeness is also independent of plant somatic growth dependence because carbon acquisition potential does not affect plants' investment into its acquisition (Figure 4.2). If it becomes more difficult to acquire, the investment into acquisition remains the same because the resource becomes more valuable.

Plant cooperativeness is $1 - \big(a/(1 - (1 - a)r_{\mathrm{p}})\big)$. We notice that plant cooperativeness decreases while fungal cooperativeness increases when plant relatedness increases. This occurs because related plants extract better terms of trade from their mycorrhizal fungi using their position as the only species capable of supplying carbon in the mutualistic system, as well as their option to acquire phosphorus if it is to their advantage.

Again, these variables impact the likelihood that this scenario occurs. If we hold dependence at zero, we find that plants receive just enough phosphorus from mycorrhizal fungi to fulfil their needs when the condition for plants to be generalists is not satisfied and $P_{\mathrm{p}} > b\mathrm{P}_{\Sigma\mathrm{f}}\big(1-(1-a)r_{\mathrm{p}}\big)(1-r_{\mathrm{f}})/\Big((1-a)C_{\Sigma\mathrm{p}}\Big)(1-br_{\mathrm{f}})$ (Figure 3). This condition is more easily satisfied than the condition for plants to be generalists by a factor $(1-r_{\mathrm{f}})/(1-br_{\mathrm{f}})$. The space where fungi can coordinate to provide just enough phosphorus to fulfil plants' needs increases when fungi are more related. Also as previously, plants are more likely to be generalists as plant relatedness increases but less likely to be generalists as somatic growth dependence increases (full expression for condition of fungi just fulfilling plant phosphorus needs in Appendix).

4.4.3 Competition between fungi maintains phosphorus transfer

When plants have very little phosphorus available, only the first force described in the previous section maintains phosphorus transfer. That is, fungi cooperate with plants because they compete with each other for plant carbon.

In this case, fungal cooperativeness approaches b as fungal relatedness approaches zero (Figure 4.2, Figure 4.3). Fungal cooperativeness falls to almost zero when relatedness is unity because fungi act as phosphorus monopolists, although this outcome is unlikely because phosphorus transfer could be maintained by the possibility that plants will become generalists, as the mutualistic system moves into the ecological scenario described in the previous section (full expression for fungal cooperativeness in Appendix).

Fungal cooperativeness is maximized at b when plant somatic growth is entirely dependent on fungal resources (Figure 4.2). When plant somatic growth is entirely independent of fungal resources, cooperativeness falls to $b(1 - r_\mathrm{f})/(1 - br_\mathrm{f})$. The fungi have less of an incentive to cooperate with plants when they cannot enrich the system in carbon.

Plant cooperativeness is again $1 - \left(a/(1 - (1 - a)r_\mathrm{p})\right)$ and thus always decreases as plant relatedness increases in our model. This results holds because plants can do nothing to increase the resource acquisition of fungi. Their only objective is to ensure the most favourable terms of trade.

In this scenario, dependence has no impact on plant cooperativeness but can either increase or decrease plant seed production. When dependence of plant somatic growth on mutualist resources is low, an increase in dependence is likely to decrease plant seed production because trade flows are relatively low, so the increase in fungal cooperativeness offers little benefit to plants. When dependence is high, an increase in dependence is more likely to increase plant seed production because the increase in fungal cooperativeness is more beneficial to plants.

4.4.4 Comparison across ecological scenarios

Fungal cooperativeness is at its lowest level when fungal relatedness is such that fungi provide just enough phosphorus to ensure that plants specialise on carbon acquisition. Then, fungal cooperativeness increases with changes in plant or fungal relatedness. This could be because fungal relatedness increases and plants become generalists.

Otherwise, it could be because fungal relatedness decreases and the fungi compete more intensely with each other for plant carbon. The highest level of fungal cooperativeness is reached when the plant is a generalist. We obtain this result because an increase in fungal cooperativeness makes plants acquire more carbon and less phosphorus directly when plants are generalists, but not when they are specialists. This makes plants more reliant on trade for phosphorus, which encourages yet more cooperation in fungi.

Plant cooperativeness also reaches its highest potential level, $2bP_{\Sigma\mathrm{f}}/\big(C_{\Sigma\mathrm{p}}P_{\mathrm{p}}(1+b)\big)$, when plants are generalists. This level of cooperativeness is a factor of $2/(1+b)$ greater than the highest possible level when plants are specialists. This appears paradoxical because plants have the least need for fungal resources when they act as generalists, but it is also the conditions where they can elicit the most cooperation from their fungal partners, as discussed in the previous paragraph.

Across all ecological scenarios, individuals that are more related to the other members of their species elicit more cooperation from their mutualistic partners. When an individual plant controls a sufficiently small proportion of the total carbon in the mutualistic system and can take up a sufficiently large quantity of phosphorus relative to the quantity available in trade, that plant is a generalist. Our results show that its seed production will be maximized when relatedness in both species is high. If the conditions on carbon and phosphorus described above are not satisfied, the plant is a specialist. Its seed production will then be maximised when relatedness amongst plants is high and relatedness amongst mycorrhizal fungi is low (Figure 4.4).

4.5 Discussion

We found that increasing relatedness between the individuals interacting with a mutualistic partner can either increase or decrease their cooperativeness. When an individual's relatedness to the members of its interacting group increases, its cooperativeness to mutualistic partners only increases if: (i) the mutualistic partner is a generalist and (ii) its ability to acquire resources is dependent on mutualistic cooperation. We also find that increased relatedness increases the ability of members of one species to elicit cooperation from members of the other species.

4.5.1 Factors mediating the effect of relatedness on cooperativeness

The prediction that cooperativeness can decrease as relatedness increases appears to contradict previous theoretical and empirical studies where higher relatedness has been shown to favour cooperation (West et al. 2007a, Bourke 2014). However, it is in line with predictions from biological markets that cooperativeness increases as the scope for partner choice increases (Noë et al. 1991, Noë & Hammerstein 1994). This discrepancy in results partly stems from differences in the goods. Much research on biological cooperation studies public or common goods, where all individuals can benefit whether or not they contribute (Coase 1960, Olson 1965, Mas-Colell et al. 1995 for definitions). This allows individuals to free-ride on the cooperativeness of others (Rankin et al. 2007, West et al. 2007a, Drescher et al. 2013). Cooperation increases when relatedness is high because contributions increase the reproductive success of genetic relatives (Diggle et al. 2007). On the other hand, partner choice models consider private or club goods, where owners can exclude others from benefits (Mas-Colell et al. 1995 for definitions). For private or club goods, volumes traded fall as the number of independent trading partners decreases (relatedness increases). They transfer fewer resources in trade because they compete less with relatives to be chosen as trading partners (West et al. 2002b, Wyatt et al. 2014). Our model studies both public and private goods, and so increased relatedness can either increase or decrease cooperativeness. Plant growth and cooperativeness are public goods shared by all of that plant's fungal partners, but a unit of carbon or phosphorus traded is a private good.

We have shown that increased dependence of resource acquisition on mutualist resources increases cooperativeness in both species, and that dependence mediates the effect of relatedness in mutualisms. In our model, a focal fungus' cooperativeness can only increase as its relatedness to other fungi increases when plants' somatic growth, and thus carbon acquisition, depends on fungal resources. This is because increased fungal cooperativeness changes a plant's strategy set by enabling the plant to fix more carbon. Related fungi can coordinate to ensure that plants fix much more carbon and rely on trade for phosphorus.

We also find that cooperativeness only increases as relatedness increases when the individuals in the partner species are generalists. That is, they do not rely exclusively on mutualistic trade to acquire the goods provided by mutualistic partners. When plants take up phosphorus from the soil, increased fungal cooperativeness changes plant resource acquisition strategy in favour of more carbon acquisition. This gives related fungi an incentive to increase cooperativeness. In contrast, the resource acquisition strategy of a specialist does not change. This removes a benefit to increased cooperativeness and makes it more likely that related individuals will be favoured to extort their mutualistic partner by demanding more and offering less in trade (Denison 2000, Cant & Johnstone 2009, Akçay & Simms 2011).

4.5.2 The plant-mycorrhizal symbiosis as a model system

We frame our model in terms of the plant-mycorrhizal symbiosis because it provides biological grounding in a system where the factors we have highlighted as important in mediating mutualistic cooperativeness all exist. Individuals preferentially reward more cooperative partners (partner choice), but mutualistic cooperativeness does not always increase with the number of independent symbiont genotypes (Violi et al. 2007, Janousková et al. 2009, Kiers et al. 2011, Hart et al. 2013, Roger et al. 2013). Further, plant somatic growth is partially dependent on mutualist resources and this affects the total resources available in the mutualistic system (Wilson & Hartnett 1998). Finally, plants can be either generalists or specialists, while mycorrhizal fungi are specialists that cannot acquire any carbon except through trade (Parniske 2008).

We now consider the impact of relaxing modelling assumptions we made to reflect the biology of this system whilst maintaining analytical tractability. First, we assumed that carbon, and not phosphorus, acquisition is dependent on mutualist resources. It makes sense that carbon fixing is more dependent on mutualistic cooperativeness because carbon fixed is only limited by leaf surface area, whereas the uptake of phosphorus is capped by the quantity available in nearby soils. However, it is also likely that the acquisition of phosphorus is somewhat dependent on the cooperativeness of mutualistic partners. This could allow highly related plants to cooperate more with their fungal mutualistic partners in order to increase phosphorus returned.

Second, we supposed that plant somatic growth increases linearly in fungal cooperativeness. Without a change in plant strategy, this means that the cost of providing additional phosphorus is always greater than the feedback benefits in increased carbon for related fungi. The cost of providing additional phosphorus is only overcome if plants become more cooperative, as they do when they are generalists. If we suppose that plant somatic growth accelerates with increased mutualistic cooperativeness, the benefits to related fungi of increased carbon flow could outweigh the costs of providing additional phosphorus even when plants are specialists. This would mean that fungal cooperativeness increases as fungal relatedness increases.

Third, we assumed that plants have phenotypic plasticity whilst mycorrhizal fungi do not. There is strong evidence for extensive phenotypic plasticity in plants (Ryser & Eek 2000, Sultan 2000), whilst the evidence in mycorrhizal fungi is inconclusive (Behm & Kiers 2014). The existence of more and less beneficial strains in the same experimental treatment suggests at least a fixed component to fungal cooperativeness (Hart et al. 2013). As discussed above, plant responsiveness helps favour increased cooperativeness in related fungi but is not essential. An analytical approach that incorporates phenotypic plasticity in both species may yield valuable insights but, to our knowledge, none has yet been developed.

4.5.3 Mechanism design in mutualisms

Previous work suggests that individuals may gain from relying on trade with mutualistic partners for essential resources (Schwartz & Hoeksema 1998; Hoeksema & Schwartz 2001, 2003; Akçay & Roughgarden 2007; Akçay & Simms 2011; Grman et al. 2012; Wyatt et al. 2014). Our work goes further, showing that individuals whose own resource acquisition is dependent on mutualistic cooperativeness can have fitness gains. This may be an important factor in the elaboration of mutualisms. In our model, dependence cannot increase under natural selection because fungal cooperativeness is genetically fixed, and so more dependent plants would be selected against. However, more dependent plants could be favoured if fungi have the ability to respond phenotypically.

Throughout this paper, we have presented the tension between the effects of relatedness and partner choice in maintaining cooperativeness. Some species have resolved it. For example, a beewolf cultivates a single strain of antibiotic-producing bacteria that provide its offspring with protection from fungal pathogens. The bacteria are vertically transmitted, so a single clonal strain is most cooperative because there is no competition over transmission (Oono et al. 2009, Friesen & Mathias 2010). This association lasts for many generations, but very occasionally beewolves select new partners from the environment (Kaltenpoth et al. 2014). When they do so, beewolves are favoured to choose from a diverse set of potential partners. This set of mechanisms grants beewolves the best of both worlds to favour symbiont cooperativeness, perhaps to the detriment of the mutualistic bacteria (Behm et al. 2014). The factors that allow certain organisms to develop mechanisms that separate the partner choice process from the cooperative interaction, as well as the implications for the further elaboration of these mutualistic systems, remain unclear.

4.5.4 Conclusions

Our analyses show that, in a given mutualistic system, high relatedness can either increase or decrease mutualistic exchange. The outcome can depend on as little as the prevailing ecological conditions. We have also highlighted two key features that mediate the effect of relatedness on mutualistic cooperativeness: (i) the dependence of resource acquisition in mutualistic partners on an individual's cooperativeness and (ii) the generalism or specialisation of an individual's mutualistic partners. This gives researchers a better understanding of the mechanisms that maintain cooperation in mutualisms by filling a conceptual gap on the tension between the benefits of partner choice and the benefits of high relatedness.

4.6 Appendix

4.6.1 Equilibrium traits of plants and mycorrhizal fungi

We derive ESS allocations to resource acquisition for plants (x) and trade for both plants and mycorrhizal fungi (q_p and q_f). First, we write down the focal plant's fitness function (w_p) substituting in the expressions derived in the main text for total carbon and phosphorus acquired ($C_{\mathrm{p(foc)t}}$ and $P_{\mathrm{p(foc)t}}$ respectively). This yields

$$w_{\mathrm{p}} = \left((1-q_{\mathrm{p}})x(d\bar{q}_{\mathrm{f}}+(1-d))\right)^{a}\left((1-x)P_{\mathrm{p}}+\frac{\bar{q}_{\mathrm{f}}P_{\Sigma\mathrm{f}}q_{\mathrm{p}}x}{\bar{q}_{\mathrm{p}}\bar{x}C_{\Sigma\mathrm{p}}}\right)^{1-a} . \tag{1a}$$

Similarly, the fitness function for a focal mycorrhizal fungus is

$$w_{\mathrm{f}} = \left(\frac{\bar{q}_{\mathrm{p}}\bar{x}C_{\Sigma\mathrm{p}}(d\bar{q}_{\mathrm{f}}+(1-d))q_{\mathrm{f}}P_{\mathrm{f}}}{\bar{q}P_{\Sigma\mathrm{f}}}\right)^{b}\left((1-q_{\mathrm{f}})P_{\mathrm{f}}\right)^{1-b} . \tag{1b}$$

We use equations (1a) and (1b) to calculate ESSs. At an ESS, each species is nearly uniform in strategy. Thus, any individual receives the global population mean fitness to first order. We take the focal plant's strategy to be the global population average, which we denote by two bars ($x=\bar{x}=\bar{\bar{x}}$, $q_{\mathrm{p}}= \bar{\bar{q}}_{\mathrm{p}}=\bar{\bar{q}}_{\mathrm{p}}$). We differentiate fitness of a focal plant with respect to its evolving variables, set individual strategies to the population average, and solve for an equilibrium using Taylor & Frank's (1996) method (mathematically: $dw_{\mathrm{p}}/dx = \partial w_{\mathrm{p}}/\partial x + r\partial w_{\mathrm{p}}/\partial\bar{x}|_{x=\bar{\bar{x}},q_{\mathrm{p}}=\bar{\bar{q}}_{\mathrm{p}}} = 0$ and $dw_{\mathrm{p}}/dq_{\mathrm{p}} = \partial w_{\mathrm{p}}/\partial q_{\mathrm{p}} + r\partial w_{\mathrm{p}}/\partial\bar{q}_{\mathrm{p}}|_{x=\bar{\bar{x}},q_{\mathrm{p}}=\bar{\bar{q}}_{\mathrm{p}}} = 0$ for plants). We solve these simultaneously to find a co-evolutionary ESS in terms of model parameters and fungal strategy (Riechert & Hammerstein 1983):

$$\bar{\bar{x}} = a+\frac{P_{\Sigma\mathrm{f}}(1-(1-a)r_{\mathrm{p}})\left(\bar{\bar{q}}_{\mathrm{f}}(1-r_{\mathrm{f}})+q_{\mathrm{f}}r_{\mathrm{f}}\right)}{C_{\Sigma\mathrm{p}}P_{\mathrm{p}}} \tag{2a}$$

and

$$\bar{\bar{q}}_{\mathrm{p}} = \frac{P_{\Sigma\mathrm{f}}(1-r_{\mathrm{p}})\left(\bar{\bar{q}}_{\mathrm{f}}(1-r_{\mathrm{f}})+q_{\mathrm{f}}r_{\mathrm{f}}\right)}{aC_{\Sigma\mathrm{p}}P_{\mathrm{p}} + P_{\Sigma\mathrm{f}}(1-(1-a)r_{\mathrm{p}})\left(\bar{\bar{q}}_{\mathrm{f}}(1-r_{\mathrm{f}})+q_{\mathrm{f}}r_{\mathrm{f}}\right)}. \tag{2b}$$

We use the expressions for $\bar{\bar{x}}$ and $\bar{\bar{q}}_{\mathrm{p}}$ from equations (2a) and (2b) in the equation for fungal fitness (1b) and similarly calculate the maxima with respect to allocation to trade, $dw_{\mathrm{f}}/dq_{\mathrm{f}} = \partial w_{\mathrm{f}}/\partial q_{\mathrm{f}} + r\partial w_{\mathrm{f}}/\partial \bar{q}_{\mathrm{f}}|_{q_{\mathrm{f}}=\bar{\bar{q}}_{\mathrm{f}}} = 0$. Substituting, we find that at a fixed point

$$\bar{\bar{q}}_{\mathrm{f}} = \frac{d(1+b+br_{\mathrm{f}})-1+\sqrt{4(1-d)db(1+br_{\mathrm{f}})+\left(1-d(1+b+br_{\mathrm{f}})\right)^2}}{C_{\Sigma\mathrm{p}}P_{\mathrm{p}}2d(1+br_{\mathrm{f}})}. \tag{2c}$$

Equations (2a-c) specify a co-evolutionary ESS $\left((x^*, q_{\mathrm{p}}^*, q_{\mathrm{f}}^*) = (\bar{\bar{x}}, \bar{\bar{q}}_{\mathrm{p}}, \bar{\bar{q}}_{\mathrm{f}})\right)$ when each of $\bar{\bar{x}}$, $\bar{\bar{q}}_{\mathrm{p}}$, and $\bar{\bar{q}}_{\mathrm{f}}$ are between 0 and 1, as all values outside this range are not feasible strategies. The values of $\bar{\bar{q}}_{\mathrm{p}}$ and $\bar{\bar{q}}_{\mathrm{f}}$ specified by equations (2b) and (2c) are always between 0 and 1. The value of $\bar{\bar{x}}$ specified by equation (2a) is between 0 and 1 if

$$P_{\mathrm{p}} > \frac{P_{\Sigma\mathrm{f}}(1-(1-a)r_{\mathrm{p}})\left(d(1+b+br_{\mathrm{f}})-1+\sqrt{4(1-d)db(1+br_{\mathrm{f}})+\left(1-d(1+b+br_{\mathrm{f}})\right)^2}\right)}{C_{\Sigma\mathrm{p}}P_{\mathrm{p}}2d(1+br_{\mathrm{f}})}. \tag{3}$$

Hence, if inequality (3) is satisfied, (2a-c) specify a co-evolutionary ESS.

We look for other strategies that are constrained maxima. That is, strategies where any alternative with higher fitness is not feasible (allocations less than 0 or greater than 1). We eliminate $\bar{\bar{x}} = 0$ and $\bar{\bar{q}}_{\mathrm{p}} = 1$ as this would leave plants without carbon, and we eliminate $\bar{\bar{q}}_\mathrm{f} = 0$ and $\bar{\bar{q}}_\mathrm{f} = 1$ as this would leave fungi without carbon in the former case and without phosphorus in the latter case. This also eliminates $\bar{\bar{q}}_\mathrm{p} = 0$ as $\bar{\bar{q}}_\mathrm{p}$ is proportional to $\bar{\bar{q}}_\mathrm{f}$.

Hence, we set $\bar{\bar{x}} = x = 1$. In this case, the phenotype of plants may or may not respond to a small change in fungal strategy. We first suppose that it does not, so

$$\left(\bar{\bar{x}},\bar{\bar{q}}_\mathrm{p},\bar{\bar{q}}_\mathrm{f}\right) = \left(1, 1-\frac{a}{1-(1-a)r_\mathrm{p}}, \frac{d(1+b-br_\mathrm{f})+br_\mathrm{f}-1+\sqrt{4db(1-d)(1-r_\mathrm{f})+\left(1-br_\mathrm{f}-d(1+b-br_\mathrm{f})\right)^2}}{2d}\right). \quad (4)$$

Now, we verify whether fitness at *x*=1 is indeed greater than at *x*<1, given the corresponding values of $\bar{q}_p$ and $\bar{q}_f$ by differentiating focal plant fitness with respect to focal plant carbon acquistion strategy whilst holding average plant carbon acquisition strategy constant (mathematically: $\partial w_\mathrm{p}/\partial x\,|_{\bar{x}=1}$) and finding parameter space where this derivative is positive. That is, where plants would be selected to increase their carbon acqusition allocation beyond one, if feasible. We find that this condition holds when

$$P_\mathrm{p} < \frac{P_{\Sigma\mathrm{f}}(1-(1-a)r_\mathrm{p})}{C_{\Sigma\mathrm{p}}2(1-a)d}\left(d(1+b-br_\mathrm{f})+br_\mathrm{f}-1+\sqrt{4db(1-d)(1-r_\mathrm{f})+\left(1-br_\mathrm{f}-d(1+b-br_\mathrm{f})\right)^2}\right). \quad (5)$$

We also find that inequality (3) is more stringent than inequality (5). When inequality (5) is satisfied and inequality (3) is not, (4) is a co-evolutionary ESS $\left((x^*, q_{\mathrm{p}}^*, q_{\mathrm{f}}^*) = (\bar{\bar{x}}, \bar{\bar{q}}_{\mathrm{p}}, \bar{\bar{q}}_{\mathrm{f}})\right)$.

If instead the phenotype of plants responds to fungal strategy when $\bar{\bar{x}} = x = 1$, fungal strategy ($\bar{q}_f$) is set so that $\bar{\bar{x}}$ in (2a) is exactly 1:

$$\left(\bar{\bar{x}}, \bar{\bar{q}}_p, \bar{\bar{q}}_f\right) = \left(1, 1 - \frac{a}{1-(1-a)r_p}, \frac{(1-a)C_{\Sigma p}P_p}{P_{\Sigma f}\left(1-(1-a)r_p\right)}\right). \tag{6}$$

We verify whether fungal fitness at $\bar{\bar{q}}_{\mathrm{f}} = (1-a)C_{\Sigma\mathrm{p}}P_{\mathrm{p}}/P_{\Sigma\mathrm{f}}(1-(1-a)r_{\mathrm{p}})$ is a maximum given the corresponding values of $\bar{\bar{x}}$ and $\bar{\bar{q}}_p$. We find that it is whenever inequality (3) is satisfied, but inequality (5) is not. Hence, under these conditions, (6) is a co-evolutionary ESS $\left((x^*, q_{\mathrm{p}}^*, q_{\mathrm{f}}^*) = (\bar{\bar{x}}, \bar{\bar{q}}_{\mathrm{p}}, \bar{\bar{q}}_{\mathrm{f}})\right)$.

5

Can natural selection favour altruism between species?

5.1 Abstract

Darwin suggested that the discovery of a trait that can only be interpreted as altruism between species would annihilate his theory of natural selection. However, it has not been formally shown whether between-species altruism can evolve by natural selection, or why this could never happen. Here, we develop a spatial population genetic model of two interacting species, showing that indiscriminate between-species helping can be favoured by natural selection. We then ask if this helping behaviour constitutes altruism between species, using a linear-regression analysis to separate the total action of natural selection into its direct and indirect (kin selected) components. We show that our model can be interpreted in two ways, as either altruism within species, or altruism between species. This ambiguity arises depending on whether or not we treat genes in the other species as predictors of an individual's fitness, which is equivalent to treating these individuals as agents (actors or recipients). Our formal analysis, which focuses upon evolutionary dynamics rather than agents and their agendas, cannot resolve which is the better approach. Nonetheless, because a within-species altruism interpretation is always possible, our analysis supports Darwin's

suggestion that natural selection does not favour traits that provide benefits exclusively to individuals of other species.

5.2 Introduction

"If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection." Darwin (1859, p.201)

Darwin's (1859) theory of natural selection explains the process and purpose of organismal adaptation. Specifically, those heritable characters that are associated with higher individual reproductive success will tend to accumulate in biological populations under the action of natural selection. Hence, Darwin argued, individual organisms will appear increasingly well designed to maximise their reproductive success. Darwin (1859, p.237) also recognised that natural selection can work indirectly, through the reproductive success of family members, so as to favour characters that promote the reproductive success of an individual's family group. Hamilton's (1963, 1964, 1970) theory of inclusive fitness expanded on this principle, showing that natural selection can favour the evolution of altruistic behaviour that reduces the actor's reproductive success provided that sufficient benefits accrue to the actor's kin.

Darwin (1859, p.201) suggested that natural selection would never favour altruism between individuals of different species. This appears to be borne out by empirical observation: whilst cooperative interactions between different species (mutualisms) are widespread in the natural world, these typically involve mechanisms that ensure return benefits accrue either to the actor or to her close kin (Foster & Wenseleers 2006, Leigh 2010, Bourke 2011). For example, plants that form symbioses with mycorrhizae provide more carbohydrates to mutualistic partners that supply more nutrients, giving the mycorrhizae an incentive to cooperate (Kiers et al. 2011). This mutualism may involve mutually beneficial helping if sufficient return benefits accrue to the helpful mycorrhiza. Alternatively, it may involve altruistic helping, favoured owing to return benefits that accrue to the mycorrhiza's close kin forming symbioses with the same root. Hence, although altruism may occur in the context of mutualisms, it appears that this altruism is occurring within rather than between species.

From a theoretical perspective, whilst some authors have argued that natural selection cannot favour altruism between species (Bourke 2011, Foster et al. 2006), others have argued that it can (Frank 1994, Fletcher & Zwick 2006, Fletcher & Doebeli 2009). Hamilton's (1963, 1964, 1970) theory of inclusive fitness highlights that it is not kinship (i.e. genealogical relationship) per se that is needed in order for altruism to be favoured, but rather that the actor and recipient are genetically similar (i.e. genetic relatedness). Frank (1994) suggested that genetic relatedness could arise between species due to the action of selection in viscous populations in a way that could favour the evolution of altruism between species (see also Gardner et al. 2007). However, a formal analysis of when such genetic associations arise, when they will favour indiscriminate helping between species, and whether this helping fits the criteria for altruism between species remains to be undertaken.

Here, we first develop an infinite stepping stone population genetic model to provide a concrete illustration of whether and how indiscriminate helping can evolve between species. Previous theory has shown that: (a) population viscosity alone can favour the evolution of indiscriminate helping within a single species because it leads to a positive genetic relatedness between interacting individuals (Hamilton 1964, Ohtsuki et al. 2006, Ohtsuki & Nowak 2006, Grafen 2007, Lehmann et al. 2007a, Taylor et al. 2007a); (b) the evolution of reciprocal helping between species can be facilitated by population structuring (Doebeli & Knowlton 1998); (c) the evolution of indiscriminate helping between species can be favoured by transmission mechanisms that systematically force pairs of helpers together across generations (Yamamura et al. 2004, Gardner et al. 2007, Fletcher & Doebeli 2009). Our aim here is to extend this previous theory, by examining whether population viscosity alone can favour indiscriminate helping between species.

We then examine whether such helping can be classified as between-species altruism using an inclusive fitness analysis. This requires dissecting the analytical conditions calculated for natural selection to favour indiscriminate between-species helping in our model into separate inclusive fitness costs and benefits. In their most general sense, the costs and benefits of an inclusive fitness analysis are defined as least-squares regressions of fitness against genetic predictors (Queller 1992, Gardner et al. 2011). We explore the consequences of allowing or disallowing the genes of other species to feature in this regression analysis, both in general and also using our stepping stone model as a concrete illustration. Our aim here is to determine both whether indiscriminate helping between species can qualify as altruism between species and whether it must be considered altruism between species.

5.3 Indiscriminate helping between species?

In this section, we ask whether indiscriminate helping between species can be favoured by natural selection despite fecundity costs to the helper. We develop an infinite stepping stone population model, derive analytical conditions for helping to be favoured in this model, and then check the robustness of these results using individual-based numerical simulations of finite populations.

5.3.1 Model

We consider two identical asexual haploid species – A and B – in a one-dimensional stepping stone model (Kimura & Weiss 1964) with infinitely many consecutively-numbered patches, each containing one individual of each species. Individuals vary only at a locus controlling social behaviour and may carry either an allele for helping (H) or carry a null allele and are non-helpers (N; Ohtsuki & Nowak 2006, Taylor et al. 2007a, Grafen & Archetti 2008, Taylor 2010). The fecundity of an individual in patch i is given by $F_i = 1 - cx_i + bx_{i'}$, where x_i is her own helping genotype ($x_i = 1$ if H, $x_i = 0$ if N) and y is the helping genotype of her social partner ($x_{i'} = 1$ if H, $x_{i'} = 0$ if N; as illustrated in Figure 5.1). Thus, $0 < c < 1$ is the marginal fecundity cost of cooperation and $b > 0$ is the marginal fecundity benefit of cooperation.

In every generation, we assume that all individuals die and that most are replaced by their clonal offspring, resulting in no genetic change within the patch. However, a small fraction of individuals are chosen at random to die without reproducing in this way, in which case their two conspecific neighbours in adjacent patches compete to

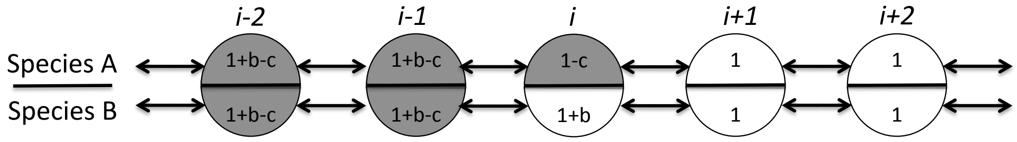


Figure 5.1 | Population structure. This figure shows a section of five patches in the population. The fecundity rate of individuals is affected by the individual of the other species with which they share a patch and they compete with individuals that reside two patches away. Shaded patches are inhabited by helpers while white patches are inhabited by non-helpers.

fill the vacant breeding spot with one of their own offspring. If the fecundity of the neighbour in patch i-1 is $F_{i\text{-}1}$ and the fecundity of the neighbour in patch i+1 is F_{i+1}, then the probability that a vacant spot in patch i is filled with an offspring of the neighbour in patch i-1 is $F_{i\text{-}1}/(F_{i\text{-}1} + F_{i+1})$ and the probability that it is filled with an offspring of the neighbour in patch i+1 is $F_{i+1}/(F_{i\text{-}1}+F_{i+1})$.

5.3.2 Evolution of helping

We consider a resident population of non-helpers into which we introduce helpers of both species at random and at low frequency. Most helpers will leave no descendants in the long term, owing to them never meeting helpers of the other species, and hence being outcompeted by their non-helping conspecific neighbours. However, there is a nonzero probability that any helper of species A will eventually meet a helper of species B. If this happens, then there may be a non-zero probability that these helpers will give rise to an expanding chain of patches that contain a helper of each species. Through analytical methods and simulations, we suggest that this will lead the local frequency of helpers to increase when:

$$b > 2 + \sqrt{8 - 4c + c^2} \tag{1}$$

(see Appendix for derivation).

More realistically, we should take into account the effects of interactions between chains of patches that contain a helper of each species, and also the effect of mutation, which is the ultimate source of genetic variation. We assume that non-helpers transform into helpers, and vice versa, at a low rate in each generation. The evolutionary dynamics are consequently complicated by the fact that non-helpers may appear within expanding chains of patches containing a helper of each species, whether due to the junction of two pre-existing chains or fresh mutational input. Thus, it is not sufficient that chains of helpers tend to increase in length (i.e. inequality (1)), but also these chains must expand faster than the subpopulations of non-helpers that appear within them. This gives rise to a more stringent condition for natural selection to favour helping:

$$\frac{(b-4)b-(c-2)^2}{(4b+(c-2)^2)(2+b-c)} > \frac{1}{2+2b-c}\,. \tag{2}$$

We obtain this result irrespective of the relative rates of mutation in each direction (see Appendix for derivation), although the derivation requires low absolute rates. These analytical results are readily confirmed by numerical simulation with higher mutation rates, also revealing the robustness of the results to relaxation of the assumption of infinite population size (Figures 5.2 and 5.3, see Appendix for details). Natural selection favours helping when the benefit is greater than approximately 7.13

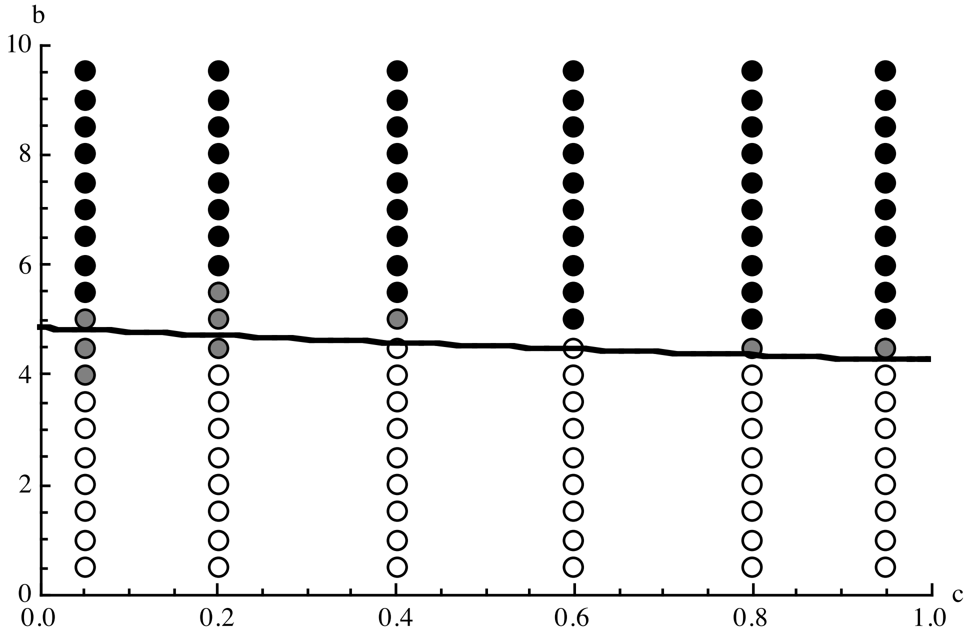


Figure 5.2 | Condition for expected local frequency of helpers to be expected to increase under natural selection. The line indicates the analytically derived condition for the expected local frequency of helpers to increase under natural selection (inequality (2) is satisfied above the line). Black dots indicate parameter values where helpers are significantly fitter than a neutral allele, white where they are significantly less fit, and grey where there is no significant difference in fitness at a 95% confidence level (see Appendix for details).

for a cost near 0 and when the benefit is greater than approximately 6.39 for a cost near 1. The required level of benefit changes almost linearly with cost. We notice that the cost has a relatively small effect on whether or not natural selection favours helping.

Paradoxically, we find that between-species helping is promoted when the fecundity cost of helping is higher, as higher values of c make conditions (1) and (2) less stringent. This is because a larger cost is associated with stronger selection, and selection is responsible for generating a statistical association between species, such that helpers of one species are more likely to be associated with helpers of the other species (see Appendix; Gardner et al. 2007). Natural selection can even favour

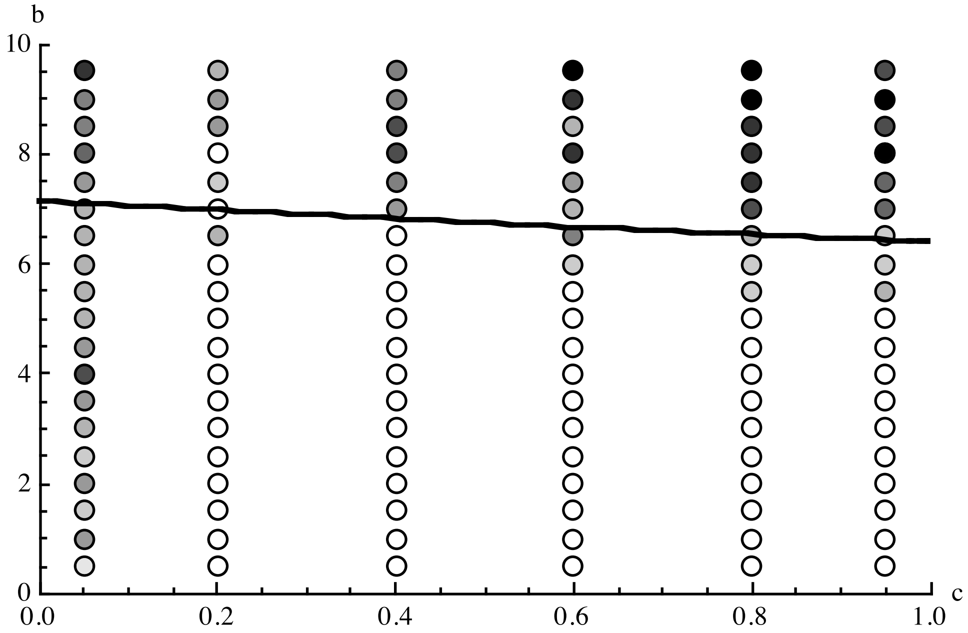


Figure 5.3 | Condition for natural selection to favour helpers. The line indicates the analytically derived condition for natural selection to favour helpers (inequality (1) is satisfied above the line). Dots indicate parameter values tested by simulation and darker dots indicate greater evolutionary success of helpers (see Appendix for details).

helping when the fecundity cost is 1, meaning that helpers who do not share patches with other helpers cannot successfully place offspring into adjacent patches. This maximises the association between helpers in the two species.

5.4 Altruism between species?

We have determined that indiscriminate helping between species can be selectively favoured in the face of fecundity costs. But can this helping be considered as altruism between species? To address this problem, we need to calculate the cost and benefit terms of Hamilton's rule. In empirical studies, fecundity and survival effects are often used as readily measured proxies for these costs and benefits. However, from a theoretical perspective, the benefit and cost terms of Hamilton's rule are not just the fecundity and/or survival effects (Rousset 2004, Gardner et al. 2011). Most generally, the benefit and cost terms of Hamilton's rule are defined as marginal fitness effects, which are computed by means of least-squares regression of fitness against genetic predictors (Queller 1992, Gardner et al. 2007, Gardner et al. 2011).

Here, we briefly review: (1) how least-squares regression methodology can be used to formally separate individual fitness into its direct versus indirect (kin selected) effects (Queller 1992; Frank 1997b,c, 1998; Gardner et al. 2007; Gardner et al. 2011); (2) how these fitness effects are used to classify social behaviours as altruistic, selfish, mutually beneficial or spiteful (Hamilton 1964, West et al. 2007b); and (3) how these fitness effects are weighted by coefficients of relatedness to yield Hamilton's rule of kin selection (Hamilton 1963, 1964, 1970; Queller 1992; Gardner et al. 2011). We then: (4) describe an ambiguity that arises in the application of these methods to our evolutionary model of helping between species; and (5) show that this ambiguity has a bearing upon whether or not such helping is classified as altruism between species.

5.4.1 Direct fitness versus indirect fitness

An individual's fitness *w* is her expected lifetime number of offspring that survive to breed in the next generation. Fitness depends not only on an individual's own genotype but also on the genotypes of her social partners. We may calculate the separate fitness effects by fitting an equation of the following form to population data by the method of least-squares:

$$w = K + \beta_{w,x|x_1,\ldots,x_n}(x - \mathrm{E}(x)) + \sum_{j=1}^{n} \beta_{w,x_j|x,x_1,\ldots,x_{j-1},x_{j+1},\ldots,x_n}(x_j - \mathrm{E}(x_j)) + \varepsilon \tag{3}$$

where *K* is a constant. The predictor *x* is the focal individual's genic value for helping and the predictors $x_1,\ldots,x_n$ are the genic values of the individual's *n* social partners, i.e. those individuals whose genotypes mediate the focal individual's fitness (e.g. Gardner et al. 2011). E[x] and E[x_j] are the overall frequency of the of the helping allele in the global population, which we assume rare, so that they are equated to zero. The partial regression coefficient $\beta_{w,x|x_1,\ldots,x_n}$ describes the effect of the individual's own genic value on her fitness, holding fixed the genic values of her *n* social partners, and defines the direct fitness effect –*C*. The partial regression coefficient $\beta_{w,x|x_1,\ldots,x_{j-1},x_{j+1},\ldots,x_n}$ describes the effect of the individual's *j*th social partner's genic value on her fitness, holding fixed the genic value of the focal individual and the genic values of her *n*-1 other social partners, and defines an indirect fitness effect B_j. We note that any partition of fitness that includes the focal individual's genic value for helping allows us to recover the total fitness effect of helping. The effects of genic values that mediate the focal individual's fitness but are not used in the partition will be redistributed into the fitness effects of the other predictors included in the analysis.

5.4.2 Classification of social behaviours

The signs of the direct and indirect fitness effects yielded by the above regression analysis are used to formally classify social behaviours. Those behaviours involving $B > 0$ and $C > 0$ are "altruistic", those involving $B > 0$ and $C < 0$ are "mutually beneficial", those involving $B < 0$ and $C > 0$ are "spiteful", and those involving $B < 0$

	Effect on recipient	
Effect on actor	+	-
+	Mutual Benefit	Selfishness
-	Altruism	Spite

Figure 5.4 | A classification of social behaviours. A classification of social behaviours based on their effect on the reproductive fitness of actors and recipients.

and $C < 0$ are "selfish" (Figure 5.4, see West et al. 2007b for a review of the history of this terminology). Importantly, these fitness costs and benefits derived from the statistical model must not be confused with the fecundity cost and benefit c and b of the evolutionary model (Rousset & Ronce 2004, West et al. 2007b, Lehmann et al. 2007a,b, Grafen 2007, Gardner et al. 2011).

5.4.3 Hamilton's rule

We can weigh the direct and indirect fitness effects ($-C$ and B_j) yielded by the above regression analysis by appropriate coefficients of genetic relatedness (r_j) to give a condition for natural selection to favour an increase in the trait of interest. This is Hamilton's (1963, 1964, 1970) rule: $-C + \sum_j B_j r_j > 0$. This can easily be seen to emerge from application of the least-squares regression model of individual fitness to Price's (1970) equation of natural selection. Price's equation states that the change in average genic value is given by:

$$\Delta \mathrm{E}(x) = \mathrm{cov}(w,x), \tag{4}$$

noting that $\mathrm{E}(w) = 1$, since the population is of fixed size across generations. Substituting the expression for fitness in equation (3) into equation (4) yields:

$$\Delta \mathrm{E}(x) = \left(\beta_{w,x|x_1,\ldots,x_n} + \sum_{j=1}^{n} \beta_{w,x_j|x,x_1,\ldots,x_{j-1},x_{j+1},\ldots,x_n} \beta_{x_j,x} \right) \mathrm{var}(x), \tag{5}$$

noting that $\mathrm{cov}(x,x) = \mathrm{var}(x)$, $\mathrm{cov}(x_j,x)/\mathrm{cov}(x,x) = \beta_{x_j,x}$, $\mathrm{cov}(\varepsilon,x) = 0$ and $\mathrm{cov}(\varepsilon,x_j) = 0$ for all j. Replacing the complicated regression terms with the $-C$ and B_j symbols defined above (Queller 1992), and noting that $r_j = \beta_{x_j,x}$ is the regression form of genetic relatedness between a focal individual and her j^{th} social partner (Orlove & Wood 1978), the condition for the genetical trait to be favoured by natural selection $\Delta\mathrm{E}(x) > 0$ is Hamilton's (1963, 1964, 1970) rule: $-C + \sum_j B_j r_j > 0$.

5.4.4 Which predictors to use?

Here we have used purely genetic predictors of fitness (Queller 1992; Gardner et al. 2011). Frank (1997a, b, 1998, 2013a, b) has clarified that any set of predictors – including, for example, phenotypes – can be used. However, we are following Fisher's (1918, 1930) genetical paradigm that partitions the action of natural selection into purely genetic effects, as this reduces ambiguity over the definition of direct versus indirect fitness effects and consequent classification of social behaviours. For example, in a scenario involving reciprocated cooperation among non-relatives, the direct fitness effect of a gene for cooperation can be positive, because it is associated with greater levels of cooperation among one's social partners, independently of the genes that they carry. Thus cooperation, in the context of reciprocity, is a mutually-beneficial behaviour (West et al. 2007b). But if cooperation phenotypes had been used as explicit predictors of individual fitness, then because the partial effect of the individual's own phenotype is negative and the partial effect of the phenotype of a social partner is positive, the reciprocated cooperation would be incorrectly diagnosed as altruistic.

Nevertheless, even restricting ourselves to purely genetical predictors of fitness, an ambiguity arises as to which set of genes we should use in our regression analysis. Specifically, should we only consider those genes belonging to social partners of the individual's own species, or should we also consider those genes belonging to heterospecific social partners? Below, we show that the genes of conspecific and heterospecific social partners both mediate the focal individual's fitness. We then investigate the consequences of taking alternative approaches to resolving the ambiguity over the use of statistical predictors of fitness.

5.4.5 Causal relationship between genes and fitness

Genes in both species mediate the focal individual's fitness (Figure 5.5a). First, her fitness is mediated by her own gene at the locus for helping as, all else being equal, she has fewer offspring if she helps more. Second, her fitness is mediated by the gene at the locus for helping carried by her heterospecific patch mate as, all else being equal, she has more offspring if her patch mate helps more. Third, her fitness is mediated by the genes carried by the conspecific individuals residing two patches away on either side, because she competes with these individuals to leave offspring whenever the patches immediately adjacent to her own become vacant. All else being equal, she has more offspring if these conspecific individuals help more. Fourth, her fitness is mediated by the genes carried by the heterospecific individuals residing two patches away on either side, because their help enhances the fitness of her competitors. All else being equal, she has fewer offspring if these heterospecific individuals help more.

This suggests that six genes mediate the individual's fitness, three belonging to her own species and three belonging to the other species. However, the causality can be traced further back in time, to other genes. The local genetic composition of the other species owes, in part, to the local genetic composition of the individual's own species in the previous generation. It also owes, in part, to the genetic composition of the individual's own species in each generation prior to that. In fact, the presence of any helper in the other species after a sufficiently long time owes entirely to the action of the individual's conspecific helpers in previous generations, as without these natural selection would eliminate helpers in the other species. This flow of causation is illustrated in Figure 5.5a.

5.4.6 Conspecific genetic predictors only

If we consider that only genes from the individual's own species may be used as predictors of her fitness, then the effects of heterospecific genes are subsumed into the effects of conspecific genes from past generations. The resulting path diagram is illustrated in Figure 5.5b. In the context of this statistical model, the partial effect of increasing the focal individual's genetic value for helping (that is, keeping all other predictors constant) is to decrease her own fitness. Hence, the direct fitness effect of helping is negative ($-C < 0$) and helping is altruistic. However, the indirect fitness effects of helping are all within species according to this statistical model, and so whilst the trait is altruistic, it is altruism within species. The inclusive fitness interpretation of this view is that, by helping, the actor suffers a direct fitness loss, but enjoys an indirect fitness benefit by increasing the local abundance of heterospecific helpers whose help will improve the reproductive success of future generations of the actor's conspecific kin. In this statistical model, the help provided by heterospecific helpers to a focal individual is interpreted as caused by previous generations of conspecifics. It cannot be interpreted as caused by the focal individual, as she cannot impact the help provided by heterospecifics in her lifetime.

5.4.7 Conspecific and heterospecific genetic predictors

Alternatively, if we consider that genes from both conspecifics and heterospecifics may be used as predictors, then we need only employ the six genes that determine a focal individual's fitness described above, as no other genes have an impact upon the individual's fitness except through those six. The resulting path diagram is illustrated in Figure 5.5c. Again, the partial effect of increasing the focal individual's genetic value for helping is to decrease her own fitness, and hence the direct fitness effect of helping is negative ($-C < 0$) and helping is altruistic. Whenever helping is favoured, we have $-C + \sum_K B_k r_k + \sum_L B_l r_l > 0$, where K is the set of all conspecific genes that mediate fitness and L is the set of all heterospecific genes that mediate fitness, and in particular $-C + \sum_K B_k r_k < 0$ (see Appendix for details). That is, the selective benefit of

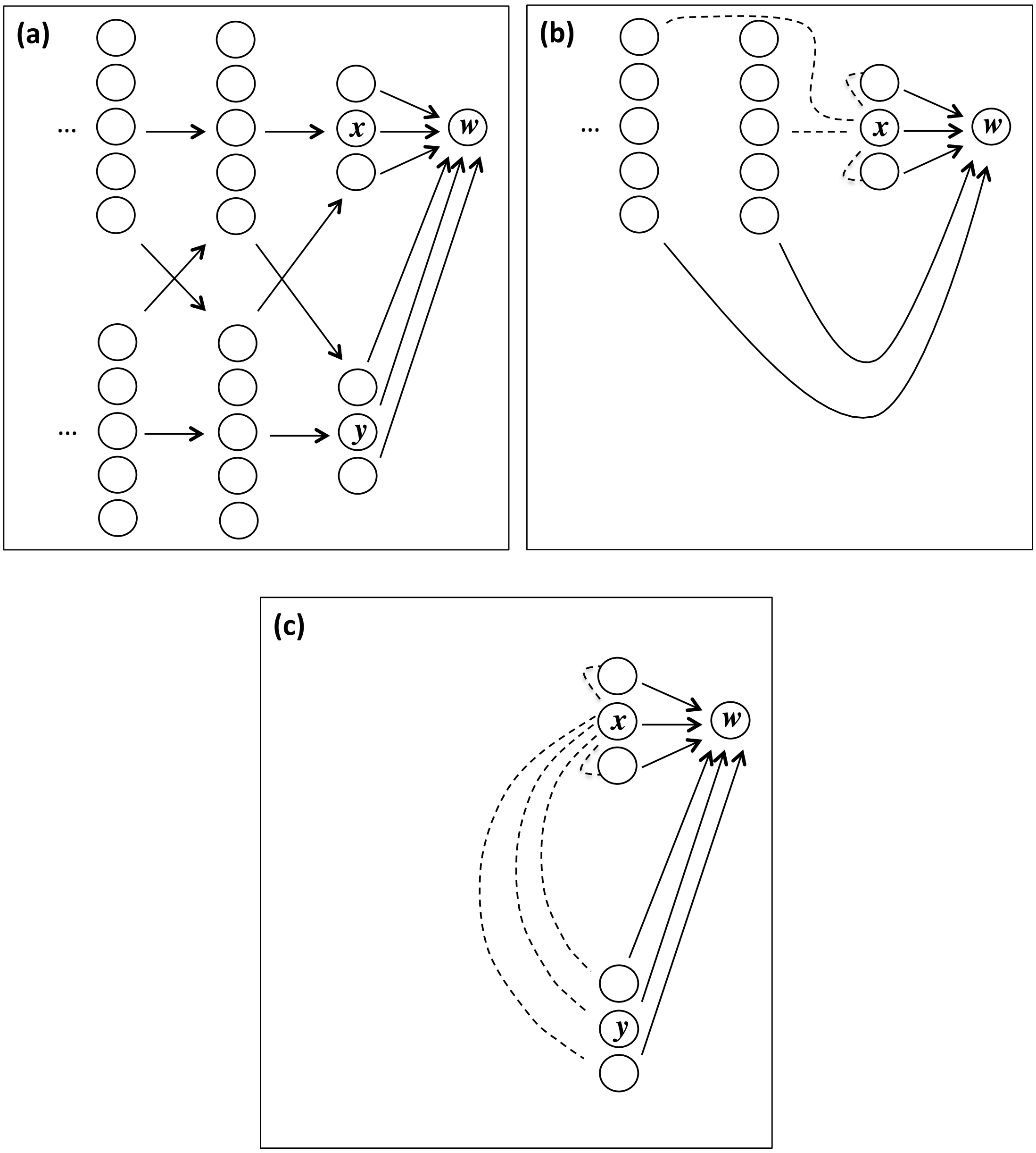


Figure 5.5 | Genetic mediators of fitness. (a) The genetic composition of past generations of both species causally impacts upon the genetic composition of the present generation of both species, and the genetic composition of the present generation of both species causally impacts upon the focal individual's fitness, *w*. A larger number of individual affect the fitness of a focal individual in each previous generation. (b) A path diagram illustrating the statistical model of fitness that uses genetic predictors from the focal individual's species only. The causal impact of genes in the other species is subsumed into the causal impact of genes in the focal individual's species from previous generations. A larger number of conspecifics affects the fitness of a focal individual in each previous generation. (c) A path diagram illustrating the statistical model of fitness that uses genetic predictors from the focal individual's species and also from the other species. The causal impact of genes in past generations of the individual's own species is subsumed into the causal impact of genes in the present generation of the focal individual's own species and in the present generation of the other species. Genetic correlations are shown as dashed lines.

helping is dependent on the help that is directed to heterospecifics, and this diagnoses the helping trait as true altruism between species. The inclusive fitness interpretation here is that the coefficient of relatedness describes the similarity in genetic propensity for helping members of the other species. Heterospecific social partners that share a focal individual's propensity for interspecific helping can be considered 'relatives' and are consequently afforded positive valuation by the actor.

5.5 Discussion

We have developed an infinite stepping stone population model to explore the evolution of indiscriminate helping between species. We have found that natural selection may build genetic associations between individuals in different species, such that helpers of one species tend to interact socially with helpers of another species, giving an indirect fitness benefit for helping. Moreover, we have found that the classification of this helping behaviour depends on the modeller's decision as to which set of genetic predictors are used in a statistical model of fitness. If genetic predictors are restricted to those genes of the individual's own species, then the helping behaviour represents within-species altruism. However, if genetic predictors are allowed to include genes from both the individual's own species and also the other species, then the helping behaviour is diagnosed as between-species altruism.

5.5.1 Indiscriminate helping between species

We have shown that natural selection can favour indiscriminate helping, even when the trait can only benefit members of another species and carries a fecundity cost to the actor. Discriminate helping, involving mechanisms such as partner choice or partner-fidelity feedback, readily evolves between species, owing to return benefits for the actor and/or her conspecific relatives (Doebeli and Knowlton 1998, West et al. 2002a, Foster & Wenseleers 2006). However, the evolution of indiscriminate helping between species has been more difficult to address. Frank's (1994) analysis suggests that indiscriminate helping between species can be favoured in principle, but his model was not fully dynamical and so the robustness of this result is unclear. Fully explicit dynamical models that have considered indiscriminate between-species helping are problematic in that they systematically force pairs of helpers together across generations through the transmission scheme (Yamamura et al. 2004, Gardner et al. 2007). That is, the rule for how individuals are transmitted depends on genotype. In contrast, in the present model we allow individuals to reproduce and disperse independently. However, the use of the term 'indiscriminate' does not mean that all individuals are equally like to receive help. A statistical association between helpers across species boundaries builds up purely by population viscosity and the action of natural selection.

We have focused upon a simple, infinite stepping stone model (Kimura & Weiss 1964), for the purpose of illustration. Investigating the impact of more complex population structure on the evolution of helping between species represents an interesting avenue for future research. Perhaps most work on social evolution in genetically structured populations has focused upon the infinite island model (Wright 1931). But the island model does not present any means for pairs of helpers from different species to retain associations whilst spreading into new territory. This is because every disperser moves to a new patch at random, independently of the destinations of the other individuals dispersing away from her natal patch. However, there is further scope for studying the evolution of helping between species on lattices, which have explicitly spatial structure in more than one dimension (Taylor 1992b).

5.5.2 Altruism between species

When is helping between species truly altruistic? Our analysis suggests that this classification issue hinges upon the set of fitness predictors that are employed in a regression analysis. Different sets of predictors lead to different partitions of fitness effects, including different estimates of the direct versus indirect components of an individual's fitness, and hence differences in classification of social behaviour as altruistic, selfish, mutually beneficial or spiteful. We have focused on genetical predictors, because using phenotypes leads to ambiguity and misinterpretation. Moreover, the phenotype is not the inherited strategy upon which natural selection acts. For example, in the context of reciprocity between non-relatives, if fitness is partitioned into the effects of own versus social partner's level of cooperation, then cooperation can appear altruistic (Fletcher & Doebeli 2009), but if it is partitioned into the effects of own versus social partner's genes, then it appears mutually beneficial (West et al. 2007b). The genetical approach is preferable, because it highlights that the rationale for cooperating in this scenario is to elicit cooperation from one's social partners, in a purely self-interested manner.

However, we have also shown that even the strictly genetical approach is beset by ambiguity over which genes are to be included as explicit predictors of fitness. In particular, do we only include genes belonging to the focal individual's own species, or do we also include genes belonging to other species? We have found that the evolution of between-species helping can be fully accounted for using either approach. If we use only conspecific genes as predictors, then we find that helping between species constitutes within-species altruism. That is, the focal actor helps cooperators of the other species in order to improve the social environment for future generations of her own kin. In contrast, if we use both conspecific and heterospecific genes as predictors, then we find that helping between species constitutes between-species altruism. That is, the focal actor aids helpers of the other species because their reproductive success – like that of conspecific relations – is associated with an increase in the population frequency of the actor's genes.

5.5.3 Actors and recipients

The decision as to which genetic predictors are to be used in the regression model of fitness amounts to deciding which individuals we are considering as the actors and the recipients of the helping behaviour (Figure 5.5). Simply having an impact upon a social partner's reproductive success does not necessarily make an individual an actor, if they might alternatively be considered a mere instrument that is used by a different individual – the true actor – in order to bring about the fitness effect. And simply having one's reproductive success mediated by a social partner does not necessarily make an individual a recipient, if they might alternatively be considered a mere instrument that is used by the actor to bring about a fitness effect for a different individual – the true recipient. This notion of agency is already implicit in any discussion of altruism: an intentional term, the use of which in scientific discourse is justified on the basis of a mathematical relationship (isomorphism) between the dynamics of natural selection and an individual-as-maximising-agent analogy (Grafen 2002, 2006a,b).

If we use only conspecific genes as predictors then we must consider only conspecific individuals in the roles of actor and recipient. That is, those heterospecific individuals who mediate a focal recipient's reproductive success must be considered mere instruments, and the causality underlying their behaviour (i.e. why they carry out the helping behaviour) must be traced back to previous generations of the focal individual's conspecific kin (the true actors), as these individuals are not dependence-separated from the focal individual's fitness (Crespi 1990, Shipley 2000). That is, these individuals affect the focal individual's fitness without having to rely on the actions of other agents. Similarly, the heterospecific individuals whose reproductive success is mediated by a focal actor must be considered mere instruments, having only instrumental value in ensuring a better social environment for future generations of the actor's conspecific kin (the true recipients). In contrast, if we use heterospecific as well as conspecific genes as predictors of fitness, then we must consider both conspecific and heterospecific individuals in the roles of actor and recipient. Note that few mutualisms admit the latter interpretation – it requires special circumstances, such as those considered in our mathematical model, where genetic correlations arise between species. Most mutualisms appear to function through phenotypic correlations, such as cooperator association, partner-fidelity feedback, or partner choice (Foster & Wenseleers 2006). Also note that we cannot use only heterospecific genes as predictors because for the same reason that we must include members of past generations if we only use conspecific predictors. All conspecific genes will never be dependence-separated from a focal individual's fitness.

Are these different interpretations equally valid? A possible justification for the conspecifics-only approach is to note that the dynamics of natural selection is framed in terms of within-species genetical change, so that it makes sense to also restrict corresponding notions of optimisation and agency to conspecifics. We also suggest that while there may be appreciable genetic relatedness across species with regard to helping genes, this might not be the case across the rest of the genome. In contrast, co-ancestry of conspecifics leads to an approximately equal relatedness across the entire genome, allowing for the evolutionary elaboration of complex adaptations.

On the other hand, a possible justification for the conspecifics and heterospecifics approach is that real-world organisms do not cease to manifest the appearance of agency and intention when we are considering the evolution of traits in other species. Consequently, it makes sense to regard individuals in all species as having agency at all times. Our formal analysis cannot address this issue, as it is framed only in terms of the dynamics of gene frequency change and not in terms of optimisation theory, which is the proper framework within which to develop notions of agency and intentionality (Grafen 2002, 2006a,b). Hence, we leave this puzzle as an open problem for future exploration.

5.6 Conclusion

To conclude, was Darwin correct to rule out the adaptive evolution of behaviours that provide benefits only for individuals of other species? We suggest that he was. Natural selection can favour the evolution of indiscriminate helping between species and, in certain circumstances such helping may justifiably be interpreted as altruism between species. However, the alternative interpretation that such helping behaviour represents mere within-species altruism is available, as restricting the set of predictors to conspecifics gives a full account of the fitness effects of the trait. Thus, benefits to individuals of other species would never provide an exclusive explanation for any behaviour that has evolved by natural selection.

5.7 Appendix

5.7.1 Evolution of Helping: condition for the expected local frequency of helpers to increase over time under natural selection

Here, we derive the condition on *b* and *c* for natural selection to favour a local population of helpers in both species. Helpers can gain offspring irrespective of whether they share patches with other helpers. Therefore, as long as the population contains helpers at a high enough frequency that there are a finite number of patches between a pair of helpers in different species, stochastic effects ensure that a local distribution of helpers consisting of a set of at least two, but potentially many more, adjacent patches that contain two helpers, one of each species, may form. At the ends of this set, there may also be sequences of patches that contain one helper and one

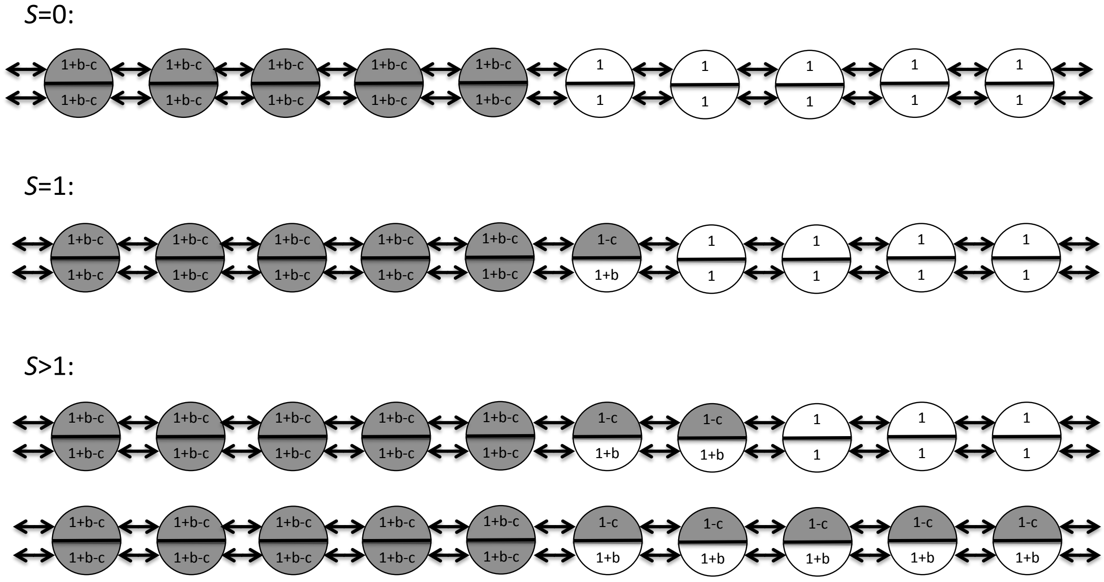


Figure 5.6 | Number of patches that contain a single helper (*s*). The number of patches with a single helper (*s*) change the probability that a helper is added or lost from the population because *s* changes the fecundity of individuals that compete for reproduction. Once we calculate the frequency of each *s*, we can calculate whether or not natural selection favours helping.

non-helper, where all of the helpers in one of these sequences are from the same species. This local distribution is illustrated in Figure 5.1.

Other local distributions of helpers may initially be present but when no two adjacent patches contain a helper of each species, natural selection eventually either eliminates helpers or gives rise to two adjacent patches that contain a helper of each species. Therefore, only helpers in a local distribution as described in the previous paragraph (and illustrated in Figure 5.1 and 5.6) can be present in the population in the long term.

If a patch contains a helper of each species and is surrounded by two patches also containing a helper of each species, then selection in that patch does not impact the total number of helpers in the population as other helpers replace deceased ones.

Therefore, we can limit our attention to the edges of the distribution of helpers. The two edges are symmetric, so we consider only one of them (patches *i*-1, *i*, and *i*+1 in Figure 5.1).

The probability that a helper replaces a non-helper and vice versa depends on the number of patches that contain a helper of one species and a non-helper of the other (see Figure 5.6 for details). We write the number of patches that contain only a single helper as *s*. For now, we assume that this number (*s*) can only change by one at a time through the replacement of an individual by the offspring of her neighbour. We relax this assumption in the next section and find that it does not affect our results. We can write the matrix of the relative rates of change in *s*

$$\begin{array}{c|cccccc} s & 0 & 1 & 2 & 3 & 4 & 5 \\ \hline 0 & -a_1 & a_1 & 0 & 0 & 0 & \ldots \\ 1 & a_2 & -a_2-a_3 & a_3 & 0 & 0 & \ldots \\ 2 & 0 & a_4 & -a_4-a_5 & a_5 & 0 & \ldots \\ 3 & 0 & 0 & a_4 & -a_4-a_5 & a_5 & \ldots \\ 4 & 0 & 0 & 0 & a_4 & -a_4-a_5 & \ldots \\ 5 & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \end{array} . \tag{6}$$

We can enter fecundity cost *c* for helpers and benefit *b* for individuals that share patches with helpers to calculate each of the values in matrix (6). The rates of increase and decrease in *s* are equal for all $s \geq 2$

$$a_4 = \frac{1+b-c}{2+2b-c} + \frac{1}{2-c} > \frac{1+b}{2+2b-c} + \frac{1-c}{2-c} = a_5 \; \forall \, b, c > 0 \, . \tag{7}$$

Hence, from the theory of Markov chains, there is a limiting distribution of the values of s. We calculate the long-term equilibrium frequency with which each value of s occurs in this distribution, p_s.

$$\begin{aligned} p_0 &= \frac{a_2(a_4 - a_5)}{a_1a_3 + a_1a_4 + a_2a_4 - (a_1 + a_2)a_5} \\ p_1 &= \frac{a_1(a_4 - a_5)}{a_1a_3 + a_1a_4 + a_2a_4 - (a_1 + a_2)a_5} \\ p_{s\geq 2} &= \frac{a_1a_3}{a_1a_3 + a_1a_4 + a_2a_4 - (a_1 + a_2)a_5} \end{aligned} \quad . \tag{8}$$

Each a_s can be decomposed into a_{s+}, the rate at which s changes by the replacement of a non-helper by a helper, and a_{s-}, the rate at which s changes by the replacement of a helper by a non-helper. The average probability that a helper replaces a non-helper is greater than the average probability that a non-helper replaces a helper if

$$p_0(a_{1+} - a_{1-}) + p_1(a_{2+} - a_{2-} + a_{3+} - a_{3-}) + p_{s\geq 2}(a_{4+} - a_{4-} + a_{5+} - a_{5-}) > 0 \; . \tag{9}$$

The values of each a_{s+} and a_{s-} can be derived directly from the model

$$\begin{aligned} &a_{1+} = 2\left(\tfrac{1+b-c}{2+b-c}\right), a_{1-} = 2\left(\tfrac{1}{2+b-c}\right), a_{2+} = \tfrac{1+b-c}{2+b-c}, a_{2-} = \tfrac{1}{2+b-c}, a_{3+} = \tfrac{1-c}{2-c}, a_{3-} = \tfrac{1+b}{2+2b-c}, \\ &a_{4+} = \tfrac{1+b-c}{2+2b-c}, a_{4-} = \tfrac{1}{2-c}, a_{5+} = \tfrac{1-c}{2-c}, a_{5-} = \tfrac{1+b}{2+2b-c} \end{aligned} \quad . \tag{10}$$

Substituting these into inequality (9) gives

$$\frac{2((b-4)b-(c-2)^2)c}{(4b+(c-2)^2)(2+b-c)} > 0 \;\; . \tag{11}$$

Simplifying, we obtain inequality (1) of the main text. If inequality (1) is satisfied, helpers are expected to increase in number over time if the population is in the local distribution described at the beginning of this section and illustrated in Figures 5.1 and 5.6. That is, at least two patches containing a helper of each species surrounded on each side by a sequence of patches that contain a helper of one of the species but not of the other.

When inequality (1) is satisfied, the probability that a helper replaces a non-helper is greater than vice versa in each species. Therefore, we suggest that the probability that the patches that initially contain a helper of each species continue to do so forever is nonzero as the number of patches with a helper of each species can be described as a random walk bounded at zero where the probability of increase is greater than the probability of decrease. Hence, when inequality (1) is satisfied, we expect the number of helpers to increase without limit over time. If inequality (1) is not satisfied, we expect helpers to eventually be eliminated.

5.7.2 Evolution of Helping: condition for the global frequency of helpers to increase under natural selection

In this section, we first analyse the effect of fresh mutational input at low frequency in the population (*a*). Then, we consider the impact of multiple instances of deceased individuals being replaced by neighbours in the same generation within a local distribution of helpers (*b*). Finally, we study the effect of local distributions of helpers meeting other helpers in the population (*c*).

(a) Further mutational input in the population

Non-helpers randomly mutate to become helpers, and vice versa. We assume that rates of mutation in both directions are sufficiently low that, after one mutation, we can determine the effect of natural selection on helping prior to the occurrence of another mutation. We can ignore non-helpers that mutate to become helpers: they are absorbed by larger distributions of helpers or eliminated by natural selection. Our simulations confirm that these assumptions do not require exceedingly low mutation rates (following section).

However, a local distribution of helpers can be disrupted by a mutation that arises in its midst (illustrated in Figure 5.7). When this happens, there are two sequences of adjacent patches with a helper in each species joined by a single patch with a helper of one species and a non-helper of the other. The non-helpers and her descendants will always share a patch with a helper of the other species, unless her descendants reach the end of the sequence of patches with a helper in both species and join the global population of non-helpers. Therefore, as long as the subpopulation of non-helpers formed by the initial mutation avoids stochastic loss, they replace helpers from within a local distribution (illustrated in Figure 5.7). Mutations are sufficiently rare that we assume local distributions grow beyond a sequence of three adjacent patches with a helper of each species before a mutation occurs. This ensures that mutations must occur at least two patches away from one end of the sequence. A sequence of at least two patches with a helper of each species must remain. Therefore, we can compare the expected rate at which new helpers are added at the far end of that sequence to the expected rate at which they are lost at the end where helpers are

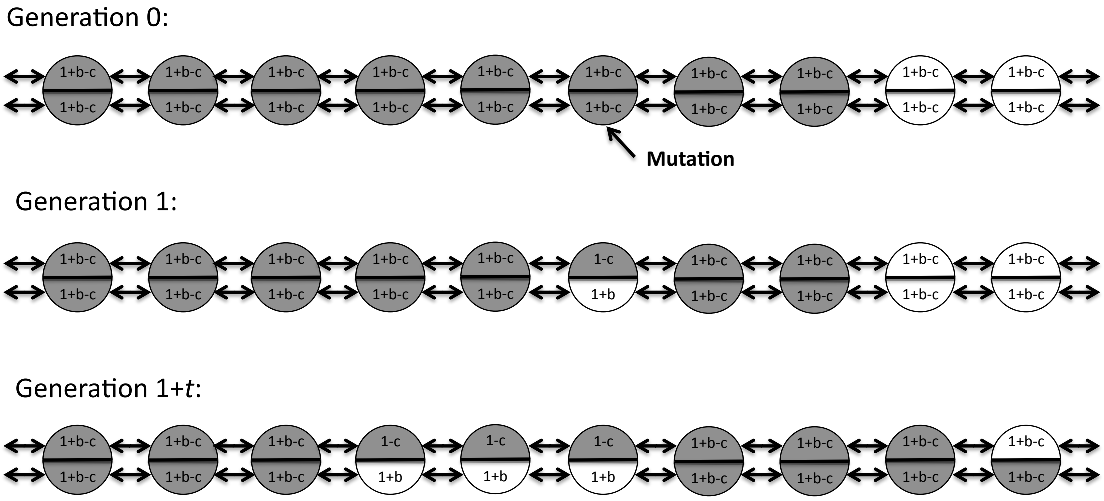


Figure 5.7 | Further mutational input in the population. At the end of generation 0, a mutant non-helper arises within a sequence of patches with a helper of each species. The mutant shares a patch with a helper but does not pay the cost of helping and so has higher fecundity than her neighbours. A subpopulation of non-helpers arises within the sequence of patches with a helper of each species. Subsequently, natural selection only favours helping if the number of helpers at the end of the sequence (right) increases faster than the number of non-helpers, in the species where the mutant has arisen.

replaced by the subpopulation of mutant non-helpers.

The rate at which helpers are lost is the rate at which non-helpers replace helpers subtracted from the rate at which helpers replace non-helpers when each receives the benefit of sharing a patch with a helper of the other species

$$\frac{1+b}{2+2b-c}-\frac{1+b-c}{2+2b-c}=\frac{c}{2+2b-c}\ . \tag{12}$$

The LHS of inequality (11) gives the expected rate at which helpers at the far end of each sequence increase in number. This is equal to twice the rate at which helpers in one species increase in number. We subtract the value in equation (12) from half the LHS of inequality (11) to find whether the rate at which helpers increase at the edge is greater than that at which they are lost in competition with the mutant subpopulation. This recovers inequality (2) from the main text.

(b) Multiple replacement by neighbours in the same generation within a local distribution of helpers

The only instance in which multiple replacement by neighbours matters is when both the last individual carrying one allele and the first carrying the other are replaced by genetically different individuals. The probability that this occurs in a single generation is therefore the probability that both are independently selected and replaced by neighbours. The effect of this double replacement is to create a subpopulation of non-helpers at the end of a sequence of helpers in one species, the effect of which we have already studied. We therefore define the rate at which individuals are selected and replaced by neighbours to be small enough that a double replacement occurs rarely enough that the effect of natural selection can be measured between any double replacements. Therefore, natural selection still favours helping when inequality (2) is satisfied.

(c) Local distributions of helpers encounter others

The evolutionary process is only affected when there are fewer than two patches containing a non-helper of each species separating the two local distributions. If there is only one patch containing a non-helper of each species, then there must be helpers of the same species in the two neighbouring patches. If the non-helper separating the two nearest helpers dies, it is certainly replaced by a helper. This gives rise to a

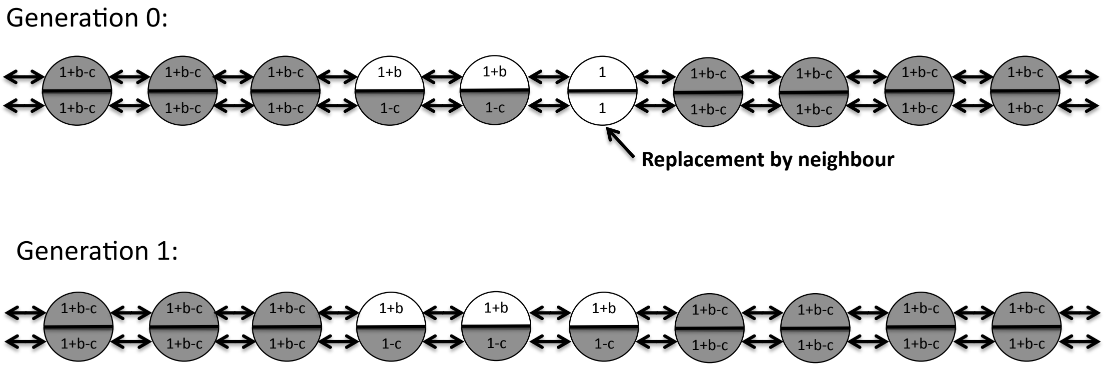


Figure 5.8 | Local distributions of helpers encounter others. This figure illustrates why the junction of two sequences of patches with a helper of each species has the same effect as a mutant arising within a sequence of patches with a helper of each species (see Figure 5.7). A subpopulation of non-helpers forms.

continuous sequence of patches that contain a helper in one species. Therefore, the effect of two local distributions of helpers joining is the same as a non-helping mutant arising in a local distribution of helpers (illustrated in Figure 5.8). We have already shown in section (*a*) that when a subpopulation of non-helpers arises within a local distribution of helpers, natural selection favours helping when inequality (2) is satisfied.

5.7.3 Simulations

(a) The effect of natural selection on helping in large populations

We run a numerical simulation of our model, relaxing the assumptions of infinite time and population size. We consider a ring of 10^6 patches. We initialize the population by randomly assigning each individual the helping allele with probability 0.02 and the non-helping allele with probability 0.98. We run the simulation for a sequence of $2*10^{10}$ replacements where a clone of the previous inhabitant does not replace a deceased individual. For each of these replacements, we select a random individual in the population. The probability that a deceased individual is replaced by a mutant offspring, an offspring of the other genetic type, is $2*10^{-5}$. If there is no mutation, the two conspecific neighbours compete to replace the deceased individual as detailed in our model. We perform five replicates for each set of parameter values displayed in Figure 5.3. We consider the last $2*10^{9}$ replacements for each replicate and count the number of times that helpers in a species have increased in number by more than 100. We assign a darker colour to the dot at parameter values where the number of helpers has increased more often, from white when helpers have never increased by 100 or more to black when this has happened each time.

We notice that at low cost, helpers often increase in frequency when our analytical results suggest that natural selection does not favour them. However, we can see (inequality (11) and equation (12)) that cost is a factor in the rate at which helpers are gained and lost by natural selection. This means that when cost is low, natural selection is very weak, and so we would expect the number of helpers to occasionally increase over this timeframe (grey dots, but not black) even when natural selection does not favour helpers.

(b) Conditions for the expected local frequency of helpers to increase

We use a cycle of 250 patches, a sequence of $2.5*10^{6}$ replacements, and assume that no mutations occur. Here, the population initially consists entirely of non-helpers except for a single patch that contains a helper of each species. We perform 2,000 replicates at each of the parameter values shown in Figure 5.2. Given an initial frequency of 1/250 in each species, we would expect a neutral allele to fix 16 times in the simulations. If there are significantly more than 16 fixations (95% confidence level), we colour the parameter values in Figure 5.2 black. If there are significantly fewer than 16 fixation, we colour the parameter values white. If the result is not significant, we colour the parameter values grey.

5.7.4 Fitness effects and relatedness when both conspecifics and heterospecifics are predictors

The fitness of a focal individual is determined by her own genotype, that of her two direct competitors, and the genotypes of the individuals share patches with each of these three. This yields 32 possible genotype combinations that determine fitness. We calculate the relative frequency of each of these combinations by considering a local distribution of helpers where there are at least five patches with a helper of each species. We use the probability distribution of s, the number of patches with a helper of one species and a non-helper of the other, derived above, to calculate the relative frequency of each genotype combination.

We calculate the fitness coefficients using least-squares regression. To that end, we write the sum of the squared differences between the actual and predicted fitness given the genotypes present, weighted by the frequency of each of the 32 genotypic combinations

$$\sum_{o=1}^{32} q_o(\delta w_o - Cx_{0(o)} + \sum_K B_k x_{k(o)} + \sum_L B_l x_{l(o)})^2 \tag{13}$$

where q_o is the frequency with which each combination occurs and $x_{0(o)}$ is the genic value of the focal individual, $x_{k(o)}$ are the genic values of conspecific predictors, $x_{l(o)}$ are those of heterospecific predictors, and δw_o is the expected deviation from average fitness of a focal individual in that genotypic combination.

We solve for the least-squares regression coefficients C, B_k, and B_l using expression (13). The relatedness terms, r_k and r_l, are the regressions of the genic value of a focal individual against that of its predictors (Gardner et al. 2011). These regressions are calculated from population data, using the long-term probabilities that the population is in particular states (Rousset & Billiard 2000, Taylor et al. 2007b). These probabilities are readily calculated using the q_o values. The regressions do not use a constant. Instead, the intercept is the frequency of the helping allele, assumed rare, in both species. The solutions are too cumbersome to reproduce here (included as a Mathematica Notebook in the Appendix to this thesis), but the inclusive fitness effect of helping is

$$-C + \sum_K B_k r_k + \sum_L B_l r_l \,. \tag{14}$$

We find that expression (14) is positive if and only if inequality (1) is satisfied. We also find that

$$-C + \sum_K B_k r_k < 0 \,. \tag{15}$$

In order for natural selection to favour helping, a local distribution of helpers must be expected to increase in number. Hence, the fitness effects in heterospecifics, $\sum_{L} B_l r_l$, are essential for natural selection to favour helping when heterospecifics are used as predictors of fitness.

6

Reconciling theory on negotiation games

6.1 Abstract

Negotiation games, in which individuals can observe and respond to a social partner's actions, have the potential to enrich evolutionary game theory. They offer a more realistic alternative to simultaneous choice (or 'sealed bid') models in some contexts, having proved useful in understanding interactions between parents who jointly invest in caring for a brood of young. However, a model by Taylor and Day has suggested (by contrast with other analyses of negotiation games) that the negotiation framework will not generally predict unique outcomes, thus severely limiting its use. We show here that this result arises only when individuals do not hold private information about their own intrinsic quality or state, both in symmetric and asymmetric contexts. Analyses that have identified a unique solution, by contrast, have been able to do so because they incorporated such variation. In addition, we demonstrate that linear rules can be generally stable in negotiation games under arbitrary fitness functions, rather than only quadratic functions as previously analysed, so long as individual variation is binary.

6.2 Introduction

When animals interact, they usually have the opportunity to respond to one another's behaviour. Yet most game-theoretical models assume that an animal's 'strategy' specifies a fixed course of action. Strategies may change over evolutionary time, but on a behavioural timescale individual actions remain constant. In economic terms, each player makes a 'sealed bid' that cannot be adjusted in response to the other's actions.

McNamara et al. (1999) addressed this limitation by introducing a novel approach, negotiation games, in which an individual's strategy takes the form of a 'response rule'. This rule specifies how the individual will change its own behaviour in response to that of its social partner. In Taylor and Day's (2004) terminology, the response rule is a reaction norm for behaviour as a function of a social partner's action. Individuals in negotiation games take turns each choosing their own action in response to their opponent's most recent choice, until these choices settle down to a stable pair of endpoints. This pair determines the payoffs that the players obtain. Negotiation games thus focus on the evolution and stability of behavioural reaction norms rather than that of the behaviours themselves.

However, while McNamara et al. (1999, 2003) and other applications of the negotiation approach (Johnstone & Hinde 2006, Johnstone 2011) identified unique evolutionarily stable strategies (ESS; Maynard-Smith & Price 1973), Taylor and Day (2004) have argued that this is not generally possible. They constructed a negotiation model of investment by two players in a common good and showed that this gave rise to a set of infinitely many evolutionary equilbria. If this is a common feature of such games, they are unlikely to generate firm and testable predictions about behaviour, limiting their use in understanding the natural world (Mock & Forbes 1992). The contradiction between the conclusions of Taylor and Day (2004) and of other negotiation models (McNamara et al. 1999, 2003; Johnstone & Hinde 2006; Johnstone 2011) suggests that either some of these analyses are flawed, or that we are missing a key difference between the models.

Here, we show that the existence (or lack) of a unique ESS depends upon whether or not individuals hold private information about their own quality or state. We extend Taylor and Day's (2004) analysis to include variation in quality, as well as allowing for asymmetry between social partners. This allows us to reconcile Taylor and Day's (2004) results with the rest of the literature on negotiation games, which incorporates such variation, by deriving conditions under which we expect multiple equilibria or a unique outcome (McNamara et al. 1999).

6.3 Model and Analyses

Following McNamara et al. (1999), we consider a population of individuals interacting in pairs, in which each individual's investment into cooperation is determined by a negotiation game played with their partner. Specifically, the individuals exchange offers over a series of rounds, where a focal individual i's offer $x_{i,t}$ in round t is a linear function of two variables: (i) its partner j's offer $x_{j,t-1}$ in the previous round; and (ii) its own quality q_i, which is unknown to its partner. The parameters of this linear function define its evolved negotiation strategy, and are: (i) a baseline offer ρ_i; (ii) responsiveness μ_i to its own quality; and (iii) responsiveness λ_{i,q_i} to its partner's previous offer given own quality. This allows both the responsiveness and the baseline offer (through μ_i), the two parameters that define investment, to vary with a focal individual's quality. Hence, we write:

$$x_{i,t} = \rho_i - \lambda_{i,q_i} x_{j,t-1} + \mu_i q_i \, . \qquad (1)$$

We assume that $|\lambda_{i,q_i}| < 1$ (McNamara et al. 1999, Taylor & Day 2004), so that an individual's offers converge to a limiting value x_i ($x_{i,t} \rightarrow x_i$ as $t \rightarrow \infty$), which is independent of initial offers and is the individual's realised investment in cooperation. Consequently, the investment in cooperation made by the focal individual satisfies the simultaneous equations $x_i = \rho_i - \lambda_{i,q_i} x_j + \mu_i q_i$ and $x_j = \rho_j - \lambda_{j,q_j} x_i + \mu_j q_j$, which we solve to yield:

$$x_i = \frac{\rho_i + \mu_i q_i - \lambda_{i,q_i} \rho_j - \lambda_{i,q_i} \mu_j q_j}{1 - \lambda_{i,q_i} \lambda_{i,q_j}} \, . \qquad (2)$$

Due to the symmetry of the negotiation process, the investment into cooperation by the focal individual's partner is obtained from equation (2) by swapping indices *i* for *j* and vice versa.

Natural selection favours those negotiation strategies $(\rho_i, \lambda_{i,q_i}, \mu_i)$ that maximise the individual's expected fitness (Grafen 1999, 2000). We assume that the focal individual's fitness function has three arguments: (i) its own investment x_i into cooperation; (ii) its partner's investment x_j into cooperation; and (iii) its own quality

q_i, a given value chosen from a probability distribution. Thus, we can express the fitness function either as $W_i(x_i, x_j, q_i)$ or $w_i(\rho_i, \lambda_{i,q_i}, \mu_i, q_i, \rho_j, \lambda_{j,q_j}, \mu_j, q_j)$ (equation (2)), where expected fitness averaged across the possible values of focal individual and social partner quality is $\bar{w}_i$. We assume that investment into cooperation by either individual leads to diminishing returns but accelerating costs.

Initially, we assume that there are only two possible qualities, denoted low and high, so that $q_1, q_2 \in \{q_{\text{low}}, q_{\text{high}}\}$. Each player is independently assigned low quality with probability $p_{q_{low}}$ $(0 < p_{q_{low}} < 1)$ and high quality with probability $p_{q_{high}}$ (= 1– $p_{q_{low}}$). We also suppose that the fitness function of both players is identical, such that we can interchange the indices *i* and *j*. Thus, without loss of generality, we consider the evolution of strategies from the perspective of player *i* only. Its strategy is specified by a set of four numbers, $(\rho_i, \lambda_{i,q_{low}}, \lambda_{i,q_{high}}, \mu_i)$. This player's expected payoff is

$$\bar{w}_i\left(\rho_i,\lambda_{i,q_{low}},\lambda_{i,q_{high}},\mu_i,\rho_j,\lambda_{j,q_{low}},\lambda_{j,q_{high}},\mu_j\right)=\sum_{q_i,q_j\in\{q_{low},q_{high}\}} p_{q_i}p_{q_j}W_i\left(x_{i,\{q_i,q_j\}},x_{j,\{q_i,q_j\}},q_i\right) \qquad (3)$$

where $x_{i,\{q_i,q_j\}}$ and $x_{j,\{q_i,q_j\}}$ denote the final negotiated levels of investment by both individuals given quality pair $\{q_i,q_j\}$.

In standard notation, we denote the marginal effect of individual *i*'s contribution on its own fitness, $\partial W_i/\partial x_i$, as $C_{\{q_1,q_2\}}$, and the marginal effect of individual *j*'s contribution on individual *i*'s fitness, $\partial W_i/\partial x_j$, as $B_{\{q_1,q_2\}}$ (Hamilton 1964, Queller 1992, Gardner et al. 2011). Using Leibniz's rule, in this case simply the method for differentiating inside an expectation, the equilibrium values of each evolving variable can then be written as

$$\begin{aligned}
\frac{\mathrm{d}\bar{w}_i}{\mathrm{d}\rho_i} &= E\left[\frac{\partial W_i}{\partial x_i}\frac{\partial x_i}{\partial \rho_i}+\frac{\partial W_i}{\partial x_j}\frac{\partial x_j}{\partial \rho_i}\right]=\sum_{q_i,q_j\in\{q_{low},q_{high}\}} p_{q_i}p_{q_j}\frac{1}{1-\lambda_{i,q_i}\lambda_{j,q_j}}\left[C_{\{q_i,q_j\}}-\lambda_{j,q_j}B_{\{q_i,q_j\}}\right]=0\\
\frac{\mathrm{d}\bar{w}_i}{\mathrm{d}\lambda_{i,q_{low}}} &= E\left[\frac{\partial W_i}{\partial x_i}\frac{\partial x_i}{\partial \lambda_{i,q_{low}}}+\frac{\partial W_i}{\partial x_j}\frac{\partial x_j}{\partial \lambda_{i,q_{low}}}\right]=\sum_{q_j\in\{q_{low},q_{high}\}} p_{q_j}\frac{-x_{i,\{q_{low},q_j\}}}{1-\lambda_{i,q_i}\lambda_{j,q_j}}\left[C_{\{q_i,q_j\}}-\lambda_{j,q_j}B_{\{q_i,q_j\}}\right]=0\\
\frac{\mathrm{d}\bar{w}_i}{\mathrm{d}\lambda_{i,q_{high}}} &= E\left[\frac{\partial W_i}{\partial x_i}\frac{\partial x_i}{\partial \lambda_{i,q_{high}}}+\frac{\partial W_i}{\partial x_j}\frac{\partial x_j}{\partial \lambda_{i,q_{high}}}\right]=\sum_{q_j\in\{q_{low},q_{high}\}} p_{q_j}\frac{-x_{i,\{q_{high},q_j\}}}{1-\lambda_{i,q_i}\lambda_{j,q_j}}\left[C_{\{q_i,q_j\}}-\lambda_{j,q_j}B_{\{q_i,q_j\}}\right]=0\\
\frac{\mathrm{d}\bar{w}_i}{\mathrm{d}\mu_i} &= E\left[\frac{\partial W_i}{\partial x_i}\frac{\partial x_i}{\partial \mu_i}+\frac{\partial W_i}{\partial x_j}\frac{\partial x_j}{\partial \mu_i}\right]=\sum_{q_i,q_j\in\{q_{low},q_{high}\}} p_{q_i}p_{q_j}\frac{q_i}{1-\lambda_{i,q_i}\lambda_{j,q_j}}\left[C_{\{q_i,q_j\}}-\lambda_{j,q_j}B_{\{q_i,q_j\}}\right]=0
\end{aligned} \quad . \quad (4)$$

In general, the conditions in equations (4) can be jointly satisfied if and only if $C_{\{q_i,q_j\}} - \lambda_{j,q_j}B_{\{q_i,q_j\}} = 0$ for all four quality combinations. Only one contribution $x_{i,\{q_i,q_j\}}$ satisfies $C_{\{q_i,q_j\}} - \lambda_{j,q_j}B_{\{q_i,q_j\}} = 0$ for a given quality combination and this contribution maximises fitness, because of the always diminishing returns and accelerating costs of investment into cooperation. When the four equations are satisfied, individual *i* achieves its maximum fitness given the quality and strategy of its partner in every possible quality combination. At equilibrium, each individual adopts the same strategy, so we drop the subscripts for the evolving parameters. This yields four equations for the two players.

> **Result 1** – The four quality-dependent fitness maximising conditions specify a unique coevolved ESS for the four parameters of the response rules $(\rho, \lambda_{q_{low}}, \lambda_{q_{high}}, \mu)$.

At the coevolved ESS, each individual is doing the best it can do against each possible opponent. There are four possible quality combinations for the interacting pair and four parameters that natural selection can act on, so the individual can achieve the best possible outcome irrespective of what rule its social partner adopts. Now, suppose that we assume no variation in quality. This means that $q_i = q_j = k$, a constant, so the conditions in equations (4) are all the same ($C_{\{k,k\}} - \lambda_{j,k} B_{\{k,k\}} = 0$). This one equation is insufficient to specify a unique solution for the parameters that define the response rule (ρ, λ_{q_k}, μ). As k is a constant, we can re-write $\rho + \mu k = \rho'$, but the single equation remains insufficient to specify a unique solution for the remaining two parameters (ρ', λ_{q_k}), as in Taylor and Day's (2004) model (Wilson 2007).

> **Result 2** – When there are no quality differences, there is a single fitness maximising outcome for *i*, given *j*'s response rule. However, there exist infinitely many rules that *i* could adopt leading to this same endpoint.

We note that this analysis extends to responsiveness to other factors or to an asymmetric game, for example an interaction between males and females or a mutualism (Johnstone & Hinde 2006, Johnstone 2011). In the former case, we simply add parameters to the response rule. In the latter case, an individual in role *i* is paired with one in role *j* and they can have different fitness functions and response rules depending on their role.

In general, a unique best response rule rests on our assumption that individuals are unable to ascertain and respond to the quality of their social partners. If they could,

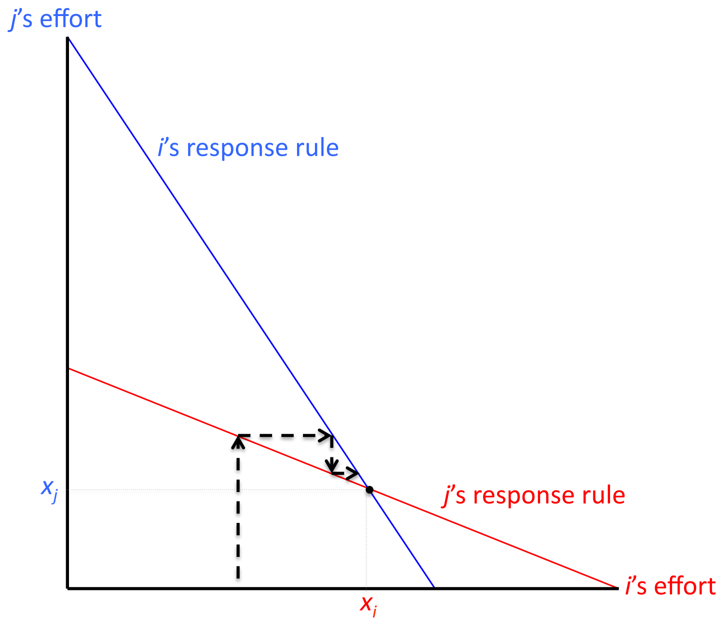


Figure 6.1 | The negotiation process given a combination of individual qualities. Both individuals adopt linear response rules. *i*'s rule uses *j*'s effort to determine its own effort. Then, *j*'s rules uses *i's* effort to determine its response. The dashed arrows show the course of negotiation, leading to the negotiated outcome at the point of intersection between the lines corresponding to the two players' response rules. At this outcome, the negotiated levels of effort are given by x_i and x_j.

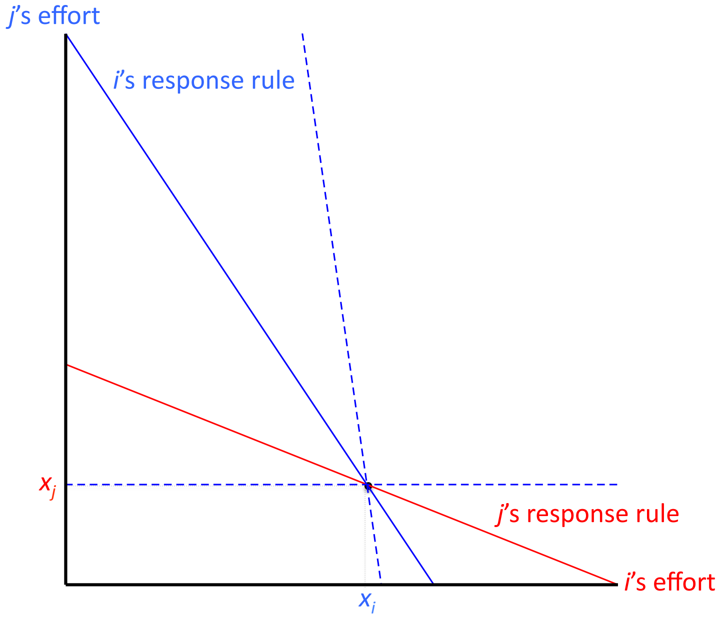


Figure 6.2 | Response rules that yield the same negotiated outcome. Without quality variation, there are infinitely many response rules that *i* might adopt that intersect *j*'s response rule at the same point, and thus yield the same outcome of negotiation. Alternative rules yielding the same outcome as the rule illustrated in Figure 1 are shown by dashed blue lines.

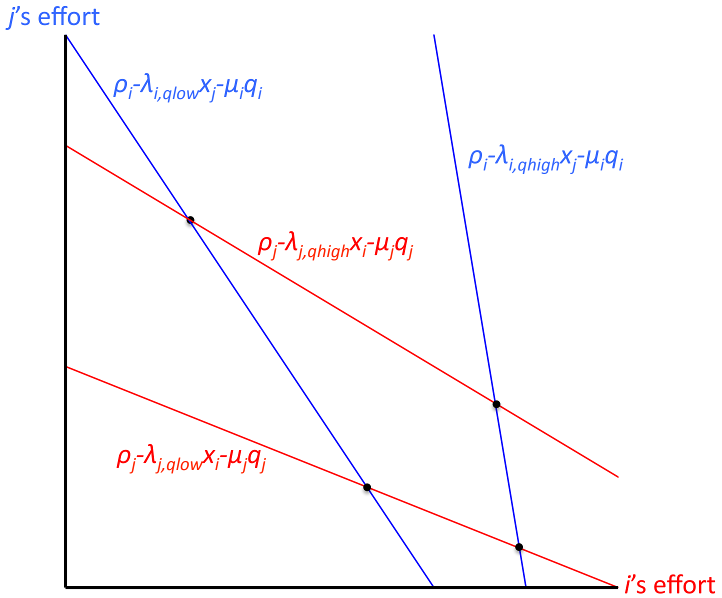


Figure 6.3 | Unique response rule is optimal with variation in quality. With two possible qualities for each individual, and thus four possible quality combinations for the pair, there are four 'optimal outcomes' for *i* given *j*'s response rule. Only one quality-dependent response rule leads to precisely these outcomes in every case.

they would be able to adopt different response rules for each quality combination. As for Result 2, infinitely many rules would yield the same endpoint of negotiation.

Figures 6.1, 6.2, and 6.3 illustrate why the negotiation model yields a unique solution if an individual has private information on its own quality. Graphically, the outcome of negotiation can be obtained by looking for the intersection between the two players' response rules (Figure 6.1), as this is equivalent to solving the two simultaneous equations that define the response rules. Since many different response rules that *i* could adopt all intersect *j*'s rule at the same point (Figure 6.2), there are many possible strategies *i* can adopt that yield the same unique fitness-maximising endpoint to the negotiation process. By contrast, with two possible qualities for each player, and thus four possible quality combinations for the pair, there are four fitness-maximising endpoints for *i* (given *j*'s response rule). There is only one quality-dependent response rule that leads to precisely these outcomes in every case (Figure 6.3).

6.3.1 An example

To illustrate, suppose that

$$W_i\left(x_i, x_j, q_i\right) = 4\left(x_i + x_j\right) - 2\left(x_i + x_j\right)^2 - \left(1 - q_i\right)x_i - 2x_i^2 \tag{6}$$

with q_i taking values $q_{\text{low}} = 0$ or $q_{\text{high}} = 1$. The first two terms in equation (6) represent the benefit of joint investment, with positive but diminishing returns for $x_i + x_j < 1$; the second two terms represent the accelerating cost of individual investment, with greater marginal cost for individuals of lower quality. In the Appendix we solve for the unique equilibrium of this game

$$\begin{aligned} \rho &= \frac{13 - 5\sqrt{5}}{8} \approx 0.227, \\ \lambda_0 = \lambda_1 &= \frac{3 - \sqrt{5}}{2} \approx 0.382, \\ \mu &= \frac{\sqrt{5} - 1}{8} \approx 0.155 \end{aligned} \quad . \tag{7}$$

6.3.2 Many possible qualities

When there are two possible qualities, and so four possible quality combinations for the pair of individuals, we have seen that the negotiation model yields four ‘optimal outcomes’ for *i* (given *j*’s response rule), which specify a unique optimal response rule. If there are $n>2$ possible quality values, then there are n^2 possible quality combinations and thus n^2 equations to satisfy. However, there will only be $n+2$ variables that define individuals i's strategy $(\rho_i, \lambda_{i,q_1}, \dots, \lambda_{i,q_n}, \mu_i)$. Hence, the optimal response rule for one individual, given the other's rule, is *overdetermined*. That is, there are more equations to be satisfied than there are response parameters. Consequently, there may be no linear response rule that ensures the optimum outcome in every case.

> **Result 3** – When there are more than two possible levels of quality, the optimal outcome for every case is only achieved if all optimal outcomes for each value of social partner quality lie on a straight line (Figure 6.4). Otherwise, any linear rule will deviate from the optimal outcome in at least one case (Figure 6.5).

When there are many possible qualities, or indeed continuous variation in quality, we might wish to allow for non-linear response rules. However, the model would then become intractable; at least, we are unable to solve for stable pairs of non-linear rules. McNamara et al. (1999, 2003), Johnstone and Hinde (2006) and Johnstone (2011) instead opted to restrict their choice of fitness function to simple quadratic forms:

$$W(x_i, x_j, q_i) = k_1 x_i^2 + k_2 x_j^2 + k_3 q_i^2 + k_4 x_i x_j + k_5 x_i q_i + k_6 x_j q_i + k_7 x_i + k_8 x_j + k_9 q_i + k_{10}\,. \qquad (8)$$

The individual's fitness maximising response rule (x_i such that $\partial W / \partial x_i = 0$) is thus

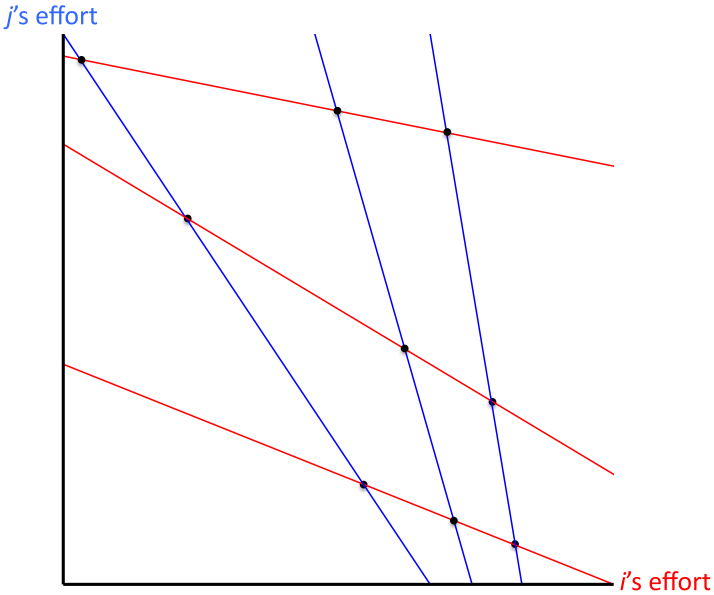


Figure 6.4 | Linear rule is optimal with three or more qualities when optimal outcomes lie on a straight line. At each level of *j*'s quality, so long as the three optimal outcomes for *i* given its own quality lie on a straight line, *i* has a unique linear quality-dependent response rule that achieves the optimal outcome in each case.

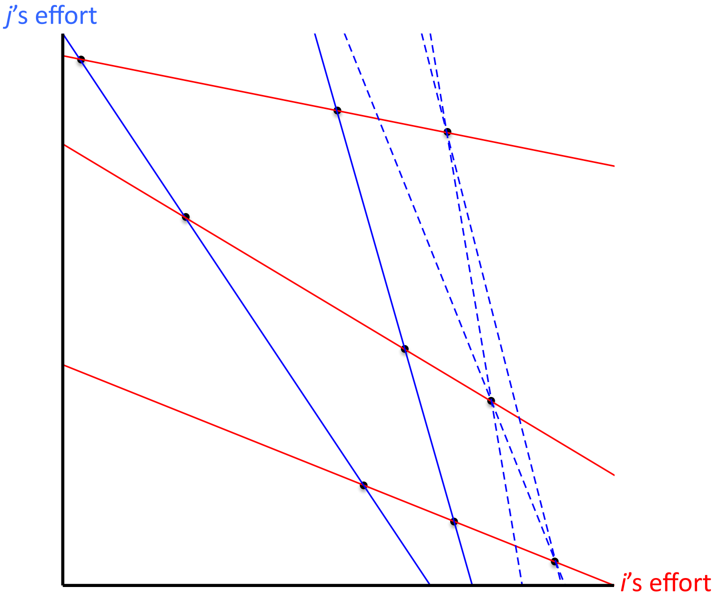


Figure 6.5 | No linear rule is optimal with three or more qualities when optimal outcomes do not lie on a straight line. If at any level of *j*'s quality, the three optimal outcomes for *i* given its own quality do not lie on a straight line, *i* cannot have a linear response rule that achieves the optimal outcome in each case. All rules will be suboptimal given at least one quality combination.

$$x_i = -\frac{k_7 + k_8\lambda_{2,q_2}}{2k_1 + k_4\lambda_{2,q_2}} - x_2\frac{k_4 + 2k_2\lambda_{2,q_2}}{2k_1 + k_4\lambda_{2,q_2}} - q_1\frac{k_5 + k_6\lambda_{2,q_2}}{2k_1 + k_4\lambda_{2,q_2}} . \qquad (9)$$

> **Result 4** – For a quadratic fitness function, the fitness maximising response of *i* varies linearly with its partner's choice of action and its slope is independent of the focal individual's quality.

Under these circumstances, we can derive stable pairs of linear response rules that are strict best responses to one another, even with continuous variation in quality (although it remains possible that there might exist alternative equilibria featuring non-linear rules).

6.4 Discussion

We have shown that the analyses of McNamara et al. (1999), Houston et al. (2005), Johnstone and Hinde (2006), Johnstone (2011) and Taylor and Day (2004) are all correct, even though their results appear contradictory. A unique ESS exists whenever private information over variation in individual quality or state is incorporated in the model. Therefore, as long as individuals hold this information, negotiation games will yield a firm prediction on the strategies eventually adopted by all members of the population. When there is no variation in quality or state, by contrast, negotiation games predict a continuum of fitness-maximising response rules. This result arises because natural selection is blind to the combination of evolved strategic variables that gives rise to an outcome of negotiation. Intuitively, infinitely many strategies can yield any given negotiation outcome, but only one strategy can yield a precise set of negotiation outcomes where each corresponds to a particular quality combination.

From a theoretical perspective, our work unifies previous results on negotiation games. In addition, we demonstrate that, so long as individual variation in quality or state is binary, linear response rules are always stable even when fitness functions are not quadratic. These results suggest that the negotiation approach is likely to both be applicable to many social interactions and yield testable predictions. Furthermore, negotiation games model extended interactions as a sequence of actions and responses, a pattern that can easily evolve (Cant & Shen 2006, Johnstone et al. 2014), rather than the stylized sequence of simultaneous un-modifiable moves more typical of classical game theory (Axelrod & Hamilton 1981). The negotiation framework appears to more closely capture reality, and thus may enrich our understanding of evolutionary games (McNamara 2013). However, the value of negotiation relies on the assumption that individuals hold private information that their partners can infer through the negotiation process (Wilson 2007). An individual with perfect information can just set their initial contribution at the endpoint of the negotiation process. Overall, we can only speculate on how generally valid the assumption of private information is. Information over quality may remain private because costly signaling does not allow individuals to advertise it honestly as it is the lowest quality individuals that benefit most from signalling, which means that any signal is vulnerable to cheating (Grafen 1990). On the other hand, at the model's ESS an individual's quality can be worked out from its first move. An individual whose strategy incorporated this information could do just as well with infinitely many alternative strategies to the ESS. Johnstone and Hinde (2006) suggested that individuals could also hold private information over offspring need, rather than just quality. Private information over two variables could make it difficult to infer what they are from a first move, thus maintaining the value of the negotiation process.

Despite uncertainty over the settings in which they are applicable, negotiation games have already contributed to our understanding of extended interactions by adding the evolution of rules that compensate for a social partner's lack of investment to the paradigm that extended interactions lead to positive reciprocity (Trivers 1971, McNamara et al. 1999, Wilson 2007), although this is no longer the exclusive explanation for cooperation amongst unrelated individuals (Clutton-Brock 2009). The prediction of compensation is very different to that of positive reciprocity, and whilst further analysis is required, it provides some basis to suggest that a large number of iterated one-shot interactions may not be equivalent to a single extended interaction. The qualitative difference between discrete and continuous action has already proved important elsewhere, notably in the costly signaling literature (Grafen 1990). There, allowing discontinuous signal levels means that an infinite number of solutions are possible (Bergstrom & Lachmann 1997, 1998; Lachmann & Bergstrom 1998, Godfray & Johnstone 2000). In negotiation games, however, the more general model that considers individual variation predicts a single ESS, thus making predictions arising from the theory easily amenable to empirical testing. However, although the distinction between continuous and discrete interactions may prove important, there are other key differences between the negotiation framework and other modelling approaches that have predicted positive reciprocity (based on Trivers' (1971) theory). For example, the strict alternation in responses and the reliance on only the partner's most recent offer (and not on the complete offer history) may prove important in explaining the results. More theoretical work is required to understand exactly which factors favour positive (or negative) reciprocity.

Historically, empirical work on negotiation games has focused on the interaction between parents (and helpers) who invest in care of a joint brood of young. This approach is particularly useful in this context, because much attention has been devoted to the way in which parents respond to changes in one another's efforts to care for young (Kosztolanyi et al. 2008, Schwagmeyer et al. 2009, Wiebe 2009), and negotiation models explain some of the variation in responses that has been revealed (McNamara et al. 2003; Johnstone & Hinde 2006; Johnstone 2011). However, many empirical results still require theoretical grounding. Large variability in partner responsiveness is often observed ranging from full compensation, through no responsiveness, to matching (Hinde 2006, Harrison et al. 2009). This spectrum of responses is not fully explained by information about costs or benefits transmitted through cooperative behaviour (Johnstone & Hinde 2006, Meade et al. 2011), leaving fertile ground for further research on negotiation games.

6.5 Appendix

Substituting into equations (4) the payoff function specified in (5), we obtain

$$4\left(1-\lambda_{j,q_j}\right)\left(1-x_i-\left(\rho_j-\lambda_{j,q_j}x_i+\mu_j q_j\right)\right)-\left(1-q_i\right)-4x_i=0 \tag{10}$$

for all $q_i, q_j \in \{q_{low}, q_{high}\}$. We can solve equation (10) for i's optimal contribution, given j's response rule:

$$x_i = \frac{\left(1-\lambda_{j,q_j}\right)\left(1-\rho_j-\mu_j q_j\right)-\tfrac{1}{4}\left(1-q_i\right)}{1+\left(1-\lambda_{j,q_j}\right)^2} \tag{11}$$

for all $q_i, q_j \in \{q_{low}, q_{high}\}$. Now, we use the expression for x_i derived in equation (2) and plug it into equation (11). We then write it out explicitly as four different equations (one for each possible combination of player qualities, remembering that in this illustrative case $q_1, q_2 \in \{0,1\}$):

$$\begin{aligned}
\frac{\rho_i-\lambda_{i,0}\rho_j}{1-\lambda_{i,0}\lambda_{j,0}} &= \frac{\left(1-\lambda_{j,0}\right)\left(1-\rho_j\right)-\tfrac{1}{4}}{1+\left(1-\lambda_{j,0}\right)^2} \\
\frac{\rho_i-\lambda_{i,0}(\rho_j+\mu_j)}{1-\lambda_{i,0}\lambda_{j,1}} &= \frac{\left(1-\lambda_{j,1}\right)\left(1-\rho_j-\mu_j\right)-\tfrac{1}{4}}{1+\left(1-\lambda_{j,1}\right)^2} \\
\frac{\rho_i+\mu_i-\lambda_{i,0}\rho_j}{1-\lambda_{i,1}\lambda_{j,0}} &= \frac{\left(1-\lambda_{j,0}\right)\left(1-\rho_j\right)-\tfrac{1}{4}}{1+\left(1-\lambda_{j,0}\right)^2} \\
\frac{\rho_i+\mu_i-\lambda_{i,1}(\rho_j+\mu_j)}{1-\lambda_{i,1}\lambda_{j,1}} &= \frac{\left(1-\lambda_{j,1}\right)\left(1-\rho_j-\mu_j\right)-\tfrac{1}{4}}{1+\left(1-\lambda_{j,1}\right)^2}
\end{aligned} \quad . \tag{12}$$

These four equations can then be simultaneously solved to obtain explicit expressions for the evolved variables in i's optimal response rule $(\rho_i, \lambda_{i,0}, \lambda_{i,1}, \mu_i)$. This leads to the optimal outcome of negotiation for any combination of player qualities, j's rule. In a similar way, we can derive expressions for the parameters of j's optimal response rule given i's rule. The solution that satisfies both sets of equations yields an evolutionarily stable pair of response rules, each of which is optimal given the other.

Here, we can adopt a simpler procedure. Since the game in our illustrative case is symmetrical and players are thus labelled arbitrarily, i's optimal evolved variables must be the same as j's, so that $\rho_i = \rho_j = \rho$, $\lambda_{i,0} = \lambda_{j,0} = \lambda_0$, $\lambda_{i,1} = \lambda_{j,1} = \lambda_1$ and $\mu_i = \mu_j = \mu$ at the ESS. The optimality conditions for both players reduce to the same set of four equations:

$$\begin{aligned}
\frac{\rho-\lambda_0\rho}{1-\lambda_0^2} &= \frac{(1-\lambda_0)(1-\rho)-\frac{1}{4}}{1+(1-\lambda_0)^2} \\
\frac{\rho-\lambda_0(\rho+\mu)}{1-\lambda_0\lambda_1} &= \frac{(1-\lambda_1)(1-\rho-\mu)-\frac{1}{4}}{1+(1-\lambda_1)^2} \\
\frac{\rho+\mu-\lambda_1\rho}{1-\lambda_1\lambda_0} &= \frac{(1-\lambda_0)(1-\rho)}{1+(1-\lambda_0)^2} \\
\frac{\rho+\mu-\lambda_1(\rho+\mu)}{1-\lambda_1\lambda_1} &= \frac{(1-\lambda_1)(1-\rho-\mu)}{1+(1-\lambda_1)^2}
\end{aligned} \quad . \tag{13}$$

These yield the solution

$$\begin{aligned}
\rho &= \frac{13-5\sqrt{5}}{8} \approx 0.227, \\
\lambda_0 = \lambda_1 &= \frac{3-\sqrt{5}}{2} \approx 0.382, \\
\mu &= \frac{\sqrt{5}-1}{8} \approx 0.155
\end{aligned} \quad . \tag{14}$$

7

Discussion

7.1 Chapter Summaries

7.1.1 Chapter 2

In Chapter 2, I developed a market model for the cooperative exchange of two resources between two species. I derived the model from a biological perspective using current knowledge of the plant-mycorrhizal symbiosis, but the model is based on previous work on trade under comparative advantage in the economic literature (Ricardo 1817, Cordella & Gabszewicz 1997, Schwartz & Hoeksema 1998).

A major obstacle in developing this model was that, whilst in many economic contexts there is a central marketplace - ensuring that all individuals pay the same price for the same goods - the same may not hold in biology. Instead, individuals engage in pairwise transactions. I therefore explored possible strategies for rewarding different partners and found the conditions under which individuals are favoured to offer the same price to all of their partners, which I named linear proportional discrimination. In my model, I demonstrated that the conditions under which individuals can be favoured to use linear proportional discrimination are likely often satisfied. This is because individuals can be favoured to use linear proportional discrimination when the quantity of resources offered for trade by different individuals follows an ideal free distribution (Kacelnik et al. 1992). This result, taken together with the positive trade flows found in my model, help validate the theoretical use of a biological market analogy based on price discrimination. However, the applicability of price discrimination mechanisms outside of the plant-mycorrhizal symbiosis remains uncertain. For example, further empirical and theoretical research is needed to determine whether microbes can easily evolve and maintain partner choice based on benefits provided (Werner et al. 2014).

I also derived results relating to biological markets that incorporate multiple partners, but do not make the simplifying assumption that their numbers are infinite. In particular, I showed that increasing the number of partners makes trade more likely and that there is a bi-directional link driving increasing specialisation and trade. These results allowed me to draw conclusions about the impact of changing ecological conditions on mutualistic partners. I found significant threshold effects on plant growth that may have implications for agricultural productivity. For this reason, it would be useful for future empirical work to test this model.

7.1.2 Chapter 3

In Chapter 3, I modified the market model from Chapter 2. I tested a hypothesis based on recent evidence that mutualists may restrict their partners' access to resources in order to make them more dependent on trade, and I asked whether the mutualists would bear costs in order to do so (Li et al. 2008, Heil et al. 2014). I used mechanisms specific to the plant-mycorrhizal symbiosis, but the general principle is widely applicable. I found that this was indeed theoretically plausible, so long as the restriction is sufficiently cost-effective and that few enough mutualists are involved in the restriction. This is because restriction is a type of public good whose benefits are shared by all restricting individuals. In addition, I discovered that restrictive behaviour actually increases the ecological conditions under which mutualistic trade occurs by making the restricted partner more dependent on this trade. Finally, I showed that restriction could even make both partners better off because it makes plants more reliant on cooperation and therefore prevents them from selfishly using bargaining power. This demonstrates that restriction could be an important stabilising factor in mutualisms and research into mechanisms by which restriction can be achieved could yield exciting new results.

7.1.3 Chapter 4

In Chapter 4, I again modified the market model from Chapter 2. In this case, I sought to resolve certain key differences in predictions between research on market mechanisms and other approaches to understanding the maintenance of mutualistic cooperation. In particular, theory of mutualisms suggests that cooperation increases when an individual's mutualistic partners are more related (Frank 1996), whereas my previous work predicted that cooperation increases as the number of genotypes increases (i.e. as relatedness decreases). I demonstrated that in a biological market model that incorporates relatedness, mutualistic exchange sometimes increase and sometimes decreases as relatedness increases. My prediction differs from previous work on biological markets based on comparative advantage because, in that work, mutualistic trade is a zero sum game (Schwartz & Hoeksema 1998, Grman et al. 2012). In other words, if one individual acquires more of a resource through trade, then another individual will have less of that resource. Therefore, more related mutualists cooperate to better exploit their partner. Instead, I incorporated the ability for mycorrhizal fungi to increase the carbon acquisition potential of their plants partners, which enables fungi to increase total resources available in the mutualistic system through their cooperativeness. This removes the zero sum feature of the mutualism and thus provides a much more complete view of the role of relatedness in symbioses. Crucially, I found that sometimes a greater number of competitors lead to greater cooperativeness, but sometimes the ability to coordinate amongst relatives leads to greater cooperativeness. My explanation of the factors mediating the effects of relatedness fills a conceptual gap and allows a more complete understanding of the maintenance of cooperation in mutualisms.

7.1.4 Chapter 5

In Chapter 5, I considered a completely different route to the evolution of mutualisms from those examined in Chapters 2, 3 and 4. Instead of a mutualism based on reciprocity and competition, I asked whether an indiscriminate costly trait that gave fecundity benefits exclusively to members of another species could be favoured by natural selection. Frank (1994) had suggested that this might be possible, but did not provide an explicit model. Using a population genetic model and simulations, I demonstrated that such an indiscriminate costly trait could indeed be favoured. This is because the helping trait is evolving in both species, helping individuals in one species are likely to be born near helping individuals in another species, and social interactions occur over different a spatial scale than competition (Grafen & Archetti 2008). Then, I asked whether this trait could be classified as true altruism between species. I found that an interpretation as altruism between species is possible, so long as individuals of the other species are treated as agents when considering the evolution of the trait in a focal species. On the other hand, if individuals from the other species are treated as mere instruments by which help is transmitted to members of the focal species in future generations, then the trait is simply altruism between conspecifics. As the development of formal notions of agency is still underway, I could not judge whether one interpretation is more correct (Grafen 2002, 2006a,b).

7.1.5 Chapter 6

In Chapter 6, I considered a more sophisticated approach to studying pairwise interactions than a simple one-shot game where the level of cooperativeness is genetically determined and cannot subsequently be modified (Houston & Davies 1985). This is the negotiation framework where individuals respond to each other's observable behaviour in a series of offers and counter-offers until a stable level of cooperative effort is reached (McNamara et al. 1999). Whilst Chapters 3 and 4 allow mycorrhizal fungi to respond to plant cooperativeness, the negotiation approach allows two-sided responsiveness and thus may enrich our understanding of evolutionary games (McNamara 2013).

However, a similar approach by Taylor and Day (2004) suggested that in general the negotiation framework does not predict a unique evolutionarily stable strategy. This would mean that the framework cannot generate firm predictions about behaviour and is therefore unlikely to generate testable hypotheses about the natural world. I demonstrated that whenever private information is available to individuals, for example knowledge over their own ability to contribute to a shared benefit, negotiations lead to a unique equilibrium outcome. This demonstrates that negotiation games yield firm, and thus testable, predictions on cooperative interactions.

7.2 General Themes

7.2.1 Mutualisms cannot be understood without a coevolutionary perspective

All of the models I presented are coevolutionary, meaning that they consider the evolutionary changes at multiple loci in response to changes at others (Janzen 1980). Coevolutionary models present fundamental challenges to modellers because the maximand of natural selection is a moving target (Van Valen 1973, Kauffman & Johnsen 1991). Nonetheless, they are essential in studying interactions between species because partner species will respond to new challenges and opportunities offered by evolutionary changes in an interacting species (Anderson & May 1982, Brundrett 2002). Cases where there is no such response are likely to be the exception, and these cases also require coevolutionary modelling to explain the special circumstances that lead individuals to evolve independently of the strategy adopted by members of an interacting species. The only likely exception to this is a situation in which evolution occurs far more slowly in one species than in the other. For example, multicellular hosts reproduce far more slowly than bacterial pathogens, so their immune systems can be taken as fixed when studying the evolution of the bacteria (Chastain et al. 2012). In a mutualistic context, the evolution of strategies rhizobia might be well predicted by assuming that the strategies of plants are fixed due to the faster life cycle of rhizobia. On the other hand, the symbiosis between plants and mycorrhizal fungi most likely needs to be considered in a co-evolutionary context because evolution probably occurs on the same timescales in both types of organism, although there is insufficient empirical evidence to assess this with certainty.

My work shows that coevolutionary processes can cause mutualists to become genetic engineers. Traits can be favoured by natural selection due to effects they have on the genetic composition of the other species (Schluter & Foster 2012). In Chapter 5, a helper's descendants receive more help than average because they are disproportionately likely to share patches with helpers of the other species. Mutualists need not only respond to evolution in the other species - they can actually cause and exploit it (Odling-Smee et al. 1996, Bäckhed et al. 2005). This process may be important in the development of mutualisms, but it requires a special set of circumstances. In my models of the mycorrhizal symbiosis and negotiation games, I assumed that an individual's strategy does not influence its, or its descendants', set of partners. This means that this individual cannot benefit disproportionately from an investment in modifying the gene pool of their mutualistic partners.

My work also highlights the fact that the effects of coevolution are not immediate (Frank 1996). Natural selection can eliminate a trait that will be beneficial, due to coevolution in the other species, long before an evolutionary response occurs. This is most clearly demonstrated by the result in Chapter 2, that no trade is evolutionarily stable except when the fitness of all members of one species is zero without trade. An individual that unilaterally starts trading will receive no return benefits. This raises questions over the origin of mutualisms. Some authors suggest that they might start as parasitic or commensal relationships and only later become mutualistic (Frank 1995, Law & Dieckmann 1998). However, it is not clear why the species that does not benefit initially would evolve adaptations to give further benefits to the exploiting species if it does not benefit from them immediately. Further research is warranted on the origin of mutualisms based on coevolution (Boyd & Richerson 1988). One avenue suggested by my work in Chapter 5 is that although more helpful individuals may not be associated initially, and may actually be selected against, natural selection on the helping trait may eventually lead to intergenerational associations between helping individuals. This mechanism leads to cooperator association, genetic correlations between individuals in two distinct species that are known to allow the evolution of mutualisms (Foster & Wenseleers 2006). These associations mean that mutualists can actually bear fitness costs and wait for future benefits to genealogical relatives due to coevolution. Although theoretically plausible, it remains uncertain whether or not mutualistic traits often evolve when a coevolutionary response in the other species is required in order to make them beneficial.

7.2.2 Phenotypic responsiveness adds further complexity

In addition to considering the role of coevolution, four of my models rely on adaptive phenotypic responsiveness, or plasticity. Purely evolutionary responses would give very different solutions and it is natural to incorporate the possibility for phenotypic changes in evolutionary models, as these changes are common in nature (Stearns 1989, West-Eberhard 1989). In fact, the entire negotiation framework I use in Chapter 6 was developed in order to allow a more realistic rendition of the adjustments made by social partners to each other's behaviour in a cooperative interaction (McNamara et al. 1999, McNamara 2013). The negotiation models both differ in their predicted outcomes from analogous models of non-modifiable behaviour, and they suggest that the fixed behaviour previously assumed is not favoured by natural selection (Houston & Davies 1985) - that is, individuals remain responsive.

Cooperation is often more easily favoured if there is a phenotypic adjustment, such as reward and punishment of cooperative versus non-cooperative types (Agrawal 2001). Many social traits can only ever be favoured if phenotypic responsiveness exists (Fordyce 2006). For instance, the restricting trait that I analyse in Chapter 3 could not be favoured by natural selection if plants could not adjust phenotypically to impairment of their phosphorus uptake pathways. The restricting trait could not offer a benefit to the restricting individuals because plants could not respond to their decreased phosphorus supply by allocating more carbon to trade. In addition, mutualistic trade in the models analysed in Chapters 2, 3, and 4 evolves more easily and is favoured under a wider range of conditions when plants can adjust their resource acquisition strategy and total quantities transferred phenotypically. Trade evolves more easily because mycorrhizal fungi can unilaterally begin to transfer phosphorus and 'know' that the plants will immediately respond by transferring carbon themselves. Trade is also stable under a broader set of conditions because mycorrhizal fungi that decrease the quantity of phosphorus they transfer immediately bear a cost when plants respond by transferring less carbon (Johnstone & Bshary 2008, Song & Feldman 2013).

In Chapter 3, phenotypic responsiveness in plant resource acquisition and cooperativeness favours cooperation. I find that this effect is even stronger in Chapter 4, where plants also make phenotypic adjustments that favour the evolution of greater cooperativeness in mycorrhizal fungi. This is because if it leads to greater carbon acquisition when mycorrhizal fungi are more cooperative, passive phenotypic responsiveness by plants offers another benefit to cooperators (Sachs et al. 2004, Foster & Wenseleers 2006). This effect ensures more cooperative fungi, particularly when plants grow poorly without fungal help. It also leads to the highest levels of cooperativeness when fungi are able to coordinate their traits through relatedness. In contrast, the work of McNamara et al. (1999, 2003) suggests that responsiveness makes individuals less cooperative and more likely to decrease their own investment in response to that of others. The models used by McNamara et al. (1999, 2003) are distinct to those in the rest of this thesis because they consider investment in shared goods, rather than resource exchange. However, another key difference is that they consider two-sided phenotypic adjustments in cooperativeness rather than phenotypic adjustments in cooperativeness for only one species. Is this a key difference that drives the prediction that phenotypic responsiveness leads to decreased cooperativeness and negative reciprocity, rather than increased cooperativeness and positive reciprocity as in my models of biological markets?

7.2.3 The market analogy offers new insights into mutualisms

I have tested and applied the market analogy to the mycorrhizal symbiosis in Chapters 2, 3, and 4 and have found this conceptual framework both theoretically sound and useful. This is valuable because it provides an explanation for mutualistic cooperation that is based neither on relatedness, which is not always present, nor reciprocity, which is probably rare (Clutton-Brock 2009, Leimar & Hammerstein 2010, Noë & Voelkl 2013). Indeed, in the words of Adam Smith (1776):

> *It is not from the benevolence of the butcher, the brewer, or the baker that we expect our dinner, but from their regard to their own self-interest. We address ourselves not to their humanity but to their self-love, and never talk to them of our own necessities, but of their advantages.*

The step from economic actors maximising their incomes to Darwinian actors acting as if striving to maximise their fitness under natural selection is easy to make.
The market analogy also allows evolutionary biologists to gain alternative insights on cooperative interactions where prevailing thought in the two disciplines leads to different conclusions. An economist would assume that the market is most efficient, and thus that aggregate fitness is maximised, when there are many unrelated participants (Smith 1776, Makowski & Ostroy 2001). On the other hand, a biologist might suggest that cooperation is greatest, and thus fitness is maximised, when interactants are highly related (Bull et al. 1991, Herre 1995, Leigh and Rowell 1995, Herre et al. 1999, Clutton-Brock 2002, Kiers et al. 2002). Similarly, an economist would assume that opportunities for trade lead to specialisation, and that specialisation would lead to a greater reliance on trade (Ricardo 1817, Hammerstein & Leimar 2006). Again, a biologist might suggest the opposite. Opportunities for trade lead individuals to seek outside options so as to increase their bargaining power, and good outside options lead to improved terms of trade but sometimes also breakdowns in cooperation (Herre et al. 1999, Denison 2000, Johstone 2000, Ferrière et al. 2002, West et al. 2002, Kiers et al. 2003, Cant & Johnstone 2009, Cant 2011). Finally, the market perspective allows us to understand changes to ecological

conditions as shifts in supply and demand. This perspective means that it is easy to identify the individuals that benefit and what their strategic responses should be (Barclay 2013). This does not imply that the insights offered by economics are conceptual leaps in biology. For example, a market is a mechanism that enables partner choice, which is well understood to promote cooperativeness (Adam 2010). Instead, I suggest that the more widespread use of economic tools could lead to the identification of novel mechanisms that help maintain cooperation (Noë 2001).

I believe that both a biologist and an economist analysing the same biological system will most often identify the same mechanisms favouring cooperative behaviour, for example in a public goods game. When predictions differ, the economic perspective may identify the wrong mechanism because assumptions that enable markets to function are not fulfilled. For example, in biological settings, I believe that partners will often have insufficient information over supply and demand for market mechanisms to function (Fu et al. 2008, Simms & Taylor 2002). However, this does not mean that the analysis of an economist is always wrong when it differs from that of a biologist. Multiple mechanisms may be acting to promote cooperation in the same biological system and it is their relative strength that matters, which is much harder to measure than a qualitative effect (Palmer et al. 2003, Sachs et al. 2004).

Indeed, in Chapter 4 I incorporated mechanisms known to favour mutualistic cooperation, such as phenotypic feedback and relatedness, into a biological market model. My model demonstrates that all of these mechanisms can act to favour cooperation in the same system. However, my model also shows that sometimes the conditions that favour cooperation under one mechanism, such as partner choice in a market, disfavour cooperation under another mechanism, such as low relatedness. Further research is needed to determine how these mechanisms interact. It may be that organisms have adapted to separate the spheres in which different mechanisms operate (Behm et al. 2014, Kaltenpoth et al. 2014).

7.2.4 Excluding free-riders is not enough to ensure cooperation

Extensive biological theory has focused on resolving the problem of cooperation. That is, the apparent paradox that individuals carry out costly cooperative behaviours that benefits others when, all else being equal, they would be better off as uncooperative free-riders (Hamilton 1963, 1964, Hardin 1968). Clearly, the potential existence of these free-riders has the potential to disrupt otherwise cooperative systems. Yet, many mechanisms exist that exclude these individuals from the benefits of cooperation, thus maintaining incentives to cooperate (Douglas 2008, West et al. 2011).

Furthermore, only certain cooperative systems suffer from a free-riding problem (Groves & Ledyard 1977, Fayle et al. 2011). These are systems where the goods provided by cooperative individuals are, in economic terminology, non-excludable. That is, once they are produced, it is not possible to exclude others from taking advantage of the benefits they offer. For example, non-producing bacteria are likely to benefit from the production of iron-scavenging molecules by others in a medium where these molecules diffuse rapidly (Redfield 2002, Kümmerli et al. 2009, Julou et al. 2013). This problem exists in Chapters 5 and 6, where the social partner benefits from a focal individual’s final cooperative investment irrespective of the social partner’s own strategy. On the other hand, in the market models in Chapters 2, 3, and 4 a focal individual can produce goods but retain them for its own use rather than trading them. In this case, the goods are clearly excludable and the obstacle to cooperation is not free-riding, as goods are produced whether or not cooperativeness is maintained by selection (Zhang & Rainey 2013, Ghoul et al. 2014). This likely means that opportunities for cooperation based on excludable goods, whether or not the exchange actually occurs, are common because there are few obstacles to their provision (McGill 2005).

The benefit of cooperative behaviour in the case of excludable goods is that it allows the efficient allocation of these goods amongst the cooperating individuals. Thus, a researcher seeking to understand the maintenance of cooperation may need to look for mechanisms other than those which exclude cheats and align interests amongst social partners (Sachs & Simms 2006). Rather, they could consider mechanisms that distribute information about resource needs of different individuals, that allow the transmission of goods between individuals, and that prevent any given individual from exerting excessive influence over the final allocation (Cohen & Shmida 1993, Morgan 2000, Oldroyd et al. 2005, Cooper 2007). Further investigation into the pathways specific to maintaining cooperation in the allocation of excludable goods would be valuable to researchers investigating social scenarios that are poorly captured by existing conceptual frameworks based on public goods dilemmas (Strassmann et al. 2000).

7.3 Conclusion

My work provides a demonstration of the diversity of mechanisms that maintain social behaviours in the natural world, even though the underlying ultimate explanations are extremely few in number. Darwin (1859) and Fisher (1930), complemented by many others, demonstrated that the process of natural selection could by itself explain all of the adaptations manifested by biological organisms. Subsequently, the work of Hamilton (1963, 1964, 1970) demonstrated that any trait favoured by natural selection must either provide lifetime direct reproductive benefits or otherwise indirect benefits, through the reproduction of genetic relatives, to its bearer. The simplicity of these ultimate explanations may have led researchers to seek equally simple proximate explanations to underlie social behaviours, such as reciprocity or limited dispersal (Trivers 1971, Hamilton 1964). Instead, I believe that we should embrace the variety and richness of mechanisms that underlie biological cooperation. To this end, I have tried to tie together economic and biological thinking. In economics, Milton Friedman (1999) wrote that it was the invisible hand of competition in the free market that allowed cooperation to arise without coercion. This additional mechanism promoting cooperation has proved useful in my biological investigations, and I hope that future research in both fields will benefit from insights generated in the other.

References

Aanen, D. K., de Fine Licht, H. H., Debets, A. J. M., Kerstes, N. A. G., Hoekstra, R. F. and Boomsma, J. J. 2009. High symbiont relatedness stabilizes mutualistic cooperation in fungus-growing termites. Science 326:1103-1106.

Adam, T. C. 2010. Competition encourages cooperation: client fish receive higher-quality service when cleaner fish compete. Anim. Behav. 79:1183-1189.

Aanen, D. K. and Hoekstra, R. F. 2007. The evolution of obligate mutualism: if you can't beat 'em, join 'em. Trends Ecol. Evol. 22:506-509.

Agarwal, B. 1997. "Bargaining" and gender relations: within and beyond the household. Fem. Econ. 3:1-51.

Agrawal, A. A. 2001. Phenotypic plasticity in the interactions and evolution of species. Science 294:321-326.

Agrawal, A. A. and Karban, R. 1997. Domatia mediate plant-arthropod mutualism. Nature 387:562-563.

Akçay, E. and Roughgarden, J. 2007. Negotiation of mutualism: rhizobia and legumes. Proc. R. Soc. Lond. B 274:25-32.

Akçay, E. and Simms, E. L. 2011. Negotiation, sanctions, and context dependency in the legume-rhizobium mutualism. Am. Nat. 178:1-14.

Akçay, E. and Van Cleve, J. 2012. Behavioural responses in structured populations pave the way to group optimality. Am. Nat. 179:257-69.

Allen, M. F., Hipps, L. E. and Wooldridge, G. L. 1989. Landscape Ecol. 2:165-171.

Amir, R. and Lambson, V. E. 2000. On the Effects of Entry in Cournot Markets. Rev. Econ. Stud. 67:235-254.

Anderson, R. M. and May, R. M. 1982. Coevolution of hosts and parasites. Parasitology 85:411-426.

Archetti, M. and Scheuring, I. 2011. Review: Evolution of cooperation in one-shot social dilemmas without assortment. J. Theor. Biol. 65:1140-1148.

Archetti, M., Scheuring, I., Hoffman, M., Frederickson, M. E., Pierce, N. E. and Yu, D. W. 2011. Economic game theory for mutualism and cooperation. Ecol. Lett. 14:1300-1312.

Archetti, M., Úbeda, F., Fudenberg, D., Green, J., Pierce, N. E. and Yu, D. W. 2011. Let the right one in: a microeconomic approach to partner choice in mutualisms. Am. Nat. 177:75-85.

Arthur, W. B., Holland, J. H., LeBaron, B., Palmer, R. G., and Tayler, P. 1997. Asset pricing under endogenous expectations in an artificial stock market. In The Economy as an Evolving Complex System II (eds. Arthur, W. B., Durlauf, S. N. and Lane, D.). Addison-Wesley, Reading, MA.

Axelrod, R. M. 1984. The Evolution of Cooperation. Basic Books, New York, NY.

Axelrod, R. A. & Hamilton, W. D. 1981. The evolution of cooperation. Science 211:1390-1396.

Bacchiega, E. 2013. A note on the effect of market power in Ricardian economies. Res. Econ. 67:111-116.

Bäckhed, F., Ley, R. E., Sonnenburg, J. L., Peterson, D. A. and Gordon, J. I. 2005. Host-bacterial mutualism in the human intestine. Science 307:1915-1920.

Baldwin, R. E. 1948. Equilbrium in international trade: a diagrammatic analysis. Q. J. Econ. 62:748-762.

Balzergue, C., Chabaud, M., Barker, D. G., Bécard, G. and Rochange, S. F. 2013. High phosphate reduces host ability to develop arbuscular mycorrhizal symbiosis without affecting root calcium spiking responses to the fungus. Front. Plant. Sci. 4:426.

Barclay, P. 2013. Strategies for cooperation in biological markets, especially for humans. Evol. Hum. Behav. 34:164-175.

Baron, D. and Myerson, R. 1982. Regulating a monopolist with unknown costs. Econometrica 50:911-930.

Batty, C. J. K., Crewe, P., Grafen, A. and Gratwick, R. 2013. Foundations of a mathematical theory of Darwinism. J. Math. Biol. 69:295-334.

Behm, J, Geurts, R. and E.T.Kiers. 2014. Parasponia – a novel system for studying mutualism stability. Trends Plant Sci.

Behm, J. E. and Kiers, E. T. 2014. A phenotypic plasticity framework for assessing intraspecific variation in arbuscular mycorrhizal fungal traits. J. Ecol. 102:315-327.

Bergmüller, R., Johnstone, R. A., Russell, A. F. and Bshary, R. 2007. Integrating cooperative breeding into theoretical concepts of cooperation. Behav. Process. 76:61-72.

Bergstrom, C. T. and Lachmann, M. 1997. Signalling among relatives. I. Is costly signaling too costly? Phil. Trans. R. Soc. Lond. B 352:609-617.

Bergstrom, C. T. and Lachmann, M. 1998. Signalling among relatives. III. Talk is cheap. Proc. Natl. Acad. Sci. USA 95:5100-5105.

Bever, J. D., Richardson, S. C., Lawrence, B. M., Holmes, J. and Watson, M. 2009. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. Ecol. Lett. 12:13-21.

Biedermann, P. H. W. and Kaltenpoth, M. 2014. New synthesis: the chemistry of partner choice in insect-microbe mutualisms. J. Chem. Ecol. 40:99.

Bliss, C. and Nalebuff, B. 1984. Dragon-slaying and ballroom dancing: the private supply of a public good. J. Public Econ. 25:1-12.

Bonabeau, E. 2002. Agent-based modeling: methods and techniques for simulating human systems. Proc. Natl. Acad. Sci. USA 99:7280-7287.

Bourke, A. F. G. 2011. Principles of Social Evolution. Oxford University Press, Oxford.

Bourke, A. F. G. 2014. Hamilton's rule and the causes of social evolution. Phil. Trans. R. Soc. B 369:20130362.

Bourke, A. F. G. 2014. The gene's-eye view, major transitions and the formal Darwinism project. Biol. Philos. 29:241-248.

Boyd, R. and Richerson, P. J. 1988. The evolution of reciprocity in sizable groups. J. Theor. Biol. 132:337-356.

Bright, M. and Bulgheresi, S. 2010. A complex journey: transmission of microbial symbionts. Nat. Rev. Microbiol. 8:218-230.

Bronstein, J. L., Dieckmann, U. and Ferrière, R. 2004. Coevolutionary dynamics and the conservation of mutualisms. In Evolutionary Conservation Biology (eds. Ferrière, R., Dieckmann, U. and Couvet, D.). Cambridge University Press, Cambridge.

Brown, J. H. and Kodric-Brown, A. 1979. Convergence, competition and mimicry in a temperate community of hummingbird-pollinated flowers. Ecology 60:1022-1035.

Brundrett, M. C. 2002. Coevolution of roots and mycorrhizas of land plants. New Phytol. 154:275-304.

Bshary, R. and Grutter, A. S. 2005. Experimental evidence that partner switching and punishment promote cooperative behaviour in cleaning mutualism. Biol. Lett. 1:396-399.

Bücking, H. and Shachar-Hill, Y. 2005. Phosphorous uptake, transport, and transfer by the arbuscular mycorrhizal fungus Glomus intraradices is stimulated by increased carbohydrate availability. New Phytol. 165:899-911.

Bull, J. J., Molineux, I. J. and Rice, W. R. 1991. Selection on benevolence in a host-parasite system. Evolution 45:875-882.

Bull, J. J. and Rice, W. R. 1991. Distinguishing mechanisms for the evolution of co-operation. J. Theor. Biol. 149:63-74.

Bull, J. J. and Wang, I.-N. 2010. Optimality models in the age of experimental evolution and genomics. J. Evol. Biol. 23:1820-1838.

Burt, A. and Trivers, R. 2006. Genes in conflict: the biology of selfish genetic elements. The Belknap Press of Harvard University Press, Cambridge, MA.

Cant, M. A. 2011. The role of threats in animal cooperation. Proc. R. Soc. Lond. B 278:170-178.

Cant, M. A. and Shen, S.-F. 2006. Endogenous timing in competitive interactions among relatives. Proc. R. Soc. Lond. B 273:171-178.

Cant, M. A. and Johnstone, R. A. 2009. How threats influence the evolutionary resolution of within-group conflict. Am. Nat. 173:759-771.

Chastain, E., Antia, R., and Bergstrom, C. T. Defensive complexity and the phylogenetic conservation of immune control. arXiv:1211-2878.

Chen, B. D., Li, X. L., Tao, H. Q., Christie, P. and Wong, M. H. 2003. The role of arbuscular mycorrhiza in zinc uptake by red clover growing in a calcareous soil spike with various quantities of zinc. Chemosphere 50:839-846.

Cheverud, J. M. 1988. A comparison of genetic and phenotypic correlations. Evolution 42:958-968.

Clutton-Brock, T. H. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. Science 296:69-72.

Clutton-Brock, T. H. 2009. Cooperation between non-kin in animal societies. Nature 462:51-57.

Clutton-Brock, T. H. and Parker, G. A. 1995. Punishment in animal societies. Nature 373:209-216.

Coase, R. H. 1937. The nature of the firm. Economica 4:386-405.

Coase, R. H. 1960. The problem of social cost. J. Law Econ. 3:1-44.

Cobb, C. W., and Douglas, P. H. 1928. A theory of production. Am. Econ. Rev. 18:139-165.

Cohen, D. and Shmida, A. 1993. The evolution of flower display and reward. Evol. Biol. 27:197-243.

Cooper, J. E. 2007. Early interactions between legumes and rhizobia: disclosing complexity in a molecular dialogue. J. Appl. Microbiol. 103:1355-1365.

Cordella, T. and Gabszewicz, J. J. 1997. Comparative advantage under oligopoly. J. Int. Econ. 43:333-346.

Cordella, T. and Gabszewicz, J. J. 1998. "Nice" trivial equilibria in strategic market games. Game. Econ. Behav. 22:162-169.

Corradi, N. and Bonfante, P. 2012. The arbuscular mycorrhizal symbiosis: origin and evolution of a beneficial plant infection. PLoS Pathog. 10.1371/journal.ppat.1002600.

Cournot, A. A. 1838. Recherches sur les principes mathematiques de la theorie des richesses. Imprimerie d'Amédée, Paris, France.

Crespi, B. J. 1990. Measuring the effect of natural selection on phenotypic interaction systems. Am. Nat. 135:32-47.

Darwin, C. R. 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.

Darwin, C. R. 1869. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. 5th ed. John Murray, London.

Davies, N. B., Krebs, J. R. and West, S. A. 2012. An Introduction to Behavioural Ecology, 4th ed. Wiley-Blackwell, Chichester.

Dawkins, R. 1976. The selfish gene. Oxford University Press, Oxford.

Dawkins, R. 1982. The extended phenotype. W. H. Freeman, Oxford.

de Mazancourt, C. and Schwartz, M. W. 2010. A resource ratio theory of cooperation. Ecol. Lett. 13:349-359.

Denison, R. F. 2000. Legume sanctions and the evolution of symbiotic cooperation by rhizobia. Am. Nat. 156:567-576.

Denison, R. F. 2013. Darwinian agriculture – how understanding evolution can improve agriculture. Princeton University Press, Princeton, NJ.

Denison, R. F., Kiers, E. T. and West, S. A. 2003. Darwinian agriculture: when can humans find solutions beyond the reach of natural selection? Q. Rev. Biol. 78:145-168.

Diggle, S. P., Griffin, A. S., Campbell, G. S. and West, S. A. 2007. Cooperation and conflict in quorum-sensing bacterial populations. Nature 450:411-414.

Dixit, A. 1980. The role of investment in entry deterrence. Econ. J. 90:95-106.

Doebeli, M. and Knowlton, N. 1998. The evolution of interspecific mutualisms. Proc. Natl. Acad. Sci. USA 95:8676–8680.

Dornbusch, R., Fischer, S. and Samuelson, P. A. 1977. Comparative advantage, trade, and payments in a Ricardian model with a continuum of goods. Am. Econ. Rev. 67:823-839.

Dornbusch, R., Fischer, S. and Samuelson, P. A. 1980. Heckscher-Ohlin trade theory with a continuum of goods. Q. J. Econ. 95:203-224.

Douglas, A. E. 2008. Conflict, cheats and the persistence of symbioses. New Phytol. 177:849-858.

Dubey, P. and Shapley, L. S. 1994. Noncooperative general exchange with a continuum of traders: two models. J. Math. Econ. 23:253-293.

Dubey, P. and Shubik, M. 1978. A theory of money and financial institutions. 28. The non-cooperative equilibria of a closed trading economy with market supply and bidding strategies. J. Econ. Theory 17:1-20.

Drescher, K., Nadell, C. D., Stone, H. A., Wingreen, N. S. and Bassler, B. L. 2014. Solutions to the public goods dilemma in bacterial biofilms. Curr. Biol. 24:50-55.

Eddington, A. S. 1928. The nature of the physical world. Cambridge University Press, Cambridge.

Edwards, D. P., Hassall, M., Sutherland, W. J. and Yu, D. W. 2006. Selection for protection in an ant-plant mutualism: host sanctions, host modularity, and the principal-agent game. Proc. R. Soc. Lond. B 273:595–602.

Eshel, I. and Feldman, M. W. 1984. Initial increase of new mutants and some continuity properties of ESS in two locus systems. Am. Nat. 124:631-640.

Ewens, W. J. 1989. An interpretation and proof of the fundamental theorem of natural selection. Theor. Popul. Biol. 36:167-180.

Ewens, W. J. 2004. Mathematical population genetics. I. Theoretical introduction. Springer, Berlin, Germany.

Ewens, W. J. 2014. Grafen, the Price equations, fitness maximization, optimization and the fundamental theorem of natural selection. Biol. Philos. 29:197-205.

Farmer, J. D. and Foley, D. 2009. The economy needs agent-based modeling. Nature 460:685-686.

Fayle, T. M., Edwards, D. P., Turner, E. C., Dumbrell, A. J., Eggleton, P. and Foster, W. A. 2012. Public goods, public services and by-product mutualism in an ant-fern symbiosis. Oikos 121:1279-1286.

Fellbaum, C. R., Gachomo E. W., Beessetty, Y., Choudhari, S., Strahan, G. D., Pfeffer, P. E., Kiers, E. T. and Bücking, H. 2012. Carbon availability triggers fungal nitrogen uptake and transport in arbuscular mycorrhizal symbiosis. Proc. Natl. Acad. Sci. USA 109:2666-2671.

Fellbaum, C. R., Mensah, J., Cloos, A., Pfeffer, P., Strahan, G., Kiers, E. T. and Bücking, H. 2014. Fungal nutrient allocation in common mycorrhizal networks is regulated by the carbon source strength of individual host plants. New Phytol. 203:646-656.

Ferrière, R., Bronstein, J. L., Rinaldi, S., Law, R. and Gauduchon, M. 2002. Cheating and the evolutionary stability of mutualism. Proc. R. Soc. Lond. B 269:773-780.

File, A. L., Klironomos, J., Maherali, H. and Dudley, S. A. 2012. Plant kin recognition enhances abundance of symbiotic microbial partner. PLoS ONE 10.1371/journal.pone.0045648.

Fisher, R. A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. Trans. R. Soc. Ed. 52:399-433.

Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.

Fletcher, J. A. and Doebeli, M. 2009. A simple and general explanation for the evolution of altruism. Proc. R. Soc. Lond. B 276:13-19.

Fletcher, J. A. and Zwick, M. 2006. Unifying the theories of inclusive fitness and reciprocal altruism. Am. Nat. 168:252-262.

Fordyce, J. A. 2006. The evolutionary consequences of ecological interactions mediated through phenotypic plasticity. J. Exp. Biol. 209:2377-2383.

Foster, K. R. and Kokko, H. 2006. Cheating can stabilize cooperation in mutualisms. Proc. R. Soc. Lond. B 273:2233-2239.

Foster, K. R. and Wenseleers, T. 2006. A general model for the evolution of mutualisms. J. Evol. Biol. 19:1283-1293.

Foster, K. R., Wenseleers, T., Ratnieks, F. L. W. and Queller, D. C. 2006. There is nothing wrong with inclusive fitness. Trends Ecol. Evol. 21:57-60.

Frank, J. L., Barry, S. and Southworth, D. 2006. Mammal mycophagy and dispersal of mycorrhizal inoculum in Oregon White Oak Woodlands. Northwest Sci. 80:264-273.

Frank, S. A. 1994. Genetics of mutualism: the evolution of altruism between species. J. Theor. Biol. 170:393-400.

Frank, S. A. 1995. The origin of synergistic symbiosis. J. Theor. Biol. 176:403-410.

Frank, S. A. 1996. Host-symbiont conflict over the mixing of symbiotic lineages. Proc. R. Soc. Lond. B 263:339-344.

Frank, S. A. 1997a. Models of symbiosis. Am. Nat. 150:S80-S99.

Frank, S. A. 1997b. Multivariate analysis of correlated selection and kin selection, with an ESS maximization method. *J. Theor. Biol.* 189:307-316.

Frank, S. A. 1997c. The Price equation, Fisher's fundamental theorem, kin selection, and causal analysis. Evolution 51:1712-1729.

Frank, S. A. 1998. Foundations of Social Evolution. Princeton University Press, Princeton, NJ.

Frank, S. A. 2011. Wright's adaptive landscape versus Fisher's fundamental theorem. In The Adaptive Landscape in Evolutionary Biology (eds. Svensson, E. and Calsbeek, R.). Oxford University Press, Oxford.

Frank, S. A. 2013a. Natural selection. VI. Partitioning the information in fitness and characters by path analysis. J. Evol. Biol. 26:457-471.

Frank, S. A. 2013b. Natural selection. VII. History and interpretation of kin selection theory. J. Evol. Biol. 26:1151-1184.

Frank, S. A. and Slatkin, M. 1992. Fisher's fundamental theorem of natural selection. Trends Ecol. Evol. 7:92-95.

Franklin, O., Näsholm, T., Högberg, P., and Högberg, M. 2014. Forests trapped in nitrogen limitation – an ecological market perspective on ectomycorrhizal symbiosis. New Phytol. 203:657-666.

Frean, M. R., and E. R. Abraham. 2004. Adaptation and enslavement in endosymbiont-host associations. Phys. Rev. E 69:051913.

Friedman, M. 1999. Introduction, I, Pencil. The Foundation for Economic Education, Inc. Irvington-on-Hudson, NY.

Friesen, M. L. and Mathias, A. 2010. Mixed infections may promote diversification of mutualistic symbionts: why are there ineffective rhizobia? J. Evol. Biol. 23:323-334.

Fruteau, C., van de Waal, E., van Damme, E. and Noë, R. 2011. Infant access and handling in sooty mangabeys and vervet monkeys. Anim. Behav. 81:153-161.

Fu, F., Hauert, C., Nowak, M. A. and Wang, L. 2008. Reputation-based partner choice promotes cooperation in social networks. Phys. Rev. E 78:026117.

Fudenberg, D. and Tirole, J. 1992. Game Theory. MIT Press, Cambridge, MA.

Gabszewicz, J. J. and Vial, J. 1972. Oligopoly “a la Cournot” in a general equilibrium analysis. J. Econ. Theory 4:381-400.

Galí, Jordi. 2008. Monetary policy, inflation, and the business cycle. Princeton University Press, Princeton, NJ.

Gamper, H. A., Hartwig, U. A. and Leuchtmann, A. 2005. Mycorrhizas improve nitrogen nutrition of Trifolium repens after 8 yr of selection under elevated atmospheric CO_2 partial pressure. New Phytol. 167:531-542.

Gardner, A. and Grafen, A. 2009. Capturing the superorganism: a formal theory of group adaptation. J. Evol. Biol. 22:659-671.

Gardner, A. and Welch, J. J. 2011. A formal theory of the selfish gene. J. Evol. Biol. 24:1801-1813.

Gardner, A. and West, S. A. 2004. Cooperation and punishment, especially in humans. Am. Nat. 164:753-764.

Gardner, A., West, S. A. and Barton, N. H. 2007. The relation between multilocus population genetics and social evolution theory. Am. Nat. 169:207-226.

Gardner, A., West, S. A. and Wild, G. 2011. The genetical theory of kin selection. J. Evol. Biol. 24, 1020-1043.

Ghoul, M., West, S. A., Diggle, S. P. and Griffin, A. S. 2014. An experimental test of whether cheating is context dependent. J. Evol. Biol. 27:551-556.

Ghoul, M., Griffin, A. S. and West, S. A. 2014. Towards an evolutionary definition of cheating. Evolution 68:318-331.

Giovannetti, M., Sbrana, C., Avio, L. and Strani, P. 2004. Patterns of below-ground plant interconnections established by means of arbuscular mycorrhizal networks. New Phytol. 164:175–181.

Godfray, H. C. J. 1995. Signalling of need between parents and young: parent-offspring conflict and sibling rivalry. Am. Nat. 146:1-24.

Godfray, H. C. J. and Johnstone, R. A. 2000. Begging and bleating: the evolution of parent-offspring signalling. Phil. Trans. R. Soc. Lond. B 355:1581-1591.

Goto, R., Okamoto, T., Kiers, E. T., Kawakita, A. and Kato, M. 2010. Selective flower abortion maintains moth cooperation in a newly discovered pollination mutualism. Ecol. Lett. 13:321-329.

Gould, S. J. and Lewontin, R. C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc R. Soc. Lond. B 205:581-598.

Grace, E. J., Cotsaftis, O., Tester, M., Smith, F. A. and Smith, S. E. 2009. Arbuscular mycorrhizal inhibition of growth in barley cannot be attributed to extent of colonization, fungal phosphorus uptake or effects on expression of plant phosphate transporter genes. New Phytol. 181:938-949.

Grafen, A. 1984. Natural selection, kin selection and group selection. In Behavioural Ecology, 2nd ed. (eds. Krebs, J. R. and Davies, N. B). Blackwell Scientific Publications, Oxford.

Grafen, A. 1990. Biological signals as handicaps. J. Theor. Biol. 144:517-546.

Grafen, A. 1999. Formal Darwinism, the individual-as-maximising-agent analogy, and bet-hedging. Proc. R. Soc. Lond B 266:799-803.

Grafen, A. 2000. Developments of Price's equation and natural selection under uncertainty. Proc. R. Soc. Lond. B 267:1223-1227.

Grafen, A. 2002. A first formal link between the Price equation and an optimization program. J. Theor. Biol. 217:75-91.

Grafen, A. 2006a. Optimisation of inclusive fitness. J. Theor. Biol. 238:541-563.

Grafen, A. 2006b. A theory of Fisher's reproductive value. J. Math. Biol. 53:15-60.

Grafen, A. 2007. An inclusive fitness analysis of altruism on a cyclical network. J. Evol. Biol. 20:2278-2283.

Grafen, A. 2014. The formal Darwinism project in outline. Biol. Philos. 29:155-174.

Grafen, A. and Archetti, M. 2008. Natural selection of altruism in inelastic viscous homogeneous populations. J. Theor. Biol. 252:694-710.

Grman, E., T. Robinson, M. P. and Klausmeier, C. A. 2012. Ecological specialization and trade affect the outcome of negotiations in mutualism. Am. Nat. 179:567-581.

Grossman, S. J. and Hart, O. D. 1983. An analysis of the principal-agent problem. Econometrica 51:7-45.

Groves, T. and Ledyard, J. 1977. Optimal allocation of public goods: a solution to the "free rider" problem. Econometrica 45:783-809.

Hadfield, J. D., Nutall, A., Osorio, D. and Owens, I. P. F. 2007. Testing the phenotypic gambit: phenotypic, genetic and environmental correlations of colour. J. Evol. Biol. 20:549-557.

Haig, D. and Westoby, M. 1988. On limits to seed production. Am. Nat. 131:757-759.

Halliday, T. R. 1983. The study of mate choice. In Mate Choice (ed. Bateson, P. G.). Cambridge University Press, Cambridge.

Hamilton, W. D. 1963. The evolution of altruistic behaviour. Am. Nat. 97:31-33.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. J. Theor. Biol. 7:1-52.

Hamilton, W. D. 1970. Selfish and spiteful behaviour in an evolutionary model. Nature 228:1218-1220.

Hammer, E. C., Pallon, J., Wallander, H. and Olsson, P. A. 2011. Tit for tat? A mycorrhizal fungus accumulates P under low plant C availability. Proc. Natl. Acad. Sci. USA 76:236-244.

Hammerstein, P. 1996. Streetcar theory and long-term evolution. Science 273:1032.

Hammerstein, P. and Hagen, E. H. 2005. The second wave of evolutionary economics in biology. Trends Ecol. Evol. 20:604-609.

Hammerstein, P. and Leimar, O. 2006. Cooperating for direct fitness benefits. J. Evol. Biol. 19:1400-1402.

Hardin, G. 1968. The tragedy of the commons. Science 162:1243-1248.

Harper, D. G. C. 1982. Competitive foraging in mallards: 'Ideal Free' ducks. Anim. Behav. 31:575-584.

Harrison, F., Barta, Z., Cuthill. I. and Szekely, T. 2009. How is sexual conflict over parental care resolved? A meta-analysis. J. Evol. Biol. 22:1800-1812.

Hart, M. M., Forsythe, J., Oshowski, B., Bücking, H., Jansa, J. and Kiers, E. T. 2013. Hiding in a crowd – does diversity facilitate persistence of a low-quality fungal partner in the mycorrhizal symbiosis? Symbiosis 59:47-56.

Heil, M., Barajas-Barron, A., Orona-Tamayo, D., Wielsch, N. and Svatos, A. 2014. Partner manipulation stabilizes a horizontally transmitted mutualism. Ecol. Lett. 17:185-192.

Heil, M., González-Teuber, M., Clement, L. W., Kautz, S., Verhaagh, M. and Silva Bueno, J. C. 2009. Divergent investment strategies of Acacia myrmecophytes and the coexistence of mutualists and exploiters. Proc. Natl. Acad. Sci. USA 106:18091-10896.

Helbing, D., Farkas, I. and Vicsek, T. 2000. Simulating dynamical features of escape panic. Nature 407:487-490.

Herre, E. A. 1995. Factors affecting the evolution of virulence: nematode parasites as a case study. Parasitology 111:179-191.

Herre, E. A., Knowlton, N., Mueller, U. G. and Rehner, S. A. 1999. The evolution of mutualisms: exploring the paths between conflict and cooperation. Trends Evol. Ecol. 14:49-53.

Hinde, C. A. 2006. Negotiation over offspring care? – a positive response to partner-provisioning rate in great tits. Behav. Ecol. 17:6-12.

Hobbes, T. 1651. Leviathan. The Clarendon Press, Oxford.

Hoeksema, J. D. and Schwartz, M. W. 2001. Modeling interspecific mutualisms as biological markets. In Economics in Nature (eds. Noë, R., van Hooff, J. A. R. A. M. and Hammerstein, P.). Cambridge University Press, Cambridge.

Hoeksema, J. D., and Schwartz, M. W. 2003. Expanding comparative-advantage biological market models: contingency of mutualism on partners' resource requirements and acquisition trade-offs. Proc. R. Soc. Lond. B 270:913-919.

Hojo, M. K., Yamamoto, A., Akino, T., Tsuji, K. and Yamaoka, R. 2014. Ants use partner specific odors to learn to recognize a mutualistic partner. PLoS ONE 10.1371/journal.pone.0086054.

Holland, J. H. and Miller, J. H. 1991. Artificial adaptive agents in economic theory. Am. Econ. Rev. 81:365-371.

Holmstron, B. 1979. Moral hazard and observability. Bell J. Econ. 10:74-91.

Houston, A. I. and Davies, N. B. 1985. The evolution of cooperation and life-history in the dunnock. In Behavioural Ecology: Ecological Consequences of Adaptive Behaviour (eds. Sibly, R. M. and Smith, R. H.). Blackwell Scientific Publications, Oxford.

Houston, A. I. and McNamara, J. M. 1988. The ideal free distribution when competitive abilities differ: an approach based on statistical mechanics. Anim. Behav. 36:166-174.

Houston, A. I., Szekely, T. and McNamara, J. 2005. Conflict between parents over care. Trends Ecol. Evol. 20:33-38.

Inman, A. J. 1990. Group foraging in starlings: distribution of unequal competitors. Anim. Behav. 40:801-810.

Jaggard, K. W., Qi, A., Ober, E. S. 2010. Possible changes to arable crop yields by 2050. Phil. Trans. R. Soc. B 365:2835-2851.

Jander, K. C., and Herre, E. A. 2010. Host sanctions and pollinator cheating in the fig tree-fig wasp mutualism. Proc. R. Soc. Lond. B 277:1481-1488.

Janetos, A. C. 1980. Strategies of female choice: a theoretical analysis. Behav. Ecol. Sociobiol. 7:107-112.

Janousková, M., Seddas, P., Mrnka, L., van Tuinen, D., Dvorácková, A., Tollot, M., Gianinazzi-Pearson, V., Vosátka, M. and Gollotte, A. 2009. Development and activity of Glomus intraradices as affected by co-existence with Glomus claroideum in one root system. Mycorrhiza 19:393-402.

Janzen, D. H. 1980. When is it coevolution? Evolution 34:611-612.

Johanssen, W. 1911. The genotype conception of heredity. Am. Nat. 45:129-159.

Johnson, D., Martin, F., Cairney, J. W. G. and Anderson, I. C. 2012. The importance of individuals: intraspecific diversity of mycorrhizal plants and fungi in ecosystems. New Phytol. 194:614-628.

Johnstone, R. A. 2000. Models of reproductive skew: a review and synthesis. Ethology 106:5-26.

Johnstone, R. A. 2004. Begging and sibling competition: how should offspring respond to their rivals. Am. Nat. 163:388-406.

Johnstone, R. A. 2011. Load lightening and negotiation over offspring care in cooperative breeders. Behav. Ecol. 22:436-444.

Johnstone, R. A. and Bshary, R. 2008. Mutualism, market effects and partner control. J. Evol. Biol. 21:879-888.

Johnstone, R. A. and Hinde, C. A. 2006. Negotiation over offspring care – how should parents respond to each other’s efforts? Behav. Ecol. 17:818-27.

Johnstone, R. A. and Keller, L. 2000. How males can gain by harming their mates: sexual conflict, seminal toxins, and the cost of mating. Am. Nat. 156:368-377.

Johnstone, R. A., Manica, A., Fayet, A. L., Caswell Stoddard, M., Rodriguez-Gironés, M. A. and Hinde, C. A. 2014. Reciprocity and conditional cooperation between great tit parents. Behav. Ecol. 25:216-222.

Jones, R. W. 1961. Comparative advantage and the theory of tariffs: a multi-country, multi-commodity model. Rev. Econ. Stud. 28:161-175.

Julou, T., Mora, T., Guillon, L., Croquette, V., Schalk, I. J., Bensimon, D. and Desprat, N. 2013. Cell-cell contacts confine public goods diffusion inside Pseudomonas aeruginosa clonal microcolonies. Proc. Natl. Acad. Sci. USA 110:12577-12582.

Kacelnik, A., Krebs, J. R. and Bernstein, C. 1992. The ideal free distribution and predator-prey populations. Trends Ecol. Evol. 7:50-55.

Kaltenpoth, M., Roeser-Mueller, K., Koehler, S., Peterson, A., Nechitaylo, T. Y., Stubblefield, J. W., Herzner, G., Seger, J. and Strohm, E. 2014. Partner choice and fidelity stabilize coevolution in a Cretaceous-age defensive symbiosis. Proc. Natl. Acad. Sci. USA 111:6359-6364.

Kant, I. 1785/1983. Grounding for the metaphysics of morals. In Ethical Philosophy (Kant, I., trans. Ellington, J. W.). Hackett, Indianapolis, IN.

Karlin, S. 1975. General two-locus selection models: some objectives, results and interpretations. Theor. Popul. Biol. 7:364-398.

Kauffman, S. A. and Johnsen, S. 1991. Coevolution to the edge of chaos: Coupled fitness landscapes, poised states, and coevolutionary avalanches. J. Theor. Biol. 149:467-505.

Kaul, I., Grunberg, I. and Stern, M. A. 1999. Defining global public goods. In Global Public Goods: International Cooperation in the 21st Century (eds. Kaul, I., Grunberg, I. and Stern, M. A.). Oxford University Press. New York, NY.

Kiers, E. T. and Denison, R. F. 2008. Sanctions, cooperation, and the stability of plant-rhizosphere mutualisms. Annu. Rev. Ecol. Evol. Syst. 39:215-236.

Kiers, E. T., Duhamel, M., Beesetty, Y., Mensah, J. A., Franken, O., Verbruggen, E., Fellbaum, C. R., Kowalchuk, G. A., Hart, M. M., Bago, A., Palmer, T. M., West, S. A., Vandenkoornhuyse, P., Jansa, J. and Bücking, H. 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. Science 333:880-882.

Kiers, E. T., Rousseau, R. A., West, S. A. and Denison, R. F. 2003. Host sanctions and the legume-rhizobia mutualism. Nature 425:78-81.

Kiers, E. T., West, S. A. and Denison, R. F. 2002. Mediating mutualisms: farm management practices and evolutionary changes in symbiont co-operation. J. Appl. Ecol. 39:745-754.

Kimura, M. and Weiss, G. H. 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. Genetics 49:561-576.

Korb, J. and Aanen, D. K. 2003. The evolution of uniparental transmission of fungal symbionts in fungus-growing termites (Macrotermitinae). Behav. Ecol. Sociobiol. 53:65-71.

Kosztolanyi, A., Cuthill, I. C. and Szekely, T. 2009. Negotiation between parents over care: reversible compensation during incubation. Behav. Ecol. 20:446-452.

Krivan, V. 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. Am. Nat. 149:164-178.

Kummel, M. and Salant, S. W. 2006. The economics of mutualisms: optimal utilization of mycorrhizal mutualistic partners by plants. Ecology 87:892-902.

Kümmerli, R., Griffin, A. S., West, S. A., Buckling, A. and Harrison, F. 2009. Viscous medium promotes cooperation in the pathogenic bacterium Pseudomonas aeruginosa. 276:3531-3538.

Lachmann, M. and Bergstrom, C. T. 1998. Signalling among relatives. II. Beyond the tower of Babel. Theor. Popul. Biol. 54:146-160.

Lack, D. L. 1948. Natural selection and family size in the starling. Evolution 2:95-110.

Law, R. and Dieckmann, U. 1998. Symbiosis through exploitation and the merger of lineages in evolution. Proc. R. Soc. Lond. B 265:1245-1253.

Lehmann, L., Keller, L. and Sumpter, J.T. 2007a. The evolution of helping and harming on graphs: the return of the inclusive fitness effect. J. Evol. Biol. 20:2284-2295.

Lehmann, L. and Rousset, F. 2014. Fitness, inclusive fitness, and optimization. Biol. Philos. 29:181-195.

Lehmann, L. Rousset, F., Roze, D. and Keller, L. 2007b. Strong reciprocity or strong ferocity? A population genetic view of the evolution of altruistic punishment. Am. Nat. 170:21-36.

Leigh, E. G., Jr. 2010a. The evolution of mutualism. J. Evol. Biol. 23:2507-2528.

Leigh, E. G., Jr. 2010b. The group selection controversy. J. Evol. Biol. 23:6-19.

Leigh, E. G., Jr. and Rowell, T. E. 1995. The evolution of mutualism and other forms of harmony at various levels of biological organization. Ecologie 26:131-158.

Leimar, O. and Hammerstein, P. 2010. Cooperation for direct fitness benefits. Phil. Trans. R. Soc. B:365:2619-2626.

Lerner, A. P. 1934. The concept of monopoly and the measurement of monopoly power. Rev. Econ. Stud. 1:157-175.

Lessells, C. M. 2005. Why are males bad for females? Models for the evolution of damaging male behavior. Am. Nat. 165:546-563.

Lewontin, R. 1961. Evolution and the theory of games. J. Theor. Biol. 1:382-403.

Lewontin, R. 1970. The units of selection. Annu. Rev. Ecol. Syst. 1:1-14.

Li, H., Smith, F. A., Dickson, S., Holloway, R. E. and Smith, S. E. 2008. Plant growth depressions in arbuscular mycorrhizal symbioses: not just caused by carbon drain? New Phytol. 178:852-862.

Lundberg, S. and Pollak, R. A. 1993. Separate spheres bargaining and the marriage market. J. Polit. Econ. 101:988-1010.

Makowski, L. and Ostroy, J. M. 2001. Perfect competition and the creativity of the market. J. Econ. Lit. 39:479-535.

Mas-Colell, A., Whinston, M. D. and Green, J. R. 1995. Microeconomic Theory. Oxford University Press, Oxford.

Maynard Smith, J. and Price, G. R. 1973. The logic of animal conflict. Nature 246:15-18.

Maynard Smith, J. and Szathmáry, E. 1995. The major transitions in evolution. Oxford University Press, Oxford.

Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, MA.

McFall-Ngai, M. 2008. Hawaiian bobtail squid. Curr. Biol. 18:R1043-R1044.

McGill, B. 2005. A mechanistic model of a mutualism and its ecological and evolutionary dynamics. Ecol. Model. 187:413-425.

McNamara, J. M. 2013. Towards a richer evolutionary game theory. J. R. Soc. Interface 10:20130544.

McNamara, J. M., Gasson, C. E. and Houston, A. I. 1999. Incorporating rules for responding into evolutionary games. Nature 401:368-371.

McNamara, J. M. and Houston, A. I. 1996. State-dependent life histories. Nature 380:215-221.

McNamara, J. M., Houston, A. I., Barta, Z. and Osorno, J.-L. 2003. Should young ever be better off with one parent than with two? Behav. Ecol. 14:301-310.

McNamara, J. M., Szekely, T., Webb, J. N. and Houston, A. I. 2000. A dynamic game-theoretic model of parental care. J. Theor. Biol. 205:605-623.

Meade, J., Nam, K. B., Lee, J. W. and Hatchwell, B. J. 2011. An experimental test of the information model for negotiation of biparental care. PLoS One 10.1371/journal.pone.0019684.

Merckx, V. and Bidartondo, M. I. 2008. Breakdown and delayed cospeciation in the arbuscular mycorrhizal mutualism. Proc. R. Soc. Lond. B 275:1029-1035.

Mikkelsen, T. N., Beier, C., Jonasson, S., Holmstrup, M., Schmidt, I. K., Ambus, P., Pilegaard, K., Michelsen, A., Albert, K., Andresen, L. C., Arndal, M. F., Bruun, N., Christensen, S., Danbæk, S., Gundersen, P., Jørgensen, P., Linden, L. G., Kongstad, J., Maraldo, K., Priemé, A., Riis-Nielsen, T., Ro-Poulsen, H., Stevnbak, K., Selsted, M. B., Sørensen, P., Larsen, K. S., Carter, M. S., Ibrom, A., Martinussen, T., Miglietta, F. and Sverdrup, H. 2008. Experimental design of multifactor climate change experiments with elevated CO_2, warming and drought: the CLIMAITE project. Funct. Ecol. 22:185-195.

Milgrom, P. and Roberts, J. 1992. Economics, organization and management. Prentice Hall, Upper Saddle River, NJ.

Mill, J. S. 1859. On Liberty. J. W. Parker and Son, London.

Moore, J. 2002. Parasites and the behaviour of animals. Oxford University Press, Oxford.

Mock, D. W. and Forbes, L. S. 1992. Parent-offspring conflict: a case of arrested development. Trends Ecol. Evol. 7:409-413.

Montesinos-Navarro, A., Segarra-Moragues, J. G., Valiente-Banuet, A. and Verdu, M. 2012. The network structure of plant-arbuscular mycorrhizal fungi. New Phytol. 194:536-547.

Moran, P. A. P. 1964. On the nonexistence of adaptive topographies. Ann. Hum. Genet. 27:383-393.

Morgan, M. T. 2000. Evolution of interactions between plants and their pollinators. Plant Species Biol. 15:249-259.

Morrow, E. H., Arnqvist, G. and Pitnick, S. 2003. Adaptation versus pleiotropy: why do males harm their mates? Behav. Ecol. 6:802-806.

Muthoo, A. 1999. Bargaining theory with applications. Cambridge University Press, Cambridge.

Nagy, R., Drissner, D., Amrhein, N., Jakobsen, I. and Bucher, M. 2009. Mycorrhizal phosphate uptake pathway in tomato is phosphorus-repressible and transcriptionally regulated. New Phytol. 181:950-959.

Nash, J. F. 1950. The bargaining problem. Econometrica 18:155-162.

Nash, J. F. 1951. Non-cooperative games. Ann. Math. 54:286-295.

Noë, R. 1990. A Veto game played by baboons: a challenge to the use of the Prisoner’s Dilemma as a paradigm for reciprocity and cooperation. Anim. Behav. 39:78-90.

Noë, R. 1992. Alliance formation among male baboons: shopping for profitable partners. In Coalitions and Alliances in Humans and Animals (eds. Harcourt, A. H. and de Waal, F. B. M.). Oxford University Press, Oxford.

Noë, R. and Hammerstein, P. 1994. Biological markets: Supply and demand determine the effect of partner choice in cooperation, mutualism, and mating. Behav. Ecol. Sociobiol. 35:1-11.

Noë, R. and Hammerstein, P. 1995. Biological markets. Tends Ecol. Evol. 10:336-339.

Noë, R. 2001. Biological markets: partner choice as the driving force behind the evolution of cooperation. In Economics in Nature. Social dilemmas, mate choice and biological markets (eds. Noë, R., van Hooff, J. A. R. A. M. and Hammerstein, P.). Cambridge University Press, Cambridge.

Noë, R., van Schaik, C. P. and van Hooff, J. A. R. A. M. 1991. The market effect: an explanation for pay-off asymmetries among collaborating animals. Ethology 87:97-118.

Noë, R. and Voelkl, B. 2013. Cooperation and biological markets: the power of partner choice. In Cooperation and its Evolution (eds. Sterelny, K., Joyce, R., Calcott, B. and Fraser, B.). MIT Press, Cambridge, MA.

O'Brien, P. K., Griffiths, T. and Hunt, P. 1991. Political components of the industrial revolution: Parliament and the English cotton textile industry, 1660-1774. Econ. Hist. Rev. New Series 44:395-423.

O'Rourke, K. H. and Williamson, J. G. 2002. After Columbus: explaining the global trade boom 1500-1800. J. Econ. Hist. 62:417-456.

Odling-Smee, F. J., Laland, K. N. and Feldman, M. W. 1996. Niche construction. Am. Nat. 147:641-648.

Odling-Smee, F. J., Laland, K. N. and Feldman, M. W. 2003. Niche construction: the neglected process in evolution. Princeton University Press, Princeton, NJ.

Ohlin, B. 1933. Interregional and international trade. Harvard University Press, Cambridge, MA.

Ohtsuki, H., Hauert, C., Lieberman, E. and Nowak, M. 2006. A simple rule for the evolution of cooperation on graphs and social networks. Nature 441:502-505.

Ohtsuki, H. and Nowak, M. 2006. Evolutionary games on cycles. Proc. R. Soc. Lond. B 273, 2249-2256.

Oldroyd, G. E. D., Harrison, M. J. and Udvardi, M. 2005. Peace talks and trade deals. Keys to long-term harmony in legume-microbe sybmioses. Plant Physiol. 137:1205-1210.

Olson, M., Jr. 1965. The logic of collective action: public goods and the theory of groups. Harvard University Press, Cambridge, MA.

Oono, R., Anderson, C. G. and Denison, R. F. 2011. Failure to fix nitrogen (N_2) by nonreproductive symbiotic rhizobia triggers sanctions that reduce fitness of their reproductive clonemates. Proc. R. Soc. Lond. B 278:2698-2703.

Oono, R., Denison, R. F. and Kiers, E. T. 2009. Tansley Review: controlling the reproductive fate of rhizobia: how universal are legume sanctions? New Phytol. 183:967-979.

Orlove, M. J. and Wood, C. L. 1978. Coefficients of relationship and coefficients of relatedness in kin selection: A covariance form for the Rho formula. J. Theor. Biol. 73:679-686.

Orzack, S. H. 2014. A commentary on the "Formal Darwinism Project": there is no grandeur in this view of life. Biol. Philos. 29:259-270.

Osborne, M. J., and A. Rubinstein. 1994. A Course in Game Theory. MIT Press, Cambridge, MA.

Paley, W. 1802. Natural Theology. R. Faulder, London.

Palmer, T. M., Stanton, M. L. and Young, T. P. 2003. Competition and coexistence: exploring mechanisms that restrict and maintain diversity within mutualist guilds. Am. Nat. 162:S63-S79.

Parker, G. A. 1983. Mate quality and mating decisions. In Mate Choice (ed. Bateson, P. G.). Cambridge University Press, Cambridge.

Parker, G. A. and Maynard Smith, J. 1990. Optimality theory in evolutionary biology. Nature 348:27-33.

Parker, G. A., and Sutherland, W. J. 1986. Ideal free distributions when individuals differ in competitive ability. Anim. Behav. 34:1222-1242.

Parniske, M. 2008. Arbuscular mycorrhiza: the mother of plant root endosymbioses. Nat. Rev. Microbiol. 6:763-775.

Peleg, B., and Shmida, A. 1992. Short-run stable matchings between bees and flowers. Games and Econ. Behav. 4:232-251.

Peleg, B., Shmida, A. and Ellner, S. 1992. Foraging graphs: constraint rules on matching between bees and flowers in a two-sided pollination market. J. Theor. Biol. 157:191-201.

Pellmyr, O. and Huth, C. J. 1994. Evolutionary stability of mutualism between yuccas and mucca moths. Nature 372:257-260.

Poisot, T., Bever, J. D., Nemri, A., Thrall, P. H. and Hochberg, M. E. 2011. A conceptual framework for the evolution of ecological specialisation. Ecol. Lett. 14:841-851.

Potts, S.G., Blesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. and Kunin, W.E. 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25:345–353.

Price, G. R. 1970. Selection and covariance. Nature 227:520-521.

Price, G. R. 1972. Fisher's 'fundamental theorem' made clear. Ann. Hum. Genet. 36:129-140.

Queller, D. C. 1992. A general model for kin selection. Evolution 46: 376-380.

Queller, D. C. and Strassman, J. E. 2009. Beyond sociality: the evolution of organismality. Phil. Trans. R. Soc. Lond. B 364:3143-3155.

Rankin, D. J., Bargum, K. and Kokko, H. 2007. The tragedy of the commons in evolutionary biology. Trends Ecol. Evol. 22:643-651.

Real, L. 1990. Search theory and mate choice. I. Models of single-sex discrimination. Am. Nat. 136:376-405.

Real, L. A. 1991. Search theory and mate choice. II. Mutual interaction, assortative mating, and equilibrium variation in male and female fitness. Am. Nat. 138:901-917.

Réale, D. and Festa-Bianchet, M. 2000. Quantitative genetics of life-history traits in a long-lived wild mammal. Heredity 85:593-603.

Reddell, P., Spain, A. V. and Hopkins, M. 1997. Dispersal of spores of mycorrhizal fungi in scats of native mammals in tropical forests of Northeastern Australia. Biotropica 29:184-192.

Refield, R. J. 2002. Is quorum sensing a side effect of diffusion sensing? Trends Microbiol. 10:365-370.

Regus, J. U., Gano, K. A., Hollowell, A. C. and Sachs, J. L. 2014. Efficiency of partner choice and sanctions in Lotus is not altered by nitrogen fertilization. Proc. R. Soc. Lond. B 281:20132587.

Ricardo, D. 1817. On the principles of political economy and taxation. John Murray, London.

Rieber, W. J. 1982. Discriminating monopoly and international trade. Econ. J. 92:365-376.

Riechert, S. E. and Hammerstein, P. 1983. Game theory in the ecological context. Annu. Rev. Ecol. Syst. 14:377-409.

Roff, D. A. 1995. The estimation of genetic correlations from phenotypic correlations: a test of Cheverud's conjecture. Heredity 74:481-490.

Roger, A., Colard, A., Angelard, C. and Sanders, I. R. 2013. Relatedness among arbuscular mycorrhizal fungi drives plant growth and intraspecific fungal coexistence. ISME J. 7:2137-2146.

Rogerson, W. 1985. The first-order approach to principal-agent problems. Econometrica 53:1357-1368.

Rosenheim, J. A., Alon, U. and Shinar, G. 2010. Evolutionary balancing of fitness-limiting factors. Am. Nat. 175:662-674.

Rousset, F. 2004. Genetic structure and selection in subdivided populations. Princeton University Press, Monographs in Population Biology, Princeton, NJ.

Rousset, F. and Billiard, S. 2000. A theoretical basis for measures of kin selection in subdivided populaitons: finite populations and localized dispersal. J. Evol. Biol. 13:814-825.

Rousset, F. and Ronce, O. 2004. Inclusive fitness for traits affecting metapopulation demography. Theor. Pop. Biol. 65:127-141.

Russell, E. S. 1916. Form and function. John Murray, London.

Ryser, P. and Eek, L. 2000. Consequences of phenotypic plasticity vs. interspecific differences in leaf and root traits for acquisition of aboveground and belowground resources. Am. J. Bot. 87:402-411.

Sachs, J. L., Mueller, U. G., Wilcox, T. P. and Bull, J. J. 2004. The evolution of cooperation. Q. Rev. Biol. 79:135-160.

Sachs, J. L., Russell, J. E., Lii, Y. E., Black, K. C., Lopez, G. and Patil, A. S. 2010. Host control over infection and proliferation of a cheater symbiont. J. Evol. Biol. 23:1919-1927.

Sachs, J. L. and Simms, E. L. 2006. Pathways to mutualism breakdown. Trends Ecol. Evol. 21:585-592.

Sarkar, S. 2014. Formal Darwinism. Biol. Philos. 29:249-257.

Sbrana, C., Fortuna, P., and Giovannetti, M. 2011. Plugging into the network: belowground connections between germlings and extraradical mycelium of arbuscular mycorrhizal fungi. Mycologia 103:307-316.

Schelling, T. C. 1960. The strategy of conflict. Harvard University Press, Cambridge, MA.

Schluter, J. and Foster, K. R. 2012. The evolution of mutualism in gut microbiota via host epithelial selection. PLoS Biol. 10.1371/journal.pbio.1001424.

Schwagmeyer, P. L., Bartlett, T. L. and Schwabl, H. G. 2009. Dynamics of house sparrow biparental care: what contexts trigger partial compensation? Ethology 114:459-468.

Schwartz, M. W., and Hoeksema, J. D. 1998. Specialization and resource trade: biological markets as a model of mutualisms. Ecology 79:1029-1038.

Selosse, M. A., Richard, F., He, X. H. and Simard, S. W. 2006. Mycorrhizal networks: des liaisons dangereuses? Trends Ecol. Evol. 21:621-628.

Selten, R. and Shmida, A. 1991. Pollinator foraging and flower competition in a game equilibrium model. In Game equilibrium models Vol. I. (ed. Selten, R.). Springer-Verlag, Berlin, Germany.

Sen, A. 1990. Gender and cooperative conflicts. In Persistent inequalities: women and world development (ed. Tinker, I.). Oxford University Press, New York, NY.

Shapley, L. S. 1977. Noncooperative General Exchange. In Theory and Measurement of Economic Externalities (ed. Lin, S. A. Y.). Academic Press, New York, NY.

Shapley, L. S., and Shubik, M. 1977. Trade using one commodity as a means of payment. J. Polit. Econ. 85:937-968.

Shelton, B. A. and John, D. 1996. The division of household labor. Annu. Rev. Sociol. 22:299-322.

Shipley, B. 2000. Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference. Cambridge University Press, Cambridge.

Shiozawa, Y. 2007. A new construction of Ricardian trade theory – a many-country, many-commodity case with intermediate goods and choice of production techniques. Evol. Inst. Econ. Rev. 3:141-187.

Shubik, M. 1972. Commodity money, oligopoly, credit and bankruptcy in a general equilibrium model. West. Econ. J. 10:24-38.

Simms, E. L. and Taylor, D. L. 2002. Partner choice in nitrogen-fixation mutualisms of legumes and rhizobia. Integr. Comp. Biol. 42:369-380.

Simms, E. L., Taylor, D. L., Povich, J., Shefferson, R. P., Urbina, M. and Tauszick, Y. 2006. An empirical test of partner choice mechanisms in a legume-rhizobium interaction. Proc. R. Soc. Lond. B 273:77-81.

Sirot, E. 2012. Negotiation may lead selfish individual to cooperate: the example of the collective vigilance game. Proc. Biol. Sci. 279:2862-2867.

Smets, F. and Wouters, R. 2003. An estimated dynamic stochastic general equilibrium model of the Euro area. J. Eur. Econ. Assoc. 1:1123-1175.

Smith, A. 1776. The Wealth of Nations. Methuen & Co., London.

Smith, F. A., Grace, E. J. and Smith, S. E. 2009. More than a carbon economy: nutrient trade and ecological sustainability in facultative arbuscular mycorrhizal symbioses. New Phytol. 182:347-358.

Smith, F. A. and Smith, S. E. 2013. How useful is the mutualism-parasitism continuum of arbuscular mycorrhizal functioning? Plant Soil 363:7-18.

Smith, S. E., Jakobsen, I, Gronlund, M. and Smith, F. A. 2011. Roles of arbuscular mycorrhizas in plant phosphorus nutrition: interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorous acquisition. Plant Physiol. 156:1050-1057.

Sober, E. and Lewontin, R. C. 1982. Artifact, cause and genic selection. Philos. Sci. 49:157-180.

Song, Z. and Feldman, M. W. 2013. Plant-animal mutualism in biological markets: evolutionary and ecological dynamics driven by non-heritable phenotypic variance. Theor. Popul. Biol. 88:20-30.

Spence, A. M. 1977. Entry, capacity investment, and oligopolistic pricing. Bell J. Econ. 8:543-544.

Spencer, H. 1864. Principles of Biology. William and Norgate, London.

Springer, S. A., Crespi, B. J. and Swanson, W. J. 2011. Beyond the phenotypic gambit: molecular behavioural ecology and the evolution of genetic architecture. Mol. Ecol. 20:2240-2257.

Staddon, P. L., Jakobsen, I. and Blum, H. 2004. Nitrogen input mediates the effect of free-air enrichment on mycorrhizal fungal abundance. Glob. Change Biol. 10:1678-1688.

Stearns, S. C. 1989. The evolutionary significance of phenotypic plasticity. BioScience 39:436-445.

Stiglitz, J. 1987. The causes and consequences of the dependence of quality on price. J. Econ. Litt. 25:1-48.

Strassmann, J. E., Zhu, Y. and Queller, D. C. 2000. Altruism and social cheating in the social amoeba Dictyostelium discoideum. Nature 408:965-967.

Subramanian, A. 1995. Putting some numbers on the TRIPS pharmaceutical debate. Int. J. Technol. Manage. 10:252-268.

Sultan, S. E. 2000. Phenotypic plasticity for plant development, function and life history. Trends Plant Sci. 5:537-542.

Sutherland, W. J., and Parker, G. A. 1985. The distribution of unequal competitors. In Behavioural ecology: ecological consequences of adaptive behaviour (eds. Sibly, R. M. and Smith, R. H.). Blackwell, Oxford.

Sutherland, W. J., Townsend, C. R. and Patmore, J. M. 1988. A test of the ideal free distribution with unequal competitors. Behav. Ecol. Sociobiol. 23:51-53.

Tanaka, Y. and Yano, K. 2005. Nitrogen delivery to maize via mycorrhizal hyphae depends on the form of N supplied. Plant Cell Environ. 28:1247-1254.

Tang-Martinez, Z. 2001. The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: a critical re-evaluation. Behav. Proc. 53:21-40.

Taylor, P. D. 1992a. Altruism in viscous populations – an inclusive fitness model. Evol. Ecol. 6:352-356.

Taylor, P. D. 1992b. Inclusive fitness in a homogeneous environment. Proc. R. Soc. Lond. B 249:299-302.

Taylor, P. D. 2010. Birth-death symmetry in the evolution of a social trait. J. Evol. Biol. 23:2569-2578.

Taylor, P. D. and Day, T. 2004. Stability in negotiation games and the emergence of cooperation. Proc. R. Soc. Lond. B 271:669-674.

Taylor, P. D., Day, T. and Wild, G. 2007a. Evolution of cooperation in a finite homogeneous graph. Nature 447:469-472.

Taylor, P. D., Day, T. and Wild, G. 2007b. From inclusive fitness to fixation probability in homogeneous structured populations. J. Theor. Biol. 249:101-110.

Taylor, P. D. and Frank, S. A. 1996. How to make a kin selection model. J. Theor. Biol. 180:27-37.

Thaler, R. H. and Sunstein, C. R. 2009. Nudge: improving decisions about health, wealth, and happiness. Yale University Press, New Haven, CT.

Tinbergen, N. 1963. On aims and methods of ethology. Z.Tierpsychol. 20:410-433.

Tirole, J. 1988. The theory of industrial organization. Cambridge, MA.

Tisserant, E., M. Malbreil, A. Kuo, A. Kohler, A. Symeonidi, R. Balestrini, P. Charron, N. Duensing, N. Frei, V. Gianinazzi-Pearson, Gilbert, L. B., Handa, Y., Herr, J. R., Hijri, M., Koul, R., Kawaguchi, M., Krajinski, F., Lammers, P. J., Masclaux, F. G., Murat, C., Morin, E., Ndikumana, S., Pagni, M., Petitpierre, D., Requena, N., Rosikiewicz, P., Riley, R., Saito, K., San Clemente, H., Shapiro, H., van Tuinen, D., Bécard, G., Bonfante, P., Paszkowski, U., Shachar-Hill, Y. Y., Tuskan, G. A., Young, J. P. W., Sanders, I. R., Henrissat, B., Rensing, S. A., Grigoriev, I. V., Corradi, N., Roux, C. and Martin, F. 2014. The genome of an arbuscular mycorrhizal fungus provides insights into the oldest plant symbiosis. Proc. Natl. Acad. Sci. USA 110:20117-20122.

Trivers, R. L. 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 46:35-57.

Tylianakis, J. M., Didham, R. K., Bascompte, J. and Wardle, D. A. 2008. Global change and species interactions in terrestrial ecosystems. Ecol. Lett. 11:1351-1363.

van Baalen, M. and Jansen, V. A. A. 2001. Dangerous liaisons: the ecology of private interest and common good. Oikos 95:211-224.

Van Valen, L. 1973. A new evolutionary law. Evol. Theor. 1:1-30.

Violi, H. A., Treseder, K. K., Menge, J. A., Wright, S. F. and Lovatt, C. J. 2007. Density dependence and interspecific interactions between arbuscular mycorrhizal fungi mediated plant growth, glomalin production, and sporulation. Can. J. Bot.-Rev. Can. Bot. 85:63-75.

von Neumann, J. and Morgenstern, O. 1944. Theory of Games and Economic Behavior. Princeton University Press, Princeton, NJ.

Walder, F., Niemann, H., Natarajan, M., Lehmann, M. F., Boller, T. and Wiemken, A. 2012. Mycorrhizal networks: common goods of plants shared under unequal terms of trade. Plant Physiol. 159:789-797.

Walras, L. 1874. Eléments d'économie politique pure ou théorie de la richesse sociale. Guillaumin & Cie, Paris, France.

Weremijewicz, J., and Janos, D. P. 2013. Common mycorrhizal networks amplify size inequality in Andropogon gerardii monocultures. New Phytol. 198:203-213.

Werner, G. D. A., Strassman, J. E., Ivens, A. B. H., Engelmoer, D. J. P.,Verbruggen, E., Queller, D. C., Noë, R., Johnson, N. C., Hammerstein, P. and Kiers, E. T. 2014. Evolution of microbial markets. Proc. Natl. Acad. Sci. USA 111:1237-1244.

West, S. A. 2009. Sex Allocation. Princeton University Press, Princeton, NJ.

West, S. A., El Mouden, C., and Gardner, A. 2011. Sixteen common misconceptions about the evolution of cooperation in human. Evol. Hum. Behav. 32:231-262.

West, S. A. and Gardner, A. 2013. Adaptation and inclusive fitness. Curr. Biol. 23:R577-R584.

West, S. A., Griffin, A. S. and Gardner, A. 2007a. Evolutionary explanations for cooperation. Curr. Biol. 17:R661-R672.

West, S. A., Griffin, A. S. and Gardner, A. 2007b. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. J. Evol. Biol. 20:415-432.

West, S. A., and Herre, E. A. 1994. The ecology of the New World fig-parasitising wasps Idarnes and implications for the evolution of the fig-pollinator mutualism. Proc. R. Soc. Lond. B 258:67-72.

West, S. A. and Kiers, E. T. 2009. Evolution: what is an Organism? Curr. Biol. 19:1080-1082.

West, S. A., Kiers, E. T., Pen I. and Denison, R. F. 2002a. Sanctions and mutualism stability: when should less beneficial mutualists be tolerated? J. Evol. Biol. 15:830-837.

West, S. A., Kiers, E. T., Simms, E. L. and Denison, R. F. 2002b. Sanctions and mutualism stability: why do rhizobia fix Nitrogen? Proc. R. Soc. Lond. B 269:685-694.

West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. Annu. Rev. Ecol. Syst. 20:249-278.

Weyl, E. G., Frederickson, M. E., Yu, D. W. and Pierce, N. E. 2010. Economic contract theory tests models of mutualism. Proc. Natl. Acad. Sci. USA 107:15712-15716.

Whitham, T. G. 1980. The theory of habitat selection: examined and extended using pemphigus aphids. Am. Nat. 115:449-466.

Wiebe, K. L. 2009. Negotiation of parental care when the stakes are high: experimental handicapping of one partner during incubation leads to short-term generosity. J. Anim. Ecol. 79:63-70.

Williams, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, NJ.

Williams, G. C. 1992. Natural selection: domains, levels, and challenges. Oxford University Press, New York, NY.

Wilson, D. S. and Wilson, E. O. 2007. Rethinking the theoretical foundations of sociobiology. Q. Rev. Biol. 82:327-348.

Wilson, E. M. K. 2007. Parental effort games. Ph.D. Thesis. University of Bristol.

Wilson, G. W. and Hartnett, D. C. 1998. Interspecific variation in plant responses to mycorrhizal colonization in tallgrass prairies. Am. J. Bot. 85:1732-1738.

Wright, S. 1931. Evolution in Mendelian populations. Genetics 16:97-159.

Wyatt, G. A. K., West, S. A. and Gardner, A. 2013. Can natural selection favour altruism between species? J. Evol. Biol. 26:1854-1865.

Wyatt, G. A. K., Kiers, E. T., Gardner, A. and West, S. A. 2014. A biological market analysis of the plant-mycorrhizal symbiosis. Evolution 68:2603-2618.

Yamamura, N., Higashi, M., Behera, N. and Wakano, J. Y. 2004. Evolution of mutualism through spatial effects. J. Theor. Biol. 226:421-428.

Zhang, X.-X. and Rainey, P. B. 2013. Exploring the sociobiology of pyoverdin-producing Pseudomonas. Evolution 67:3161-3174.

Appendix

This Appendix contains:

1. The inclusive fitness partition of helping referred to in section 5.7.4 (p. 167).
2. Wyatt, G. A. K., West, S. A. and Gardner, A. 2013. Can natural selection favour altruism between species? J. Evol. Biol. 26:1854-1865.
3. Wyatt, G. A. K., Kiers, E. T., Gardner, A. and West, S. A. 2014. A biological market analysis of the plant-mycorrhizal symbiosis. Evolution 68:2603-2618.

Inclusive Fitness Calculation

Frequency and Population States

We calculate the states in which we might expect to see the population (to find the frequency with which we observe each fitness). psplus refers to a state where s is greater than or equal to the value given. p5image refers to the number of times that we will observe 5 patches with a helper of one species and a non-helper of the other when we observe 5 patches.

$$\text{a1plus} = 2 * \left(\frac{1 + b - c}{2 + b - c}\right);$$

$$\text{a1minus} = 2 * \left(\frac{1}{2 + b - c}\right);$$

$$\text{a2plus} = \frac{1 + b - c}{2 + b - c};$$

$$\text{a2minus} = \frac{1}{2 + b - c};$$

$$\text{a3plus} = \frac{1 - c}{2 - c};$$

$$\text{a3minus} = \frac{1 + b}{2 + 2 * b - c};$$

$$\text{a4plus} = \frac{1 + b - c}{2 + 2 * b - c};$$

$$\text{a4minus} = \frac{1}{2 - c};$$

$$\text{a5plus} = \frac{1 - c}{2 - c};$$

$$\text{a5minus} = \frac{1 + b}{2 + 2 * b - c};$$

```
a1 = a1plus + a1minus;
a2 = a2plus + a2minus;
a3 = a3plus + a3minus;
a4 = a4plus + a4minus;
a5 = a5plus + a5minus;
```

$$\text{p0} = \frac{\text{a2} * (\text{a4} - \text{a5})}{\text{a1} * \text{a3} + \text{a1} * \text{a4} + \text{a2} * \text{a4} - (\text{a1} + \text{a2}) * \text{a5}} \;\text{// FullSimplify;}$$

$$\text{p1} = \frac{\text{a1} * (\text{a4} - \text{a5})}{\text{a1} * \text{a3} + \text{a1} * \text{a4} + \text{a2} * \text{a4} - (\text{a1} + \text{a2}) * \text{a5}} \;\text{// FullSimplify;}$$

$$\text{p2} = \frac{\text{a1} * \text{a3} * (\text{a4} - \text{a5})}{\text{a4} * (\text{a1} * \text{a3} + \text{a1} * \text{a4} + \text{a2} * \text{a4} - (\text{a1} + \text{a2}) * \text{a5})} \;\text{// FullSimplify;}$$

$$\text{p3} = \text{p2} * \frac{\text{a5}}{\text{a4}} \;\text{// FullSimplify;}$$

$$\text{p4} = \text{p3} * \frac{\text{a5}}{\text{a4}} \;\text{// FullSimplify;}$$

$$\text{p5} = \text{p4} * \frac{\text{a5}}{\text{a4}} \;\text{// FullSimplify;}$$

$$\text{p1plus} = \frac{\text{p2}}{1 - \frac{\text{a5}}{\text{a4}}} + \text{p1} \;\text{// FullSimplify;}$$

$$\text{p2plus} = \frac{\text{p2}}{1 - \frac{\text{a5}}{\text{a4}}} \;\text{// FullSimplify;}$$

$$\text{p3plus} = \frac{\text{p3}}{1 - \frac{\text{a5}}{\text{a4}}} \;\text{// FullSimplify;}$$

$$\text{p4plus} = \frac{\text{p4}}{1 - \frac{\text{a5}}{\text{a4}}} \;\text{// FullSimplify;}$$

$$\text{p5image} = \left(\frac{(\text{a4})^2}{(\text{a4} - \text{a5})^2}\right) * \frac{\text{p5}}{2} \;\text{// FullSimplify;}$$

Regression of Fitness against the 6 Predictors of Fitness

We are looking at the behaviour of a long chain of cooperators, therefore the two ends of the chain are equivalent. We consider only what happens at the right end of the chain. These chains get very long, so most of the time that we are looking at at least one cooperator, all 10 patches will be cooperators. We say that we observe this state of the population k times (when all predictors are cooperators), and all the other states are calculated relative to this. We can say that we observe this state k times because while there are infinitely many cooperators, each chain will only be finitely long.

$$\begin{aligned}
\text{regression} = {} & (0) + \left(\frac{1}{2 - c} + \frac{1}{2} - 1 - \text{Aminus2}\right)^2 \left(\frac{\text{p1plus}}{2}\right) + \left(\frac{1}{2 - c} + \frac{1}{2} - 1 - \text{Aminus2}\right)^2 \left(\frac{\text{p2plus}}{2}\right) + \\
& \left(\frac{1}{2} + \frac{1 - c}{2 - c} - 1 - \text{Aminus2} - \text{A0}\right)^2 \left(\frac{\text{p3plus}}{2}\right) + \left(\frac{1}{2} + \frac{1 - c}{2 - c} - 1 - \text{Aminus2} - \text{A0}\right)^2 \left(\frac{\text{p4plus}}{2}\right) + \\
& (0 - \text{Aminus2} - \text{A0} - \text{Aplus2})^2 \,(\text{p5image}) + \left(\frac{1}{2 + b} + \frac{1}{2} - 1 - \text{Bminus2}\right)^2 \left(\frac{\text{p1plus}}{2}\right) + \\
& \left(\frac{1}{2 + b - c} + \frac{1}{2} - 1 - \text{Bminus2} - \text{Aminus2}\right)^2 (\text{p0}) + \left(\frac{1}{2 + b - c} + \frac{1}{2} - 1 - \text{Bminus2} - \text{Aminus2}\right)^2 \left(\frac{\text{p1}}{2}\right) + \\
& \left(\frac{1 - c}{2 + b - 2 * c} + \frac{1 - c}{2 - c} - 1 - \text{Bminus2} - \text{Aminus2} - \text{A0}\right)^2 \left(\frac{\text{p2}}{2}\right) + \\
& \left(\frac{1 - c}{2 + b - 2 * c} + \frac{1 - c}{2 - c} - 1 - \text{Bminus2} - \text{Aminus2} - \text{A0}\right)^2 \left(\frac{\text{p3}}{2}\right) + \\
& \left(\frac{1 - c}{2 + b - 2 * c} + \frac{1}{2} - 1 - \text{Bminus2} - \text{Aminus2} - \text{A0} - \text{Aplus2}\right)^2 \left(\frac{\text{p4plus}}{2}\right) + \\
& \left(\frac{1}{2 + b} + \frac{1}{2} - 1 - \text{Bminus2}\right)^2 \left(\frac{\text{p2plus}}{2}\right) + \left(\frac{1}{2 + b - c} + \frac{1}{2} - 1 - \text{Bminus2} - \text{Aminus2}\right)^2 \left(\frac{\text{p1}}{2}\right) +
\end{aligned}$$

$$
\begin{aligned}
&\left(\frac{1}{2+b-c}+\frac{1}{2}-1-\text{Bminus2}-\text{Aminus2}\right)^2(\text{p0})+\\
&\left(\frac{1-c}{2+b-2\ast c}+\frac{1-c}{2-c}-1-\text{Bminus2}-\text{Aminus2}-\text{A0}\right)^2\left(\frac{\text{p1}}{2}\right)+\\
&\left(\frac{1-c}{2+b-2\ast c}+\frac{1-c}{2-c}-1-\text{Bminus2}-\text{Aminus2}-\text{A0}\right)^2\left(\frac{\text{p2}}{2}\right)+\\
&\left(\frac{1-c}{2+b-2\ast c}+\frac{1}{2}-1-\text{Bminus2}-\text{Aminus2}-\text{A0}-\text{Aplus2}\right)^2\left(\frac{\text{p3plus}}{2}\right)+\\
&\left(\frac{1}{2}+\frac{1+b}{2+b}-1-\text{Bminus2}-\text{B0}\right)^2\left(\frac{\text{p3plus}}{2}\right)+\\
&\left(\frac{1+b}{2+2\ast b-c}+\frac{1+b}{2+b}-1-\text{Bminus2}-\text{B0}-\text{Aminus2}\right)^2\left(\frac{\text{p2}}{2}\right)+\\
&\left(\frac{1+b}{2+2\ast b-c}+\frac{1+b}{2+b}-1-\text{Bminus2}-\text{B0}-\text{Aminus2}\right)^2\left(\frac{\text{p1}}{2}\right)+\\
&\left(\frac{1}{2}+\frac{1+b-c}{2+b-c}-1-\text{Bminus2}-\text{B0}-\text{Aminus2}-\text{A0}\right)^2(\text{p0})+\\
&\left(\frac{1}{2}+\frac{1+b-c}{2+b-c}-1-\text{Bminus2}-\text{B0}-\text{Aminus2}-\text{A0}\right)^2\left(\frac{\text{p1}}{2}\right)+\\
&\left(\frac{1}{2}+\frac{1+b-c}{2+b-2\ast c}-1-\text{Bminus2}-\text{B0}-\text{Aminus2}-\text{A0}-\text{Aplus2}\right)^2\left(\frac{\text{p2plus}}{2}\right)+\\
&\left(\frac{1}{2}+\frac{1+b}{2+b}-1-\text{Bminus2}-\text{B0}\right)^2\left(\frac{\text{p4plus}}{2}\right)+\\
&\left(\frac{1+b}{2+2\ast b-c}+\frac{1+b}{2+b}-1-\text{Bminus2}-\text{B0}-\text{Aminus2}\right)^2\left(\frac{\text{p3}}{2}\right)+\\
&\left(\frac{1+b}{2+2\ast b-c}+\frac{1+b}{2+b}-1-\text{Bminus2}-\text{B0}-\text{Aminus2}\right)^2\left(\frac{\text{p2}}{2}\right)+\\
&\left(\frac{1}{2}+\frac{1+b-c}{2+b-c}-1-\text{Bminus2}-\text{B0}-\text{Aminus2}-\text{A0}\right)^2\left(\frac{\text{p1}}{2}\right)+\\
&\left(\frac{1}{2}+\frac{1+b-c}{2+b-c}-1-\text{Bminus2}-\text{B0}-\text{Aminus2}-\text{A0}\right)^2(\text{p0})+\\
&\left(\frac{1}{2}+\frac{1+b-c}{2+b-2\ast c}-1-\text{Bminus2}-\text{B0}-\text{Aminus2}-\text{A0}-\text{Aplus2}\right)^2\left(\frac{\text{p1plus}}{2}\right)+\\
&(0-\text{Bminus2}-\text{B0}-\text{Bplus2})^2(\text{p5image})+\\
&\left(\frac{1+b}{2+2\ast b-c}+\frac{1}{2}-1-\text{Bminus2}-\text{B0}-\text{Bplus2}-\text{Aminus2}\right)^2\left(\frac{\text{p4plus}}{2}\right)+\\
&\left(\frac{1+b}{2+2\ast b-c}+\frac{1}{2}-1-\text{Bminus2}-\text{B0}-\text{Bplus2}-\text{Aminus2}\right)^2\left(\frac{\text{p3plus}}{2}\right)+\\
&\left(\frac{1}{2}+\frac{1+b-c}{2+2\ast b-c}-1-\text{Bminus2}-\text{B0}-\text{Bplus2}-\text{Aminus2}-\text{A0}\right)^2\left(\frac{\text{p2plus}}{2}\right)+\\
&\left(\frac{1}{2}+\frac{1+b-c}{2+2\ast b-c}-1-\text{Bminus2}-\text{B0}-\text{Bplus2}-\text{Aminus2}-\text{A0}\right)^2\left(\frac{\text{p1plus}}{2}\right)+\\
&(0-\text{Bminus2}-\text{B0}-\text{Bplus2}-\text{Aminus2}-\text{A0}-\text{Aplus2})^2(\text{k});
\end{aligned}
$$

```
regressionBminus2 = D[regression, Bminus2] // FullSimplify;
regressionB0 = D[regression, B0] // FullSimplify;
regressionBplus2 = D[regression, Bplus2] // FullSimplify;
regressionAminus2 = D[regression, Aminus2] // FullSimplify;
regressionA0 = D[regression, A0] // FullSimplify;
regressionAplus2 = D[regression, Aplus2] // FullSimplify;
```

```
Solve[{regressionBminus2 == 0, regressionB0 == 0, regressionBplus2 == 0,
    regressionAminus2 == 0, regressionA0 == 0, regressionAplus2 == 0},
   {Bminus2, B0, Bplus2, Aminus2, A0, Aplus2}];
```

Now, we simplify the 6 coefficients.

```
Bminus2simp = Bminus2 /. % // FullSimplify
```

```
{(b ((-2 + c)^24 + 8 b (-2 + c)^19 (-48 - 2 c (-43 + c (29 + (-9 + c) c)) + (-2 + c)^3 c k) -
        b^2 (-2 + c)^17 (8480 + c (-17 680 + 2816 k +
                c (15 056 - 3 c (2248 + c (-510 + 47 c)) - 4736 k + 16 c (184 + c (-52 + 5 c)) k))) -
        2 b^9 (-2 + c)^3 (317 194 240 + c (3 932 160 (-339 + 116 k) +
                c (-1 179 648 (-2399 + 1184 k) + c (c^9 (53 833 + 33 820 k) + 49 152
                        (-83 983 + 36 396 k) - 8 c^8 (161 890 + 93 039 k) + 64 c^7 (219 124 + 110 343 k) -
                       8192 c (-555 321 + 140 902 k) + 512 c^2 (-7 481 797 + 456 572 k) -
                       48 c^6 (1 876 553 + 789 744 k) + 128 c^3 (18 957 469 + 1 867 104 k) +
                       64 c^5 (5 974 757 + 1 964 107 k) - 32 c^4 (35 437 837 + 7 949 644 k))))) -
        2 b^4 (-2 + c)^13 (520 960 + c (640 (-2179 + 536 k) + c (1 688 448 - 704 768 k + c
                  (128 (-9603 + 4571 k) + c (570 528 - 260 416 k +
                        c (-165 216 + 27 338 c - 1999 c^2 + 8 (7772 + c (-854 + 19 c)) k)))))) +
        8 b^3 (-2 + c)^15 (-14 256 + c (33 928 - 7072 k + c (4 (-8741 + 3300 k) + c
                  (20 514 - 9640 k + c (-7057 + 3596 k + c (1333 - 636 k + c (-109 + 40 k))))))) -
        2 b^5 (-2 + c)^11 (3 412 992 + c (1536 (-6613 + 1820 k) +
                c (-768 (-18 409 + 8176 k) + c (32 (-385 079 + 181 356 k) +
                      c (7 239 456 - 2 918 336 k + c (-2 854 520 + 816 096 k + c (721 488 -
                               105 616 k - 32 c (3305 + 34 k) + c^2 (6869 + 1272 k))))))) +
        8 b^6 (-2 + c)^9 (-4 122 624 + c (-3072 (-4399 + 1312 k) + c (3072 (-6923 + 3204 k) +
                 c (256 (84 485 - 39 012 k) + c (32 (-482 301 + 171 446 k) +
                        c (256 (30 298 - 6377 k) + c (-2 665 830 + 165 296 k + c (593 719 + 49 760
                                     k + c (-77 157 + 4442 c + 4 (-4441 + 412 c) k))))))))) -
        2 b^7 (-2 + c)^7 (59 473 920 + c (49 152 (-4335 + 1372 k) + c (-24 576 (-15 227 +
                       7252 k) + c (2048 (-212 615 + 96 012 k) + c (-3584 (-102 273 + 32 206 k) +
                        c (32 (-7 029 539 + 1 049 508 k) + c (98 487 008 + 471 744 k +
                                c (-8 (3 714 911 + 529 444 k) + c (5 851 448 - 675 716 c + 34 695 c^2 +
                                         8 (197 558 + c (-32 804 + 2121 c)) k))))))))) -
        2 b^11 (-216 006 656 + c (-2 097 152 (-447 + 178 k) + c (524 288 (-4075 + 2144 k) +
                 c (-262 144 (-13 351 + 5192 k) + c (327 680 (-13 673 + 2006 k) +
                        c (4096 (1 088 549 + 71 124 k) + c (-4096 (823 243 + 178 460 k) +
                                c (512 (3 718 381 + 1 211 644 k) + c (-789 685 408 + 235 331 760 c -
                                         48 523 504 c^2 + 6 471 528 c^3 - 489 126 c^4 + 15 069 c^5 + 8
                                          (-40 849 600 + c (14 520 656 + c (-3 466 688 + c (527 000 +
                                                   c (-45 228 + 1613 c))))) k))))))))) + 4 b^13
          (1 048 576 + c (1 048 576 (-3 + 2 k) + c (-262 144 (-23 + 12 k) + c (32 768 (-291 + 28 k) +
                       c (16 384 (713 + 132 k) + c (-2048 (5011 + 1660 k) + c (2560 (2439 + 1048 k) +
                                c (-128 (19 959 + 10 460 k) + c (662 576 + 418 048 k + c (c (3878 +
                                                   375 c + 5600 k) - 8 (11 731 + 9224 k))))))))))) +
        2 b^12 (-2 + c) (-15 728 640 + c (-524 288 (-95 + 56 k) + c (1 048 576 (-90 + 49 k) + c
                  (-524 288 (-271 + 49 k) + c (-32 768 (5069 + 558 k) + c (4096 (34 433 + 9556 k) +
                              c (-512 (163 877 + 63 464 k) + c (256 (133 051 + 64 224 k) +
                                     c (-16 (564 553 + 327 856 k) + c (1 427 992 + 990 464 k + c
                                                 (-107 398 + 1319 c - 94 112 k + 2800 c k))))))))))) +
        b^8 (-2 + c)^5 (-320 077 824 + c (-393 216 (-3167 + 1048 k) + c (786 432 (-3071 +
                       1493 k) + c (-32 768 (-96 623 + 42 696 k) + c (4096 (-750 933 + 211 166 k) +
                          c (-512 (-4 367 689 + 437 676 k) + c (-64 (18 678 809 + 1 069 512 k) +
                                c (458 354 592 + 86 381 824 k + c (-24 (5 080 397 + 1 537 968 k) +
                                       c (21 307 316 + 8 644 416 k + c (-2 197 530 + 101 507 c +
                                                   16 (-68 098 + 3591 c) k))))))))))) +
        b^10 (-2 + c)^2 (449 839 104 + c (4 194 304 (-431 + 170 k) + c (-524 288 (-7221 +
                       3784 k) + c (262 144 (-21 515 + 8468 k) + c (-32 768 (-197 393 + 31 826 k) +
                          c (-8192 (691 689 + 31 120 k) + c (1024 (3 613 727 + 711 064 k) +
                                c (-512 (3 445 887 + 1 071 100 k) + c (144 (4 172 159 +
```

```
                                                        1 693 456 k) + c (- 256 (552 305 + 271 677 k) +
                                                        c (384 (56 533 + 32 315 k) + c (- 1 943 400 + 76 499 c +
                                                           16 (- 78 164 + 3359 c) k)))))))))))))) /
   (2 (2 + b) (2 + b - 2 c) (2 + b - c) (2 + 2 b - c) (- 2 + c) (- 4 b (- 2 + c)^3 +
        (- 2 + c)^4 +
        b^2
          (16 +
             c (- 16 + 5 c)))
     ((- 2 + c)^16 + 2 b (- 2 + c)^14 (16 + c (- 3 + 4 k)) +
        b^2
          (- 2 + c)^12
          (448 +
             39 c^2 +
             56 c (- 3 + 4 k)) -
        8 b^3 (- 2 + c)^10 (- 448 + c (84 (3 - 4 k) + c (- 117 + 2 c (14 + 5 k)))) +
        b^4
          (- 2 + c)^8
          (17 920 +
             c (4480 (- 3 + 4 k) + c (9360 - 320 c (14 + 5 k) + 9 c^2 (87 + 32 k)))) -
        2 b^5 (- 2 + c)^6 (- 28 672 + c (- 8960 (- 3 + 4 k) +
                c (- 24 960 + 1280 c (14 + 5 k) - 72 c^2 (87 + 32 k) + c^3 (767 + 348 k)))) +
        b^6 (- 2 + c)^4 (114 688 + c (43 008 (- 3 + 4 k) + c (149 760 + c (3 c (25 056 + c (- 6136 + 495 c)) +
                          32 c (864 + 29 (- 9 + c) c) k - 10 240 (14 + 5 k))))) - 4 b^7 (- 2 + c)^2
          (- 32 768 + c (- 14 336 (- 3 + 4 k) + c (- 59 904 + c (5120 (14 + 5 k) + c (- 576 (87 + 32 k) +
                               c (24 (767 + 348 k) + c (- 2970 + 97 c + 8 (- 232 + 15 c) k))))))) +
        4 b^8 (16 384 + c (8192 (- 3 + 4 k) + c (39 936 + c (- 4096 (14 + 5 k) +
                          c (576 (87 + 32 k) - c (32 (767 + 348 k) +
                                c (c (388 + 55 c + 480 k) - 4 (1485 + 928 k)))))))))}
```

```
B0simp = B0 /. %% // FullSimplify
```

```
{- (b ((- 2 + c)^20 + 4 b (- 2 + c)^16 (40 + c (- 50 + 20 c - 3 c^2 + 2 (- 2 + c)^2 k)) - 4 b^2 (- 2 + c)^14
           (- 724 + c (- 3 c (205 + c (- 59 + 7 c)) + 32 (34 - 9 k) + 4 c (80 + c (- 26 + 3 c)) k)) +
         4 b^11 (65 536 + c (- 131 072 + 217 088 c - 321 536 c^2 + 328 960 c^3 -
                   214 016 c^4 + 85 616 c^5 - 19 784 c^6 + 2278 c^7 - 85 c^8 +
                   32 (32 + c (16 + c (- 22 + 5 c))) (128 + c (- 128 + c (88 + c (- 40 + 7 c)))) k)) +
         2 b^3 (- 2 + c)^11 (- 31 296 + c (70 688 - 18 560 k + c (- 68 192 + 32 064 k + c
                            (37 984 - 20 160 k - c (13 140 - 5792 k + c (- 2636 + 247 c + 4 (174 + c) k)))))) -
         2 b^5 (- 2 + c)^8 (- 559 104 + c (- 14 336 (- 89 + 38 k) + c (672 (- 2087 + 1200 k) +
                        c (80 (13 085 - 4832 k) + c (- 544 736 + 44 800 k +
                                  c (184 124 - 36 962 c + 3419 c^2 + 4 (8268 + c (- 3492 + 403 c)) k)))))) +
         2 b^10 (- 2 + c) (- 851 968 + c (- 98 304 (- 19 + 16 k) + c (4096 (- 711 + 304 k) +
                        c (2048 (1941 + 208 k) + c (- 768 (5079 + 1600 k) +
                                  c (2 485 376 - 990 480 c + 234 840 c^2 - 29 638 c^3 + 1479 c^4 +
                                       16 (65 792 + c (- 32 016 + c (8544 + c (- 1058 + 35 c)))) k)))))) +
         4 b^4 (- 2 + c)^9 (- 112 128 + c (282 368 - 88 064 k + c (8 (- 40 101 + 20 368 k) +
                        c (225 860 - 111 168 k + c (- 107 318 + 33 984 k +
                                  c (33 445 - 2848 k + c (- 6271 + 554 c + 4 (- 250 + 49 c) k))))))) +
         b^8 (- 2 + c)^2 (17 301 504 + c (1 310 720 (- 41 + 20 k) + c (- 12 288 (- 7221 + 4112 k) +
                        c (16 384 (- 6673 + 1888 k) + c (512 (204 427 + 8064 k) +
                                  c (- 1024 (71 783 + 18 162 k) + c (36 098 032 - 11 977 568 c +
                                            2 561 776 c^2 - 319 824 c^3 + 17 719 c^4 + 16 (869 680 +
                                                 c (- 356 784 + c (86 376 + c (- 11 372 + 613 c)))) k))))))) +
         2 b^6 (- 2 + c)^6 (1 978 368 + c (458 752 (- 11 + 5 k) + c (- 896 (- 7223 + 4144 k) +
                        c (128 (- 45 901 + 15 136 k) +
                             c (3 906 248 - 89 600 k + c (- 64 (27 907 + 6055 k) + c (526 458 + 203 264 k +
                                            c (- 91 150 + 7087 c + 136 (- 326 + 27 c) k)))))))) -
         2 b^7 (- 2 + c)^4 (- 4 964 352 + c (- 32 768 (- 428 + 203 k) + c (2560 (- 8035 + 4592 k) +
```

$$
\begin{array}{l}
\qquad\qquad\qquad c\ (256\ (85\,991 - 25\,952\ k) + c\ (-32\ (557\,889 + 8512\ k) + c\ (64\ (161\,495 + 38\,707 \\
\qquad\qquad\qquad\qquad\qquad\qquad k) + c\ (-16\ (252\,983 + 98\,008\ k) + c\ (32\ (31\,841 + 15\,444\ k) + \\
\qquad\qquad\qquad\qquad\qquad\qquad c\ (-149\,846 + 9807\ c - 80\,672\ k + 5356\ c\ k)))))))))) + \\
\qquad 2\ b^{9}\ (9\,961\,472 + c\ (262\,144\ (-129 + 64\ k) + c\ (-8192\ (-7577 + 4304\ k) + \\
\qquad\qquad\qquad c\ (4096\ (-21\,103 + 5728\ k) + c\ (1024\ (93\,097 + 4992\ k) + \\
\qquad\qquad\qquad\qquad c\ (-1024\ (76\,949 + 19\,998\ k) + c\ (32\ (1\,459\,909 + 557\,200\ k) + \\
\qquad\qquad\qquad\qquad\qquad c\ (-16\ (1\,210\,125 + 563\,432\ k) + c\ (5\,454\,768 + 2\,888\,704\ k - \\
\qquad\qquad\qquad\qquad\qquad\qquad c\ (993\,656 + 566\,976\ k + c\ (-105\,382 + 4927\ c + \\
\qquad\qquad\qquad\qquad\qquad\qquad\qquad 8\ (-7556 + 317\ c)\ k)))))))))))))\ / \\
((2 + b)\ (2 + b - 2\ c)\ (2 + b - c)\ (2 + 2\ b - c)\ (-2 + c)\ ((-2 + c)^{16} + \\
\quad 2 \\
\quad\ b \\
\quad\ (-2 + c)^{14} \\
\quad\ (16 + c\ (-3 + 4\ k)) + b^{2} \\
\quad\ (-2 + c)^{12} \\
\quad\ (448 + 39\ c^{2} + 56\ c\ (-3 + 4\ k)) - 8 \\
\quad\ b^{3} \\
\quad\ (-2 + c)^{10} \\
\quad\ (-448 + c\ (84\ (3 - 4\ k) + c\ (-117 + 2\ c\ (14 + 5\ k)))) + b^{4} \\
\quad\ (-2 + c)^{8} \\
\quad\ (17\,920 + c\ (4480\ (-3 + 4\ k) + c\ (9360 - 320\ c\ (14 + 5\ k) + 9\ c^{2}\ (87 + 32\ k)))) - 2 \\
\quad\ b^{5} \\
\quad\ (-2 + c)^{6} \\
\quad\ (-28\,672 + c\ (-8960\ (-3 + 4\ k) + \\
\qquad\qquad c\ (-24\,960 + 1280\ c\ (14 + 5\ k) - 72\ c^{2}\ (87 + 32\ k) + c^{3}\ (767 + 348\ k)))) + b^{6}\ (-2 + c)^{4} \\
\quad\ (114\,688 + c\ (43\,008\ (-3 + 4\ k) + c\ (149\,760 + c\ (3\ c\ (25\,056 + c\ (-6136 + 495\ c)) + \\
\qquad\qquad\qquad 32\ c\ (864 + 29\ (-9 + c)\ c)\ k - 10\,240\ (14 + 5\ k))))) - 4\ b^{7}\ (-2 + c)^{2} \\
\quad\ (-32\,768 + c\ (-14\,336\ (-3 + 4\ k) + c\ (-59\,904 + c\ (5120\ (14 + 5\ k) + c\ (-576\ (87 + 32\ k) + \\
\qquad\qquad\qquad\quad c\ (24\ (767 + 348\ k) + c\ (-2970 + 97\ c + 8\ (-232 + 15\ c)\ k))))))) + \\
\quad 4\ b^{8}\ (16\,384 + c\ (8192\ (-3 + 4\ k) + c\ (39\,936 + c\ (-4096\ (14 + 5\ k) + c \\
\qquad\qquad\qquad (576\ (87 + 32\ k) - c\ (32\ (767 + 348\ k) + \\
\qquad\qquad\qquad\qquad c\ (c\ (388 + 55\ c + 480\ k) - 4\ (1485 + 928\ k))))))))))\}
\end{array}
$$

```
Bplus2simp = Bplus2 /. %%% // FullSimplify
```

$$
\begin{array}{l}
\{(b\ ((-2 + c)^{24} + 8\ b\ (-2 + c)^{19}\ (-48 - 2\ c\ (-43 + c\ (28 + (-8 + c)\ c)) + (-2 + c)^{3}\ c\ k) - \\
\qquad b^{2}\ (-2 + c)^{17}\ (8480 + c\ (-17\,680 + 2816\ k + \\
\qquad\qquad c\ (14\,384 - 4736\ k + c\ (-6024 + 1466\ c - 149\ c^{2} + 16\ (176 + c\ (-44 + 5\ c))\ k)))) - \\
\qquad 2\ b^{5}\ (-2 + c)^{11}\ (3\,412\,992 + c\ (1536\ (-6613 + 1820\ k) + \\
\qquad\qquad c\ (-1536\ (-8831 + 4088\ k) + c\ (32\ (-361\,147 + 168\,028\ k) + \\
\qquad\qquad\qquad c\ (7\,260\,992 - 2\,051\,264\ k + c\ (-3\,324\,280 + 1\,018\,824\ c - 184\,264\ c^{2} + \\
\qquad\qquad\qquad\qquad 14\,799\ c^{3} + 8\ (23\,164 + c\ (16\,750 + c\ (-6092 + 641\ c)))\ k)))))) + \\
\qquad 4\ b^{3}\ (-2 + c)^{15}\ (-28\,512 + c\ (67\,856 - 14\,144\ k + c\ (8\ (-8339 + 3300\ k) + c\ (37\,332 - \\
\qquad\qquad\qquad 18\,064\ k + c\ (-13\,742 + 5560\ k + c\ (3014 - 824\ k + c\ (-295 + 32\ k))))))) + \\
\qquad 2\ b^{4}\ (-2 + c)^{13}\ (-520\,960 + c\ (-640\ (-2179 + 536\ k) + c\ (64\ (-25\,223 + 11\,012\ k) + \\
\qquad\qquad\quad c\ (96\ (11\,849 - 5660\ k) + c\ (-565\,520 + 190\,016\ k + \\
\qquad\qquad\qquad\quad c\ (191\,688 - 26\,208\ k + c\ (-38\,846 - 2000\ k + 91\ c\ (39 + 8\ k)))))))) + \\
\qquad 4\ b^{6}\ (-2 + c)^{9}\ (-8\,245\,248 + c\ (-6144\ (-4399 + 1312\ k) + c\ (24\,576\ (-1667 + 801\ k) + \\
\qquad\qquad\quad c\ (-512\ (-80\,047 + 36\,196\ k) + c\ (32\ (-973\,409 + 235\,804\ k) + c\ (17\,924\,304 - \\
\qquad\qquad\qquad\qquad 73\,728\ k + c\ (-4\ (1\,830\,361 + 324\,776\ k) + c\ (1\,963\,930 + 583\,776\ k + \\
\qquad\qquad\qquad\qquad\quad 3\ c^{2}\ (7085 + 2928\ k) - 8\ c\ (38\,482 + 14\,261\ k))))))))) + \\
\qquad b^{10}\ (-2 + c)^{2}\ (449\,839\,104 + c\ (4\,194\,304\ (-431 + 170\ k) + c\ (-524\,288 \\
\qquad\qquad\qquad (-7013 + 3784\ k) + c\ (2\,359\,296\ (-2311 + 868\ k) + \\
\qquad\qquad\qquad\quad c\ (-16\,384\ (-401\,975 + 31\,028\ k) + c\ (-8192\ (769\,835 + 121\,824\ k) + \\
\qquad\qquad\qquad\qquad c\ (1024\ (4\,438\,129 + 1\,318\,264\ k) + c\ (-1536\ (1\,551\,233 + 584\,916\ k) + \\
\qquad\qquad\qquad\qquad\quad c\ (885\,768\,624 + 382\,474\,496\ k + c^{4}\ (125\,791 + 87\,152\ k) - \\
\qquad\qquad\qquad\qquad\qquad 8\ c^{3}\ (423\,283 + 251\,528\ k) + 64\ c^{2}\ (575\,113 + 305\,210\ k) - \\
\qquad\qquad\qquad\qquad\qquad 192\ c\ (1\,173\,815 + 563\,052\ k)))))))))) -
\end{array}
$$

$$2\,b^{7}\,(-2+c)^{7}\,(59\,473\,920+c\,(49\,152\,(-4335+1372\,k)+c\,(-24\,576\,(-14\,723+7252\,k)+$$
$$c\,(2048\,(-203\,011+89\,404\,k)+c\,(1792\,(206\,817-43\,916\,k)+c\,(-32\,(8\,010\,719+$$
$$241\,340\,k)+c\,(64\,(2\,037\,896+419\,019\,k)+c\,(-8\,(5\,770\,507+$$
$$1\,827\,092\,k)+c\,(16\,(666\,151+256\,551\,k)+c\,(-1\,435\,220+$$
$$84\,949\,c+72\,(-8556+545\,c)\,k))))))))))+$$
$$2\,b^{12}\,(-2+c)\,(-15\,728\,640+c\,(-524\,288\,(-95+56\,k)+c\,(262\,144\,(-345+196\,k)+$$
$$c\,(-655\,360\,(-211+28\,k)+$$
$$c\,(-16\,384\,(10\,607+1996\,k)+c\,(4096\,(38\,999+12\,852\,k)+$$
$$c\,(-512\,(198\,403+79\,624\,k)+c\,(256\,(169\,717+78\,288\,k)+$$
$$c\,(-16\,(748\,357+395\,184\,k)+c\,(1\,929\,272-138\,934\,c+$$
$$111\,c^{2}+16\,(74\,320+c\,(-6938+175\,c))\,k))))))))))+$$
$$4\,b^{13}\,(1\,048\,576+c\,(1\,048\,576\,(-3+2\,k)+c\,(-524\,288\,(-11+6\,k)+c\,(32\,768$$
$$(-283+12\,k)+c\,(294\,912\,(41+10\,k)+c\,(-2048\,(5507+1948\,k)+$$
$$c\,(512\,(13\,981+5848\,k)+c\,(-128\,(23\,439+11\,308\,k)+$$
$$c\,(48\,(16\,373+9136\,k)+c\,(-88\,(1273+856\,k)+$$
$$c\,(4982+375\,c+5600\,k)))))))))))-$$
$$2\,b^{9}\,(-2+c)^{3}\,(317\,194\,240+c\,(3\,932\,160\,(-339+116\,k)+c\,(-37\,748\,736$$
$$(-73+37\,k)+c\,(16\,384\,(-243\,049+102\,740\,k)+$$
$$c\,(4096\,(1\,118\,515-195\,644\,k)+c\,(-1536\,(2\,742\,747+187\,148\,k)+$$
$$c\,(128\,(23\,216\,743+5\,436\,800\,k)+c\,(-32\,(48\,468\,153+16\,231\,516\,k)+$$
$$c\,(32\,(18\,183\,305+7\,247\,262\,k)+c\,(-16\,(9\,467\,527+4\,216\,416$$
$$k)+c\,(25\,789\,136-2\,553\,888\,c+109\,439\,c^{2}+12$$
$$(1\,046\,768+9\,c\,(-12\,562+593\,c))\,k)))))))))))-$$
$$2\,b^{11}\,(-216\,006\,656+c\,(-2\,097\,152\,(-447+178\,k)+c\,(524\,288\,(-3973+2144\,k)+$$
$$c\,(-262\,144\,(-12\,933+4840\,k)+c\,(32\,768\,(-137\,829+10\,700\,k)+$$
$$c\,(4096\,(1\,177\,645+184\,628\,k)+c\,(-4096\,(962\,501+283\,772\,k)+c\,(512$$
$$(4\,676\,121+1\,749\,964\,k)+c\,(-224\,(4\,731\,095+2\,029\,392\,k)+$$
$$c\,(400\,(835\,019+398\,760\,k)+c\,(-71\,961\,904+9\,808\,936$$
$$c-718\,046\,c^{2}+17\,765\,c^{3}+8\,(-4\,765\,632+c$$
$$(729\,368+c\,(-62\,444+2117\,c)))\,k)))))))))))+$$
$$b^{8}\,(-2+c)^{5}\,(-320\,077\,824+c\,(-393\,216\,(-3167+1048\,k)+c\,(196\,608\,(-11\,921+$$
$$5972\,k)+c\,(-524\,288\,(-5800+2497\,k)+c\,(2048\,(-1\,517\,077+288\,940\,k)+$$
$$c\,(512\,(4\,893\,611+259\,892\,k)+c\,(-64\,(23\,791\,423+5\,312\,872\,k)+$$
$$c\,(32\,(20\,860\,311+6\,847\,480\,k)+c\,(-8\,(25\,325\,291+9\,973\,584\,k)+$$
$$c\,(40\,148\,260+17\,641\,792\,k+c\,(-4\,642\,674-2\,215\,712\,k+$$
$$7\,c\,(33\,617+17\,328\,k))))))))))))))\,/$$
$$(2\,(2+b)\,(2+b-2\,c)\,(2+b-c)\,(2+2\,b-c)\,(-2+c)\,(-4\,b\,(-2+c)^{3}+$$
$$(-2+$$
$$c)^{4}+$$
$$b^{2}\,(16+c\,(-16+5\,c)))\,((-2+c)^{16}+2$$
$$b$$
$$(-2+c)^{14}$$
$$(16+$$
$$c\,(-3+4\,k))+$$
$$b^{2}\,(-2+c)^{12}\,(448+39\,c^{2}+56\,c\,(-3+4\,k))-$$
$$8$$
$$b^{3}$$
$$(-2+c)^{10}$$
$$(-448+$$
$$c\,(84\,(3-4\,k)+c\,(-117+2\,c\,(14+5\,k))))+$$
$$b^{4}\,(-2+c)^{8}\,(17\,920+c\,(4480\,(-3+4\,k)+c\,(9360-320\,c\,(14+5\,k)+9\,c^{2}\,(87+32\,k))))-$$
$$2$$
$$b^{5}$$
$$(-2+c)^{6}$$
$$(-28\,672+$$
$$c\,(-8960\,(-3+4\,k)+$$
$$c\,(-24\,960+1280\,c\,(14+5\,k)-72\,c^{2}\,(87+32\,k)+c^{3}\,(767+348\,k))))+$$

```
        b^6 (-2 + c)^4 (114 688 + c (43 008 (-3 + 4 k) + c (149 760 + c (3 c (25 056 + c (-6136 + 495 c)) +
                      32 c (864 + 29 (-9 + c) c) k - 10 240 (14 + 5 k))))) - 4 b^7 (-2 + c)^2
          (-32 768 + c (-14 336 (-3 + 4 k) + c (-59 904 + c (5120 (14 + 5 k) + c (-576 (87 + 32 k) +
                         c (24 (767 + 348 k) + c (-2970 + 97 c + 8 (-232 + 15 c) k))))))) +
        4 b^8 (16 384 + c (8192 (-3 + 4 k) + c (39 936 + c (-4096 (14 + 5 k) +
                      c (576 (87 + 32 k) - c (32 (767 + 348 k) +
                             c (c (388 + 55 c + 480 k) - 4 (1485 + 928 k))))))))))}
```

```
Aminus2simp = Aminus2 /. %%%% // FullSimplify
```

```
{- (c (-4 (-2 + c)^22 (-1 + c) - 2 b (-2 + c)^20 (-96 + c (124 - 30 c + c^2 + 16 (-1 + c) k)) - b^2 (-2 + c)^18
          (-4256 + c (6768 - 3164 c + 616 c^2 - 29 c^3 + 16 (-88 + c (104 + (-18 + c) c)) k)) +
       4 b^3 (-2 + c)^16 (14 432 + c (-27 376 + 7104 k + c (18 752 - 9760 k +
                    c (394 (-17 + 8 k) + c (1200 - 392 k + c (-59 + 34 k)))))) - b^4 (-2 + c)^14
         (-535 104 + c (64 (18 503 - 5440 k) + c (16 (-66 495 + 34 336 k) + c (552 432 - 253 696 k +
                      c (-173 852 + 48 448 k + c (28 208 - 4736 k + c (-1455 + 352 k))))))) +
       4 b^9 (-2 + c)^4 (105 054 208 + c (32 768 (-12 767 + 4446 k) + c (-16 384
                   (-50 057 + 25 308 k) + c (512 (-2 083 837 + 953 660 k) +
                      c (256 (3 962 237 - 1 141 136 k) + c (-718 827 232 + 65 945 984 k -
                             5 c^6 (5705 + 3508 k) + 144 c^3 (256 109 + 89 036 k) +
                             160 c (2 347 091 + 194 940 k) + c^5 (634 367 + 341 440 k) -
                             8 c^4 (788 825 + 354 738 k) - 32 c^2 (4 413 076 + 1 004 621 k)))))) -
       2 b^13 (-2 + c) (4 718 592 + c (524 288 (-28 + 17 k) + c (-393 216 (-67 + 38 k) +
                    c (8192 (-4123 + 1044 k) + c (8192 (3799 + 274 k) + c (-512 (39 299 + 13 428 k) +
                             c (8 898 304 - 2 589 728 c + 460 376 c^2 - 42 370 c^3 + 1223 c^4 +
                                 64 (76 688 + c (-28 194 + c (5511 + c (-491 + 10 c)))) k)))))) -
       4 b^5 (-2 + c)^12 (-896 128 + c (2 276 160 - 722 048 k + c (96 (-26 321 + 13 508 k) +
                    c (1 717 976 - 774 432 k + c (8 (-96 373 + 25 152 k) +
                           c (56 (3831 - 355 k) + c (-31 602 - 568 k + c (1723 + 132 k)))))))) +
       8 b^14 (-4 + c)^2 (8192 + c (4096 (-5 + 4 k) + c (-512 (-67 + 32 k) +
                    c (256 (-161 + 8 k) + c (32 (1047 + 368 k) + c (-48 (365 + 244 k) +
                                 c (c (-923 + 60 c - 640 k) + 6 (919 + 752 k)))))))) +
       4 b^6 (-2 + c)^10 (4 472 064 + c (1536 (-8383 + 2787 k) + c (17 015 104 -
                    8 689 920 k + c (2432 (-5867 + 2623 k) +
                      c (8 273 536 - 2 130 688 k + c (4 (-810 443 + 57 512 k) + c (795 468 +
                                 58 944 k + c (-107 399 + 5967 c + 56 (-359 + 29 c) k)))))))) -
       2 b^7 (-2 + c)^8 (-33 767 424 + c (-24 576 (-4441 + 1518 k) + c (4096 (-40 855 + 20 784 k) +
                    c (166 503 488 - 74 533 632 k + c (128 (-920 007 + 241 742 k) + c (64 (922 955 -
                                 63 979 k) + c (-48 (419 909 + 37 724 k) + c (4 380 364 + 951 184 k +
                                    c (-542 124 + 29 265 c - 173 632 k + 11 624 c k))))))))) +
       4 b^8 (-2 + c)^6 (48 439 296 + c (368 640 (-473 + 164 k) + c (-2048 (-148 667 + 75 384 k) +
                    c (128 (-2 733 207 + 1 234 100 k) + c (290 661 472 - 79 542 016 k +
                           c (128 (-1 378 819 + 107 259 k) + c (8 (9 567 251 + 862 104 k) +
                                 c (-12 (1 900 653 + 430 376 k) + c (4 402 757 + 1 490 368 k +
                                        4 c (-123 733 - 53 306 k + c (6219 + 3127 k)))))))))) +
       b^10 (-2 + c)^2 (677 904 384 + c (1 048 576 (-2831 + 983 k) + c (-131 072 (-49 283 + 24 844 k) +
                    c (8192 (-1 144 163 + 531 876 k) + c (-2048 (-4 885 773 + 1 484 072 k) +
                           c (512 (-15 761 923 + 1 702 140 k) + c (1536 (3 192 673 + 233 102 k) +
                                 c (-128 (17 288 761 + 3 908 092 k) + c (32 (22 644 845 + 8 022 208
                                            k) + c (3 c (8 334 892 + c (-733 436 + 28 157 c)) +
                                           16 c (878 984 + c (-90 016 + 3949 c)) k -
                                           64 (2 593 805 + 1 204 376 k)))))))))) +
       b^12 (156 237 824 + c (2 097 152 (-313 + 132 k) + c (-524 288 (-2719 + 1496 k) +
                    c (32 768 (-64 717 + 27 996 k) +
                       c (-8192 (-285 201 + 58 264 k) + c (-4096 (471 119 + 14 548 k) +
                              c (4096 (289 491 + 67 834 k) + c (-128 (4 171 997 + 1 679 780 k) +
                                    c (48 (3 584 243 + 1 939 568 k) + c (-32 (1 188 049 +
                                              777 944 k) + c (5 330 984 - 403 464 c + 10 513 c^2 +
                                              16 (249 528 + c (-21 082 + 641 c)) k)))))))))) -
       2 b^11 (-2 + c) (197 132 288 + c (65 011 712 (-13 + 5 k) + c (-4 718 592 (-389 +
                      206 k) + c (8192 (-329 027 + 148 804 k) +
```

```
                    c (-4096 (-714 047 + 183 668 k) + c (9216 (-259 397 + 10 828 k) +
                          c (1536 (952 955 + 142 596 k) + c (-32 (20 668 143 + 6 398 540 k) + c
                               (215 342 384 + 95 557 824 k + c (-40 (1 214 351 + 679 288 k) +
                                  c (7 080 012 + 4 699 872 k + c (-581 402 - 446 872 k +
                                    c (19 057 + 17 260 k))))))))))))))) /
   (2 (2 + b) (2 + b - 2 c) (2 + b - c) (2 + 2 b - c) (-2 + c) (-4 b (-2 + c)^3 +
       (-2 + c)^4 +
       b^2
        (16 + c (-16 + 5 c)))
     ((-2 + c)^16 + 2 b (-2 + c)^14 (16 + c (-3 + 4 k)) +
       b^2
        (-2 + c)^12
        (448 + 39 c^2 + 56 c (-3 + 4 k)) - 8
        b^3
        (-2 + c)^10
        (-448 + c (84 (3 - 4 k) + c (-117 + 2 c (14 + 5 k)))) + b^4
        (-2 + c)^8
        (17 920 +
          c (4480 (-3 + 4 k) + c (9360 - 320 c (14 + 5 k) + 9 c^2 (87 + 32 k)))) -
       2 b^5 (-2 + c)^6 (-28 672 + c (-8960 (-3 + 4 k) + c (-24 960 + 1280 c (14 + 5 k) -
                 72 c^2 (87 + 32 k) + c^3 (767 + 348 k)))) + b^6 (-2 + c)^4
        (114 688 + c (43 008 (-3 + 4 k) + c (149 760 + c (3 c (25 056 + c (-6136 + 495 c)) +
                     32 c (864 + 29 (-9 + c) c) k - 10 240 (14 + 5 k))))) - 4 b^7 (-2 + c)^2
        (-32 768 + c (-14 336 (-3 + 4 k) + c (-59 904 + c (5120 (14 + 5 k) + c (-576 (87 + 32 k) +
                        c (24 (767 + 348 k) + c (-2970 + 97 c + 8 (-232 + 15 c) k))))))) +
       4 b^8 (16 384 + c (8192 (-3 + 4 k) + c (39 936 + c (-4096 (14 + 5 k) + c
                       (576 (87 + 32 k) - c (32 (767 + 348 k) +
                           c (c (388 + 55 c + 480 k) - 4 (1485 + 928 k))))))))))}
```

```
A0simp = A0 /. %%%%% // FullSimplify
```

```
{(c (-4 (-2 + c)^18 (-1 + c) - 2 b (-2 + c)^16 (-80 + c (100 - 22 c + c^2 + 16 (-1 + c) k)) -
       b^2 (-2 + c)^14 (-2912 + c (4384 - 1904 c + 392 c^2 - 19 c^3 + 16 (-72 + c (80 + (-10 + c) c)) k)) +
       4 b^3 (-2 + c)^12 (7968 + c (8 (-1761 + 584 k) +
                c (9088 - 5760 k + c (-3384 + 653 c - 32 c^2 + 2 (668 + c (-68 + 7 c)) k)))) +
       2 b^4 (-2 + c)^10 (116 768 + c (32 (-7443 + 2816 k) + c (24 (8471 - 5136 k) + c (16 (-6869 +
                       2532 k) + c (37 626 - 3680 k + c (-6586 + 375 c + 48 (-7 + c) k)))))) +
       2 b^8 (-2 + c)^2 (11 976 704 + c (16 384 (-2396 + 1059 k) + c (512 (129 037 - 71 760 k) +
                 c (256 (-308 677 + 103 528 k) + c (71 822 560 - 1 839 104 k +
                       c (-48 120 672 + 22 759 128 c - 7 292 256 c^2 + 1 499 108 c^3 -
                          178 968 c^4 + 9585 c^5 + 16 (-637 088 + c (521 736 + c (-213 308 +
                                      c (50 054 + c (-6397 + 348 c))))) k)))))) + 8 b^12
        (8192 + c (16 384 (-1 + k) + c (512 (51 - 16 k) + c (-256 (139 + 40 k) + c (32 (1027 + 512 k) +
                       c (-32 (583 + 310 k) + c (6146 + 5 c (-211 + 14 c - 64 k) + 2848 k))))))) -
       2 b^11 (-2 + c) (262 144 + c (32 768 (-16 + 15 k) + c (2048 (389 - 136 k) + c
                  (-512 (1957 + 424 k) + c (1024 (835 + 378 k) + c (-64 (7093 + 3890 k) +
                             c (141 192 - 22 858 c + 1395 c^2 + 64 (1231 + c (-169 + 5 c)) k))))))) -
       2 b^5 (-2 + c)^8 (-603 136 + c (256 (5473 - 2241 k) + c (64 (-23 221 + 13 620 k) + c
                  (48 (21 923 - 7652 k) + c (64 (-8053 + 430 k) +
                       c (32 (4890 + 703 k) + c (-25 142 - 7040 k + c (1589 + 580 k)))))))) +
       b^10 (7 602 176 + c (131 072 (-177 + 101 k) + c (-28 672 (-1395 + 784 k) + c
                  (4096 (-12 877 + 2216 k) + c (2560 (20 781 + 3712 k) +
                       c (-256 (150 745 + 58 146 k) + c (19 307 920 + 9 644 288 k +
                             c^4 (7761 + 3664 k) - 16 c^3 (9875 + 5514 k) +
                             8 c^2 (168 185 + 97 776 k) - 32 c (200 863 + 112 568 k)))))))) +
       4 b^6 (-2 + c)^6 (1 125 376 + c (3584 (-823 + 353 k) + c (3 738 032 - 2 139 904
                 k + c (16 (-204 053 + 68 888 k) +
                    c (2 068 108 - 68 160 k + c (-8 (110 963 + 20 240 k) + c (236 509 +
```

```
                    77 104 k + c (-34 889 - 14 720 k + 3 c (741 + 344 k))))))))) -
   2 b^7 (-2 + c)^4 (-6 111 232 + c (-4096 (-4383 + 1925 k) + c (768 (-34 463 + 19 392 k) +
              c (27 420 864 - 9 142 784 k + c (64 (-331 187 + 8328 k) + c (64 (182 543 +
                    36 892 k) + c (-16 (270 573 + 94 976 k) + c (76 (13 323 + 5996 k) +
                      c (-135 390 + 8093 c - 69 104 k + 4300 c k))))))))) -
   4 b^9 (-2 + c) (4 128 768 + c (212 992 (-61 + 31 k) + c (-2048 (-10 761 + 6076 k) +
              c (512 (-53 975 + 13 704 k) + c (640 (41 381 + 3440 k) +
                  c (-32 (577 585 + 178 198 k) + c (8 992 352 + 4 000 352 k +
                      c (-20 (146 745 + 77 656 k) + c (608 250 + 352 304 k +
                          c (-72 032 + 3717 c + 6 (-7186 + 361 c) k))))))))))))) /
 (((2 + b) (2 + b - 2 c) (2 + b - c) (2 + 2 b - c) (-2 + c) ((-2 + c)^16 +
   2
    b
    (-2 + c)^14
    (16 + c (-3 + 4 k)) + b^2
    (-2 + c)^12
    (448 + 39 c^2 + 56 c (-3 + 4 k)) - 8
    b^3
    (-2 + c)^10
    (-448 + c (84 (3 - 4 k) + c (-117 + 2 c (14 + 5 k)))) + b^4
    (-2 + c)^8
    (17 920 + c (4480 (-3 + 4 k) + c (9360 - 320 c (14 + 5 k) + 9 c^2 (87 + 32 k)))) - 2
    b^5
    (-2 + c)^6
    (-28 672 + c (-8960 (-3 + 4 k) +
          c (-24 960 + 1280 c (14 + 5 k) - 72 c^2 (87 + 32 k) + c^3 (767 + 348 k)))) +
   b^6 (-2 + c)^4 (114 688 + c (43 008 (-3 + 4 k) + c (149 760 + c (3 c (25 056 + c (-6136 + 495 c)) +
                32 c (864 + 29 (-9 + c) c) k - 10 240 (14 + 5 k))))) - 4 b^7 (-2 + c)^2
    (-32 768 + c (-14 336 (-3 + 4 k) + c (-59 904 + c (5120 (14 + 5 k) + c (-576 (87 + 32 k) +
                  c (24 (767 + 348 k) + c (-2970 + 97 c + 8 (-232 + 15 c) k))))))) +
   4 b^8 (16 384 + c (8192 (-3 + 4 k) + c (39 936 + c (-4096 (14 + 5 k) +
                c (576 (87 + 32 k) - c (32 (767 + 348 k) +
                      c (c (388 + 55 c + 480 k) - 4 (1485 + 928 k))))))))))}
```

```
Aplus2simp = Aplus2 /. %%%%%% // FullSimplify
```

```
{(c (4 (-2 + c)^22 (-1 + c) + 2 b (-2 + c)^20 (-96 + c (124 - 30 c + c^2 + 16 (-1 + c) k)) +
      b^2 (-2 + c)^18 (-4256 + c (6736 - 3116 c + 592 c^2 - 25 c^3 + 16 (-88 + c (104 + (-18 + c) c)) k)) +
      b^4 (-2 + c)^14 (-535 104 + c (1 158 592 - 1 021 808 c + 529 808 c^2 - 170 252 c^3 + 28 552 c^4 -
            1531 c^5 + 64 (-5440 + c (8432 + c (-3684 + c (565 + (-20 + c) c)))) k)) -
      8 b^3 (-2 + c)^16 (7216 + c (16 (-845 + 222 k) + c (9112 - 4848 k + c (-3205 +
                c (566 + 13 c (-2 + k) - 172 k) + 1528 k)))) - 4 b^6 (-2 + c)^10 (4 472 064 +
         c (1536 (-8023 + 2787 k) + c (192 (83 459 - 43 084 k) + c (128 (-108 590 + 41 573 k) +
                c (128 (67 843 - 7956 k) + c (-4 (927 285 + 91 928 k) + c (986 592 -
                          143 133 c + 8458 c^2 + 8 (28 664 + c (-5573 + 375 c)) k))))))) +
      2 b^7 (-2 + c)^8 (-33 767 424 + c (-73 728 (-1401 + 506 k) + c (12 288 (-12 733 + 6480 k) +
              c (64 (2 565 913 - 916 332 k) + c (768 (-166 967 + 14 701 k) + c (71 523 616 +
                        9 073 984 k + c (-26 776 208 + 6 275 276 c - 823 340 c^2 + 46 051 c^3 +
                          8 (-869 560 + c (266 714 + c (-40 260 + 2411 c))) k))))))) +
      2 b^13 (-2 + c) (4 718 592 + c (524 288 (-26 + 17 k) + c (-131 072 (-221 + 98 k) +
              c (-352 256 (145 + 4 k) + c (24 576 (2549 + 710 k) +
                    c (-512 (98 307 + 37 780 k) + c (26 197 760 - 8 574 752 c +
                          1 613 656 c^2 - 134 306 c^3 + 247 c^4 + 64 (181 392 +
                            c (-66 802 + c (14 431 + c (-1519 + 40 c)))) k))))))) +
      8 b^5 (-2 + c)^12 (-448 064 + c (1 101 600 - 361 024 k + c (16 (-75 043 + 39 228 k) +
              c (828 916 - 341 904 k + c (-390 660 + 61 248 k +
                    c (115 888 + 6092 k + c (-18 271 - 3196 k + c (1077 + 250 k))))))) +
      8 b^14 (-131 072 + c (-131 072 (-3 + 2 k) + c (65 536 (-13 + 6 k) + c
```

$$
\begin{aligned}
&(20\,480\ (77+4\ k)+c\ (-1024\ (1979+600\ k)+\\
&\quad c\ (256\ (6551+2596\ k)+c\ (-256\ (3443+1542\ k)+c\ (283\,760-49\,810\ c+\\
&\quad 3067\ c^2+160\ c^3+32\ (4454+c\ (-909+80\ c))\ k))))))))-\\
&4\ b^8\ (-2+c)^6\ (48\,439\,296+c\ (24\,576\ (-6647+2460\ k)+c\ (-6144\ (-46\,121+23\,112\ k)+\\
&\quad c\ (128\ (-2\,737\,295+919\,156\ k)+c\ (328\,943\,584-21\,982\,976\ k+\\
&\quad c\ (-128\ (1\,768\,361+255\,137\ k)+c\ (8\ (13\,636\,859+3\,752\,424\ k)+\\
&\quad c\ (-4\ (8\,831\,221+3\,132\,504\ k)+c\ (7\,263\,921+2\,961\,216\ k+\\
&\quad c\ (-853\,822-380\,168\ k+7\ c\ (6269+2940\ k)))))))))))+\\
&4\ b^9\ (-2+c)^4\ (-105\,054\,208+c\ (-32\,768\ (-11\,867+4446\ k)+c\ (49\,152\ (-15\,515+\\
&\quad 7652\ k)+c\ (-512\ (-2\,125\,813+679\,036\ k)+c\ (256\ (-4\,667\,989+246\,480\ k)+\\
&\quad c\ (32\ (30\,546\,471+4\,715\,156\ k)+c\ (-32\ (17\,984\,363+5\,099\,932\ k)+\\
&\quad c\ (237\,584\,432+86\,170\,272\ k+c\ (-16\ (4\,165\,657+1\,734\,236\ k)+\\
&\quad c\ (16\ (752\,726+344\,649\ k)+c\ (-1\,261\,035-621\,728\ k+\\
&\quad 6\ c\ (9733+5094\ k))))))))))))-b^{10}\ (-2+c)^2\\
&(677\,904\,384+c\ (1\,048\,576\ (-2621+983\ k)+c\ (-131\,072\ (-46\,023+22\,348\ k)+\\
&\quad c\ (24\,576\ (-397\,737+122\,828\ k)+c\ (-6144\ (-2\,000\,075+92\,024\ k)+\\
&\quad c\ (-512\ (22\,737\,083+3\,594\,212\ k)+c\ (512\ (15\,802\,043+4\,530\,170\ k)+\\
&\quad c\ (-128\ (31\,702\,465+11\,604\,524\ k)+c\ (32\ (45\,090\,053+\\
&\quad 18\,943\,648\ k)+c\ (-64\ (5\,512\,697+2\,554\,152\ k)+c\\
&\quad (56\,078\,756+28\,229\,760\ k-36\ c\ (143\,997+78\,496\ k)+\\
&\quad c^2\ (210\,639+124\,816\ k))))))))))))-\\
&b^{12}\ (156\,237\,824+c\ (2\,097\,152\ (-289+132\ k)+c\ (-2\,621\,440\ (-535+264\ k)+c\\
&\quad (294\,912\ (-8637+1724\ k)+\\
&\quad c\ (8192\ (432\,469+37\,928\ k)+c\ (-4096\ (874\,463+230\,804\ k)+\\
&\quad c\ (4096\ (630\,597+228\,274\ k)+c\ (-896\ (1\,471\,179+621\,724\ k)+\\
&\quad c\ (144\ (3\,253\,801+1\,530\,320\ k)+c\ (-96\ (1\,164\,635+604\,296\\
&\quad k)+c\ (16\,597\,608+9\,624\,448\ k+c\ (-1\,299\,208+\\
&\quad 33\,321\ c-881\,312\ k+31\,504\ c\ k))))))))))))+\\
&2\ b^{11}\ (-2+c)\ (197\,132\,288+c\ (1\,048\,576\ (-741+310\ k)+c\ (-13\,631\,488\\
&\quad (-128+63\ k)+c\ (8192\ (-365\,755+91\,652\ k)+\\
&\quad c\ (4096\ (970\,931+28\,620\ k)+c\ (-1024\ (3\,812\,833+836\,852\ k)+\\
&\quad c\ (512\ (5\,408\,909+1\,789\,868\ k)+c\ (-32\ (43\,847\,039+17\,505\,196\ k)+\\
&\quad c\ (48\ (10\,412\,101+4\,674\,276\ k)+c\ (-8\ (15\,150\,395+7\,478\,936\\
&\quad k)+c\ (4\ (4\,700\,219+2\,547\,320\ k)+c\ (-1\,644\,986+\\
&\quad 59\,293\ c-992\,344\ k+41\,356\ c\ k))))))))))))))\ /\\
&(2\ (2+b)\ (2+b-2\ c)\ (2+b-c)\ (2+2\ b-c)\ (-2+c)\ (-4\ b\ (-2+c)^3+\\
&\quad (-2+c)^4+\\
&\quad b^2\\
&\quad (16+\\
&\quad c\ (-16+5\ c)))\\
&\quad ((-2+c)^{16}+2\ b\ (-2+c)^{14}\ (16+c\ (-3+4\ k))+\\
&\quad b^2\\
&\quad (-2+c)^{12}\\
&\quad (448+\\
&\quad 39\ c^2+\\
&\quad 56\ c\ (-3+4\ k))-\\
&\quad 8\ b^3\ (-2+c)^{10}\ (-448+c\ (84\ (3-4\ k)+c\ (-117+2\ c\ (14+5\ k))))+\\
&\quad b^4\\
&\quad (-2+c)^8\\
&\quad (17\,920+\\
&\quad c\ (4480\ (-3+4\ k)+c\ (9360-320\ c\ (14+5\ k)+9\ c^2\ (87+32\ k))))-\\
&\quad 2\ b^5\ (-2+c)^6\ (-28\,672+c\ (-8960\ (-3+4\ k)+\\
&\quad c\ (-24\,960+1280\ c\ (14+5\ k)-72\ c^2\ (87+32\ k)+c^3\ (767+348\ k))))+\\
&\quad b^6\ (-2+c)^4\ (114\,688+c\ (43\,008\ (-3+4\ k)+c\ (149\,760+c\ (3\ c\ (25\,056+c\ (-6136+495\ c))+\\
&\quad 32\ c\ (864+29\ (-9+c)\ c)\ k-10\,240\ (14+5\ k)))))-4\ b^7\ (-2+c)^2\\
&\quad (-32\,768+c\ (-14\,336\ (-3+4\ k)+c\ (-59\,904+c\ (5120\ (14+5\ k)+c\ (-576\ (87+32\ k)+\\
&\quad c\ (24\ (767+348\ k)+c\ (-2970+97\ c+8\ (-232+15\ c)\ k)))))))+\\
&\quad 4\ b^8\ (16\,384+c\ (8192\ (-3+4\ k)+c\ (39\,936+c\ (-4096\ (14+5\ k)+\\
&\quad c\ (576\ (87+32\ k)-c\ (32\ (767+348\ k)+
\end{aligned}
$$

y Intercept

It is clear that when none of the predictors are cooperators, the fitness of the focal individual is the population average. Therefore, we can trivially write that c=0.

Relatedness

The relatedness of the focal individual to itself is 1. The relatedness of the individual in position Aminus2 (top left) to the focal individual is also 1. We can calculated relatedness from the case where the cooperators are rare. Therefore, relatedness can simply be calculated as the probability of the individual in any of the positions being cooperators given that the focal individual is a cooperator. Clearly, this increases with k, but does not quite reach one for any of the other predictors of fitness.

```
rAminus2A0 = 1;
rA0A0 = 1;
```

$$\text{rAplus2A0} = \left(k + \text{p5image} + \frac{\text{p4plus}}{2} + \frac{\text{p3plus}}{2} + \frac{\text{p2plus}}{2} + \frac{\text{p1plus}}{2}\right) \Big/ \left(k + \frac{\text{p3plus}}{2} + \frac{\text{p4plus}}{2} + \text{p5image} + \frac{\text{p2}}{2} + \frac{\text{p3}}{2} + \frac{\text{p4plus}}{2} + \frac{\text{p1}}{2} + \frac{\text{p2}}{2} + \frac{\text{p3plus}}{2} + \text{p0} + \frac{\text{p1}}{2} + \frac{\text{p2plus}}{2} + \text{p0} + \frac{\text{p1}}{2} + \frac{\text{p1plus}}{2} + \frac{\text{p2plus}}{2} + \frac{\text{p1plus}}{2}\right);$$

$$\text{rBminus2A0} = \left(k + \frac{\text{p2}}{2} + \frac{\text{p3}}{2} + \frac{\text{p4plus}}{2} + \frac{\text{p1}}{2} + \frac{\text{p2}}{2} + \frac{\text{p3plus}}{2} + \text{p0} + \frac{\text{p1}}{2} + \frac{\text{p2plus}}{2} + \text{p0} + \frac{\text{p1}}{2} + \frac{\text{p1plus}}{2} + \frac{\text{p2plus}}{2} + \frac{\text{p1plus}}{2}\right) \Big/ \left(k + \frac{\text{p3plus}}{2} + \frac{\text{p4plus}}{2} + \text{p5image} + \frac{\text{p2}}{2} + \frac{\text{p3}}{2} + \frac{\text{p4plus}}{2} + \frac{\text{p1}}{2} + \frac{\text{p2}}{2} + \frac{\text{p3plus}}{2} + \text{p0} + \frac{\text{p1}}{2} + \frac{\text{p2plus}}{2} + \text{p0} + \frac{\text{p1}}{2} + \frac{\text{p1plus}}{2} + \frac{\text{p2plus}}{2} + \frac{\text{p1plus}}{2}\right);$$

$$\text{rB0A0} = \left(k + \text{p0} + \frac{\text{p1}}{2} + \frac{\text{p2plus}}{2} + \text{p0} + \frac{\text{p1}}{2} + \frac{\text{p1plus}}{2} + \frac{\text{p2plus}}{2} + \frac{\text{p1plus}}{2}\right) \Big/ \left(k + \frac{\text{p3plus}}{2} + \frac{\text{p4plus}}{2} + \text{p5image} + \frac{\text{p2}}{2} + \frac{\text{p3}}{2} + \frac{\text{p4plus}}{2} + \frac{\text{p1}}{2} + \frac{\text{p2}}{2} + \frac{\text{p3plus}}{2} + \text{p0} + \frac{\text{p1}}{2} + \frac{\text{p2plus}}{2} + \text{p0} + \frac{\text{p1}}{2} + \frac{\text{p1plus}}{2} + \frac{\text{p2plus}}{2} + \frac{\text{p1plus}}{2}\right);$$

$$\text{rBplus2A0} = \left(k + \frac{\text{p2plus}}{2} + \frac{\text{p1plus}}{2}\right) \Big/ \left(k + \frac{\text{p3plus}}{2} + \frac{\text{p4plus}}{2} + \text{p5image} + \frac{\text{p2}}{2} + \frac{\text{p3}}{2} + \frac{\text{p4plus}}{2} + \frac{\text{p1}}{2} + \frac{\text{p2}}{2} + \frac{\text{p3plus}}{2} + \text{p0} + \frac{\text{p1}}{2} + \frac{\text{p2plus}}{2} + \text{p0} + \frac{\text{p1}}{2} + \frac{\text{p1plus}}{2} + \frac{\text{p2plus}}{2} + \frac{\text{p1plus}}{2}\right);$$

Inclusive Fitness Calculation

```
IFcalculation = Bminus2simp * rBminus2A0 + B0simp * rB0A0 + Bplus2simp * rBplus2A0 +
   Aminus2simp * rAminus2A0 + A0simp + Aplus2simp * rAplus2A0 // FullSimplify
```

$$\left\{\left(4\, b\, \left((-4+b)\, b - (-2+c)^2\right) c^2\right) \Big/ \left((2+b-c)\, \left((-2+c)^4 + 2\, b\, (-2+c)^2\, (4 + c\, (3 + 2\, k)) + b^2\, (16 + c\, (24 + c + 16\, k))\right)\right)\right\}$$

The condition for this to be greater than 0 is exactly the
same as what we calculated in the population genetics framework,
although it does not use simplifications. Therefore, for example,
the function is decreasing in k,
which is unsurprising because if k is large then almost all of the cooperators have
a fitness equal to 1. However, the postive/negative condition is unchanged.

Altruism between species?

We can easily check that the within species effect cannot be positive when individuals in both species are used as predictors

```
withinspecieseffect =
 Aminus2simp * rAminus2A0 + A0simp + Aplus2simp * rAplus2A0 // FullSimplify
```

```
{(4 b c^2 (-4 (-2 + c)^24 (-1 + c) - 2 b (-2 + c)^22 (-104 + c (132 - 30 c + c^2 + 16 (-1 + c) k)) -
        b^2 (-2 + c)^20 (-5024 + c (7760 - 3404 c + 620 c^2 - 27 c^3 + 16 (-96 + c (112 + (-18 + c) c)) k)) +
        2 b^3 (-2 + c)^18 (37 376 + c (64 (-1067 + 266 k) + c (43 896 - 22 784 k + c
                    (-14 648 + 2446 c - 115 c^2 + 8 (848 + c (-95 + 7 c)) k)))) - b^4 (-2 + c)^16
          (-766 016 + c (256 (6337 - 1804 k) + c (16 (-85 597 + 43 760 k) + c (667 568 - 294 400 k +
                      c (-197 852 + 47 648 k + c (30 472 - 1563 c + 200 (-16 + c) k)))))) -
        4 b^5 (-2 + c)^14 (-1 431 232 + c (3 461 024 - 1 070 208 k + c (-3 618 864 + 1 820 608
                    k + c (2 327 072 - 974 080 k + c (-994 468 + 202 432 k +
                          c (264 364 - 6008 k + c (-37 419 - 3140 k + 14 c (145 + 19 k)))))))) -
        2 b^7 (-2 + c)^10 (-69 543 936 + c (-3072 (-69 155 + 23 292 k) + c (3072 (-100 631 + 48 929 k) +
                  c (256 (1 158 364 - 444 087 k) + c (256 (-799 301 + 132 665 k) + c (16 (6 252 625 +
                                    171 308 k) + c (-16 (2 060 163 + 330 812 k) + c (6 852 820 - 808 896
                                          c + 41 877 c^2 + 4 (430 332 + c (-64 390 + 3863 c)) k)))))))) +
        4 b^6 (-2 + c)^12 (8 056 576 + c (256 (-85 913 + 28 004 k) + c (27 465 728 - 13 587 584
                    k + c (-21 981 968 + 8 775 296 k + c (72 (170 579 - 30 788 k) +
                          c (-4 639 940 - 52 096 k + c (4 (273 197 + 37 858 k) +
                                c (-141 639 - 31 376 k + c (7685 + 2126 k))))))))) +
        4 b^8 (-2 + c)^8 (115 974 144 + c (49 152 (-8011 + 2748 k) + c (-6144 (-106 753 +
                      51 004 k) + c (1024 (-717 193 + 266 100 k) + c (603 018 080 - 94 966 784 k +
                          c (-16 (22 576 739 + 779 904 k) + c (544 (280 715 + 47 738 k) +
                                c (-12 (3 646 817 + 963 072 k) + c (8 045 685 + 2 701 528 k +
                                      c (-858 772 + 41 019 c - 339 344 k + 18 294 c k)))))))))) +
        32 b^15 (131 072 + c (65 536 (-7 + 4 k) + c (-32 768 (-29 + 14 k) + c (16 384 (-93 + 7 k) +
                      c (23 552 (77 + 16 k) + c (-512 (2941 + 1042 k) + c (128 (6605 + 3002 k) +
                                c (-64 (4846 + 2671 k) + c (69 218 + 45 984 k + c (-7851 - 6720 k +
                                          5 c (36 + 5 c + 80 k))))))))))) - 4 b^9 (-2 + c)^6
          (-298 811 392 + c (-16 384 (-68 461 + 23 652 k) + c (24 576 (-85 867 + 40 320 k) +
                  c (-8192 (-330 157 + 119 529 k) + c (128 (-20 113 901 + 3 091 040 k) +
                          c (64 (28 493 239 + 1 031 890 k) + c (-32 (29 366 837 + 5 090 058 k) +
                                  c (343 167 256 + 92 655 680 k + c (-4 (21 480 017 + 7 400 784 k) +
                                          c (13 996 180 + 5 716 672 k + 6 c^2 (9581 + 5037 k) -
                                              7 c (191 339 + 89 452 k))))))))))) +
        16 b^14 (-2 + c) (-2 490 368 + c (-65 536 (-131 + 72 k) + c (163 840 (-107 + 50 k) +
                  c (-8192 (-3299 + 372 k) + c (-1024 (30 037 + 4736 k) + c (2048 (12 041 + 3755
                                  k) + c (-128 (105 965 + 44 038 k) + c (32 (155 489 + 79 268 k) +
                                    c (-2 (576 699 + 353 456 k) + c (150 517 + 113 136 k +
                                              c (-8161 - 10 c + 40 (-218 + 5 c) k))))))))))) +
        b^12 (-2 + c) (-1 889 533 952 + c (-1 048 576 (-8059 + 3008 k) + c (1 048 576
                    (-18 949 + 8812 k) + c
                    (-524 288 (-62 653 + 20 176 k) + c (16 384 (-2 508 169 + 254 752 k) +
                          c (65 536 (595 137 + 52 081 k) + c (-4096 (6 776 221 + 1 512 590 k) +
                                c (1024 (14 293 953 + 4 589 752 k) + c (-32 (176 269 777 +
                                              70 452 944 k) + c (240 (6 472 719 + 3 053 488 k) +
                                              c (-294 249 040 + 35 785 928 c - 2 436 258 c^2 + 65 097
                                                  c^3 + 16 (-10 035 696 + c (1 408 296 + c (-112 474 +
                                                  3757 c))) k))))))))))) + b^10 (-2 + c)^4
          (2 358 771 712 + c (524 288 (-18 597 + 6412 k) + c (-262 144 (-78 210 + 36 119 k) +
                  c (98 304 (-301 377 + 107 392 k) + c (2048 (15 660 511 - 2 408 512 k) +
                          c (-1024 (25 590 691 + 874 028 k) + c (256 (62 192 229 + 10 764 262 k) +
                                c (-64 (110 413 819 + 30 086 472 k) + c (64 (35 049 839 +
                                              12 248 998 k) + c (-96 (5 139 369 + 2 138 992 k) +
                                              c (71 173 812 + 34 149 088 k + c (-6 039 352 + 226 817
                                                  c + 8 (-411 644 + 17 543 c) k)))))))))))) -
        2 b^13 (-350 224 384 + c (-1 048 576 (-1483 + 596 k) + c (1 048 576 (-3531 + 1670 k) +
                  c (-262 144 (-24 001 + 7000 k) + c (16 384 (-495 167 + 25 152 k) +
                          c (8192 (963 447 + 134 830 k) + c (-4096 (1 394 539 + 378 096 k) +
```

```
                         c (13 312 (228 279 + 83 518 k) + c (- 288 (4 065 003 + 1 809 008 k) +
                                c (318 385 328 + 166 142 976 k + c (- 176 (331 855 +
                                      201 104 k) + c (6 644 456 - 393 374 c + 7311 c^2 + 32
                                      (147 796 + c (- 10 831 + 310 c)) k)))))))))))) -
    4 b^11 (- 2 + c)^2 (- 875 036 672 + c (- 262 144 (- 15 149 + 5172 k) + c (262 144
              (- 35 303 + 16 057 k) + c (- 65 536 (- 227 314 + 80 469 k) +
                c (2048 (- 8 825 489 + 1 389 568 k) + c (1024 (16 341 355 + 479 166 k) + c
                        (- 256 (45 758 107 + 7 813 058 k) + c (128 (47 864 302 + 13 080 519 k) +
                            c (- 320 (7 376 915 + 2 601 516 k) + c (8 (82 039 383 +
                                      34 563 268 k) + c (- 68 (1 870 979 + 911 640 k) +
                                      c (16 185 170 + 9 005 064 k + c^2 (38 072 + 28 134 k) -
                                      17 c (70 525 + 44 816 k))))))))))))))) /
((2 + b) (2 + b - 2 c) (2 + b - c) (2 + 2 b - c) (- 2 + c) (- 4 b (- 2 + c)^3 +
    (- 2 +
       c)^4 +
    b^2 (16 + c (- 16 + 5 c))) ((- 2 + c)^4 + 2 b
     (- 2 + c)^2
     (4 +
        c
         (3 + 2 k)) +
    b^2 (16 + c (24 + c + 16 k))) ((- 2 + c)^16 +
    2
     b
     (- 2 + c)^14
     (16 +
        c (- 3 + 4 k)) +
    b^2 (- 2 + c)^12 (448 + 39 c^2 + 56 c (- 3 + 4 k)) -
    8
     b^3
     (- 2 + c)^10
     (- 448 +
        c (84 (3 - 4 k) + c (- 117 + 2 c (14 + 5 k)))) +
    b^4 (- 2 + c)^8 (17 920 + c (4480 (- 3 + 4 k) + c (9360 - 320 c (14 + 5 k) + 9 c^2 (87 + 32 k)))) -
    2
     b^5
     (- 2 + c)^6
     (- 28 672 +
        c (- 8960 (- 3 + 4 k) +
           c (- 24 960 + 1280 c (14 + 5 k) - 72 c^2 (87 + 32 k) + c^3 (767 + 348 k)))) +
    b^6 (- 2 + c)^4 (114 688 + c (43 008 (- 3 + 4 k) + c (149 760 + c (3 c (25 056 + c (- 6136 + 495 c)) +
                32 c (864 + 29 (- 9 + c) c) k - 10 240 (14 + 5 k))))) - 4 b^7 (- 2 + c)^2
     (- 32 768 + c (- 14 336 (- 3 + 4 k) + c (- 59 904 + c (5120 (14 + 5 k) + c (- 576 (87 + 32 k) +
                   c (24 (767 + 348 k) + c (- 2970 + 97 c + 8 (- 232 + 15 c) k))))))) +
    4 b^8 (16 384 + c (8192 (- 3 + 4 k) + c (39 936 + c (- 4096 (14 + 5 k) +
                c (576 (87 + 32 k) - c (32 (767 + 348 k) +
                      c (c (388 + 55 c + 480 k) - 4 (1485 + 928 k))))))))))}
```

```
withinspecieseffect[[1]];
```

```
Reduce[% > 0 && 1 > c > 0 && b > 0 && k > 0, {b, c, k}]
```

```
False
```

ORIGINAL ARTICLE

doi:10.1111/evo.12466

A BIOLOGICAL MARKET ANALYSIS OF THE PLANT-MYCORRHIZAL SYMBIOSIS

Gregory A. K. Wyatt,[1,2] E. Toby Kiers,[3] Andy Gardner,[4] and Stuart A. West[1]

[1]*Department of Zoology, University of Oxford, Oxford OX1 3PS, United Kingdom*

[2]*E-mail: gregory.wyatt@zoo.ox.ac.uk*

[3]*Institute of Ecological Sciences, Faculty of Earth and Life Sciences, Vrije Universiteit, De Boelelaan 1085, 1081 HV, Amsterdam, The Netherlands*

[4]*School of Biology, University of St Andrews, Dyers Brae, St Andrews KY16 9TH, United Kingdom*

Received December 11, 2013
Accepted May 27, 2014

It has been argued that cooperative behavior in the plant-mycorrhizal mutualism resembles trade in a market economy and can be understood using economic tools. Here, we assess the validity of this "biological market" analogy by investigating whether a market mechanism—that is, competition between partners over the price at which they provide goods—could be the outcome of natural selection. Then, we consider the conditions under which this market mechanism is sufficient to maintain mutualistic trade. We find that: (i) as in a market, individuals are favored to divide resources among trading partners in direct relation to the relative amount of resources received, termed linear proportional discrimination; (ii) mutualistic trade is more likely to be favored when individuals are able to interact with more partners of both species, and when there is a greater relative difference between the species in their ability to directly acquire different resources; (iii) if trade is favored, then either one or both species is favored to give up acquiring one resource directly, and vice versa. We then formulate testable predictions as to how environmental changes and coevolved responses of plants and mycorrhizal fungi will influence plant fitness (crop yields) in agricultural ecosystems.

KEY WORDS: **Bargaining power, Cournot competition, Darwinian agriculture, mutualism, partner choice, Ricardian economics.**

Mutualistic cooperation between species poses a problem for evolutionary theory (Sachs et al. 2004; Foster and Wenseleers 2006; Leigh 2010). The problem is that—all else being equal—cheats who reduce their investment in a cooperative trait, while enjoying the benefits of others' investment, will be favored by natural selection (West et al. 2007; Ghoul et al. 2014). Consequently, natural selection will act to disfavor costly cooperation. Within a species, genetic relatedness between social partners may result in kin selection that directly favors selflessness (Hamilton 1964), whereas the emergence and stability of cooperation between species requires additional mechanisms (Foster and Wenseleers 2006, but see Frank 1994; Wyatt et al. 2013).

A number of empirical studies have shown that mutualistic cooperation can be stabilized when one of the partners exerts control over the other (Agrawal and Karban 1997; Korb and Aanen 2003; Edwards et al. 2006; Johnstone and Bshary 2008; McFall-Ngai 2008). That is, members of the controlled species either irreversibly commit to their mutualistic partner or cannot choose at all, and the controlling partner employs some mechanism to enforce or select for cooperation (Noë 1990; Bull and Rice 1991; Pellmyr and Huth 1994; West and Herre 1994; West et al. 2002a, b; Kiers et al. 2003; Frean and Abraham 2004; Goto et al. 2010; Jander and Herre 2010; Archetti et al. 2011). For example, legume species invest fewer resources into root nodules containing rhizobia that fix less nitrogen (Kiers et al. 2003; Simms et al. 2006; Oono et al. 2009, 2011; Regus et al. 2014).

In contrast, in the mutualism formed between plants and mycorrhizal fungi, neither partner wields total control. Here, every individual may interact with multiple partners simultaneously: multiple mycorrhizal fungi can colonize a single plant host, and each of these fungal individuals can potentially interact with multiple plant hosts (Selosse et al. 2006; Kiers and Denison 2008). Empirical work has shown that plants supply more carbohydrates to fungal partners that provide more phosphorus, and vice versa (Hammer et al. 2011; Kiers et al. 2011; Fellbaum et al. 2012, 2014). Biological market theory has emerged as a tool to study

EVOLUTION
INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

Evolution 68-9: 2603–2618

how cooperation can be stabilized in many-to-many interactions (Noë et al. 1991; Noë 1992; Noë and Hammerstein 1994, 1995; Werner et al. 2014), having originally been applied to systems where control is wielded by a single partner class (Selten and Shmida 1991; Peleg and Shmida 1992; Peleg et al. 1992). The strength of biological market theory is to make networks of two-way trading connections tractable by treating them as if partners were trading goods within a central marketplace (Noë and Hammerstein 1994).

However, the validity of this biological market approach in analyzing many-to-many interactions has yet to be formally evaluated. First, previous theory assumes the reward functions used by at least one class of partner (Schwartz and Hoeksema 1998; Hoeksema and Schwartz 2001, 2003; Kummel and Salant 2006). The question of which rewarding schemes natural selection will lead to has not been addressed. Natural selection could easily lead to consistent pricing across partners, or it could instead lead to discriminatory pricing, where different individuals face a different reward function. Second, previous theoretical models have assumed that mutually beneficial trade is made, rather than investigating when trade would be evolutionarily stable (Schwartz and Hoeksema 1998; Hoeksema and Schwartz 2001, 2003; Grman et al. 2012). There are many situations where trade or cooperation would be mutually beneficial but is not favored by natural selection, as famously illustrated by the Prisoner's Dilemma. Third, previous biological market models have assumed that markets comprise either very few or else infinitely many traders (Schwartz and Hoeksema 1998; Hoeksema and Schwartz 2001, 2003; Akçay and Roughgarden 2007; de Mazancourt and Schwartz 2010; Akçay and Simms 2011; Grman et al. 2012). Incorporating the more realistic assumption of finite markets with a variable number of participants may lead to single individuals exerting partial control over the overall supply of a good—termed "bargaining power" (Johnson et al. 2012). This could lead to the collapse of trade (Baldwin 1948; Rieber 1982).

Here, we assess the validity of the biological market analogy, developing a market model based on current knowledge of the mycorrhizal symbiosis. We derive the conditions under which individuals receive the same market exchange rate for their goods and under which trade is maintained. When these conditions are satisfied, we apply an economic model where individuals compete to supply goods and services in biological settings. We use our market model to explore the selective forces behind specialization in mutualisms. Finally, we consider the specific application of our model to the mycorrhizal symbiosis and the implications for agricultural scenarios. Specifically, we examine the consequences of: (i) variation in the number of trading partners of each species; (ii) the addition of phosphorus fertilizers; and (iii) rising CO_2 levels.

Model and Analyses

We develop a model for the cooperative exchange of two resources between two species. We phrase our model in terms of the plant-mycorrhizal mutualism in which carbon from the host is exchanged for phosphorus from the fungus. Here, we consider only exchange of these two resources, although in reality the fungal partner can provide other nutrients, such as nitrogen. While we examine cases of particular relevance to that interaction, our aim is to keep our overall model general so that it can be applied to other mutualisms. Consequently, in the general formulation of our model we allow mycorrhizal fungi to acquire carbon directly, even though in the arbuscular mycorrhizal (AM) symbiosis, the fungal partner is an obligate biotroph that is completely dependent on its host for carbon (Parniske 2008). Our approach allows us to explore the reasons natural selection has favored reliance on host-derived carbon. To explain why mycorrhizal fungi do not acquire carbon directly, we must work out the fitness consequences for hypothetical fungi that can directly obtain carbon and show that natural selection will have eliminated them. This approach of considering a wider range of possibilities leads to a better understanding of the phenomena actually observed (Eddington 1928).

DIRECT RESOURCE ACQUISITION

We consider a population of plants and mycorrhizal fungi that require carbon and phosphorus for growth. We assume that there is a linear trade-off between the resources invested into carbon and phosphorus acquisition, although other trade-offs would yield qualitatively identical solutions (Hoeksema and Schwarz 2003). Specifically, we assume that individuals acquire a proportion x of the maximum amount of carbon that they can acquire and a proportion 1-x of the maximum amount of phosphorus. These maximum amounts are C_p and P_p for plants, and C_m and P_m for mycorrhizae (in practice, $C_m = 0$ for mycorrhizal fungi). In principle, increased growth in mutualism could mean that these maximum amounts increase. We neglect such effects because the primary purpose of our model is to investigate the influence of partner discrimination in mutualisms. Hence, plants acquire $x_p C_p$ units of carbon and (1-x_p)P_p units of phosphorus, whilst mycorrhizal fungi acquire $x_m C_m$ units of carbon and (1-x_m)P_m units of phosphorus. The maximum amount of a resource that an individual can acquire depends on two factors—the availability of that resource in the environment and the inherent ability of individuals of that species to acquire it. For biological realism, we also give mycorrhizal fungi a small initial endowment of carbon, I. This reflects the trace amounts of carbon that fungal spores require to develop, as well as their ability to maintain at least some carbon independence from trade with specific host plants, for example by drawing down from common mycorrhizal networks (Giovannetti et al. 2004; Sbrana et al.

2011). Nonetheless, it is clear that this amount must be small as mycorrhizal fungi grow poorly except in symbiosis.

MUTUALISTIC TRADE

In addition to acquiring carbon and phosphorus directly, we allow plants and mycorrhizal fungi to engage in mutualistic trade. Each plant has n_m mycorrhizal fungi as trading partners and each fungus has n_p plants. Plants transfer a proportion q_p of their directly acquired carbon to mycorrhizal partners and the fungi transfer a proportion q_m of their directly acquired phosphorus to plants.

What strategy for sharing resources between trading partners does natural selection favor? In principle, an individual could transfer all traded resources to one partner, could share equally between all partners, or could use any intermediate strategy. To determine the optimal sharing strategy across all partners, we only need to work out the relative amounts transferred to any pair of partners. This works because it allows us to consider the amount allocated to any given partner versus any other. With this information, we can calculate the ratios allocated between a sequence of as many partners as a focal individual has (a:b:c:d:e:f etc.). A plant is favored to allocate a proportion f_{p1} of an amount of carbon C_t to fungus m_1 and a proportion 1-f_{p1} of the amount C_t to m_2, so as to maximize phosphorus received in return. The phosphorus received from each fungus is a proportion, f_{m1} or f_{m2}, of the phosphorus that each fungus trades, P_{t1} and P_{t2}, respectively. The proportions f_{m1} and f_{m2} are functions of the focal plant's ($f_{p1}C_t$ or $(1\text{-}f_{p1})C_t$) and all other plants' (C_{re1} or C_{re2}) carbon allocation to that fungus. The focal plant maximizes its phosphorus from trade when the equation $P_r = f_{m1}\left(f_{p1}C_t, C_{re1}\right)P_{t1} + f_{m2}\left(\left(1 - f_{p1}\right)C_t, C_{re2}\right)P_{t2}$ is maximized. In the Appendix we show that:

Result 1—Individuals are favored use a rule that allocates resources among partners of the other species in direct proportion to the relative amount of benefits they receive from each partner, when others do likewise. Specifically, a linear "proportional discrimination" (Tang-Martinez 2001) allocation is an evolutionarily stable strategy (ESS, Maynard Smith and Price 1973).

To illustrate, we find that in populations using linear proportional discrimination, if a plant receives two-thirds of the benefits it acquires through trade from one mycorrhizal fungus and one-third from another, it sends two-thirds of the total carbon it allocates for trade to the former and one-third to the latter. No other strategy arising in such a population can invade. Plants that either allocate all carbon to one partner or split carbon equally between all partners would have a lower fitness and hence be eliminated by natural selection.Linear proportional discrimination leads to individuals that receive the same exchange rate for resources or services traded in many mutualistic contexts, including our model (see Appendix for details). We still need to show that quantities traded in our model can be nonzero. We do this by showing that when members of both species are simultaneously maximizing their fitness, their evolved strategy includes sending resources to members of the other species. Henceforth, we assume that all individuals adopt a linear proportional discrimination allocation, as it is an ESS.

EVOLUTION OF RESOURCE ACQUISITION AND TRANSFER

After acquisition and trading of resources, each individual has a final amount of carbon (C_f) and phosphorus (P_f). These amounts jointly determine fitness. We choose fitness functions so that: (i) an individual's fitness is zero unless they possess both resources; (ii) increasing the level of either resource gives diminishing marginal fitness returns; (iii) there are constant returns to scale, so that a change in fitness due to different trading dynamics can be measured against a consistent baseline as resource availability changes. Specifically, we assume that plant fitness is given by $w_p = C_{fp}{}^{a}P_{fp}{}^{1\text{-}a}$, and mycorrhizal fitness is given by $w_m = C_{fm}{}^{b}P_{fm}{}^{1\text{-}b}$, where the exponents $0 < a < 1$ and $0 < b < 1$ mediate the marginal fitness effects of additional resources. These functions are commonly used to satisfy the above requirements in the economics literature and are termed "Cobb-Douglas functions" (Cobb and Douglas 1928).

We now re-write these fitness functions, replacing the final amounts of carbon and phosphorus (C_f and P_f) with explicit expressions for the amounts acquired and traded for (see Table 1 for a list of parameters and evolved strategies used in the analysis). We consider a focal plant with a strategy pair (x_p, q_p), which may not be the ESS, in a population with mean proportions of carbon acquired x'_p and x'_m, and allocations to trade q'_p and q'_m where resource acquisition and trading allocations are uncorrelated.

The plant acquires an amount x_pC_p of carbon and retains a fraction 1-q_p of this, so that it has a final quantity of carbon given by $C_{fp} = x_pC_p(1\text{-}q_p)$. The plant also acquires an amount of phosphorus $(1\text{-}x_p)P_p$ directly and receives an amount of phosphorus $P_r = P_t n_m s_p$ via trade, where P_t is the quantity phosphorus each mycorrhizal fungus trades, n_m is the total number of mycorrhizal fungi hosted by the plant and s_p is the share of the traded phosphorus the focal plant acquires (see Appendix for a derivation of s_p in terms of model parameters and strategies). Mycorrhizal fungi each acquire, on average, a quantity $(1\text{-}x'_m)P_m$ of phosphorus and allocate a proportion q'_m of it to trade. Hence, the average quantity of phosphorus allocated to trade by each fungus is $P_t = (1\text{-}x'_m)P_m q'_m$. This means that the total quantity of phosphorus the focal plants trades for is $P_r = (1\text{-}x'_m)P_m q'_m n_m s_p$. The final quantity of phosphorus available to plants is the sum of the quantity they take up from the soil and the quantity they acquire via trade, so $P_{fp} = (1\text{-}x_p)P_p + (1\text{-}x'_m)P_m q'_m n_m s_p$. Now, we replace C_{fp} and P_{fp} in the focal plant's

Table 1. Parameters and evolved strategies used in the analysis.

Symbol:	Definition:
$C_{p/m}$:	Quantity of carbon available for an individual plant/mycorrhizal fungus to acquire
C_t:	Quantity of carbon traded by an individual plant
C_{re}:	Quantity of phosphorus received in trade by an individual mycorrhizal fungus, excluding what it receives from the focal plant
I:	Initial carbon endowment of mycorrhizal fungi
$P_{p/m}$:	Quantity of phosphorus available for an individual plant/mycorrhizal fungus to acquire
P_r:	Quantity of phosphorus received in trade by an individual plant
P_t:	Quantity of phosphorus traded by an individual mycorrhizal fungus
$n_{p/m}$:	The number of heterospecific trading partners available to each plant/mycorrhizal fungus
a:	Exponent that mediates the marginal effect of additional carbon or phosphorus on plant fitness
b:	Exponent that mediates the marginal effect of additional carbon and phosphorus on mycorrhizal fungus fitness
$x_{p/m}$:	Proportion of resources that plants/mycorrhizal fungi allocate to acquiring carbon. They allocate the remainder of their resources to acquiring phosphorus. $'$ denotes the average across the population
$q_{p/m}$:	Proportion of carbon/phosphorus that plants/mycorrhizal fungi allocate to trade. $'$ denotes the average across the population

fitness function with the equations in this paragraph to yield

$$w_p = (x_p C_p(1-q_p))^a((1-x_p)P_p + n_m(1-x'_m)P_m q'_m s_p)^{(1-a)}. \tag{1a}$$

Similarly, a focal mycorrhizal fungus' fitness is

$$w_m = (I + x_m C_m + n_p x'_p C_p q'_p s_m)^b((1-x_m)P_m(1-q_m))^{(1-b)}. \tag{1b}$$

We then study the evolution of the four variables that determine resource acquisition (x_p and x_m) and transfer (q_p and q_m). We find the ESSs (x_p*, q_p*) for plants and (x_m*, q_m*) for fungal partners. The ESS for plants determines that for mycorrhizal fungi and vice versa, so we denote pairs of coevolutionary ESSs as (x_p*, q_p*, x_m*, q_m*). Four ESS scenarios are possible: (i) there is no mutualistic trade ($q_p = q_m = 0$); (ii) plants acquire only carbon directly ($x_p = 1$) and mycorrhizal fungi acquire only phosphorus directly ($x_m = 0$); (iii) plants acquire only carbon directly ($x_p = 1$), but mycorrhizal fungi acquire both phosphorus and carbon directly ($0 < x_m < 1$); (iv) plants acquire both phosphorus and carbon directly ($0 < x_p < 1$), but mycorrhizae acquire only phosphorus directly ($x_m = 0$) (see Appendix for details). Scenario (iii) cannot occur in nature, but as discussed above it is essential to consider the scenario in order to explain why it does not occur.

We use our model and the ESSs it yields to explore three questions. First, when is mutualistic trade evolutionarily stable? Second, when is one of the partners favored to acquire only one resource, and hence rely completely on the other species for the other resource? Third, what are the consequences for agricultural yields due to changes in partner numbers (n_p and n_m), atmospheric carbon concentrations (C_p and C_m), and phosphorus fertilizer availability (P_p and P_m)?

Under what conditions do individuals engage in mutualistic trade?

We find a pair of coevolutionary ESSs with trade (q_p, $q_m > 0$) when

$$\frac{bC_p P_m}{P_p((1-b)I + bC_m)} > \frac{n_p n_m}{(n_p - 1)(n_m - 1)}. \tag{2}$$

This result shows that a market analogy is valid, as natural selection can both maintain trade and lead to all individuals receiving the same market exchange rate for their goods in our model. The result also shows that we should only expect trade when ecological parameters satisfy the conditions in inequality (2), even though mutually beneficial trade is possible under all parameter values in our model.

Result 2—Mutualistic trade is promoted when individuals in both species have less access to the resource that they can acquire by trade (P_p, C_m, or I decreases) or are more efficient at acquiring the resource that they cannot acquire by trade (C_p or P_m increases) (Fig. 1). These changes increase the benefit of acquiring resources by trade.

Result 2 is in line with previous predictions that mutual dependence increases the likelihood of mutualistic cooperation (Foster and Wenseleers 2006; Leigh 2010) and trade (Cordella and Gabszewicz 1997).

Result 3—Mutualistic trade is promoted when the number of potential competitors in each species (n_p or n_m) increases (Fig. 1). The increase in mycorrhizal partner numbers decreases a single individual's control over total phosphorus traded (i.e., its bargaining power). With this increase, a focal mycorrhizal fungus benefits less from manipulating the total amount of phosphorus in the market to increase its value (Cordella and Gabszewicz 1998). Instead, it benefits relatively more from competing intensely for carbon by trading phosphorus, thus promoting trade.

To illustrate result 3, consider the scenario where n mycorrizal fungi providing an equal amount of phosphorus to a plant. Each fungus therefore gets a fraction $1/n$ of the traded carbon. Now suppose that one mycorrhizal fungus doubles its supply of phosphorus to the plant, thus receiving $2/(n+1)$ of the traded carbon in return. The carbon returned to that fungus is increased by a factor $2n/(n+1)$, which increases with larger n (Fig. 2). A similar result has already been derived in the economics literature (Cordella and Gabscewicz 1997). However, it runs counter to widespread thinking in biology that cooperation is more likely to be outcompeted by selfishness as the number of social partners increases (Frank 1994).

Result 4—The absence of trade is always evolutionarily stable, except when at least one species can acquire only one resource without trading (C_p, P_p, C_m, and I, or $P_m = 0$). In general, if individuals in one of the species are not trading, it does not pay for members of the other species to engage in mutualistic trade. However, if individuals in one species cannot acquire one resource by other means, they must trade to survive. This illustrates that biological cooperation is easier to maintain than to initiate, as has been shown elsewhere (Axelrod and Hamilton 1981).

When does selection favor specialization?

We now explore the conditions that favor specialization. Here, we use specialization to mean when individuals of a species acquire only one resource, and rely on trade for the other.

Result 5—Whenever trade is favored, either one or both species are favored to stop acquiring one resource directly, and only acquire it through trade ($x_p = 1$ or $x_m = 0$ at each pair of trading ESSs). The reverse also holds. Whenever individuals in one species are favored to adopt a strategy where they forsake acquiring one resource directly, trade is favored.

We find that when trade is favored, plants are favored to acquire carbon, but not phosphorus, when

$$P_p \leq \frac{bC_p(n_p-1)(n_p-1+a)(n_m-1)n_m P_m}{n_p((1-a)C_p(n_p-1)n_p n_m + I(1-b)(n_p-1+a)n_m^2 - (1-a)bC_p(n_p-1)n_p)} \tag{3a}$$

(Fig. 3). When trade is favored, mycorrhizal fungi are favored to acquire phosphorus, but not carbon, when

$$C_p \geq \frac{(bC_m - I(1-b))(n_p-1+a)n_m^2}{(1-a)(n_p-1)n_p(n_m-b)}. \tag{3b}$$

Result 6—Specialization is more favored as individuals become less efficient at acquiring the resource they trade for (P_p, C_m, and/or I are small relative to P_m and/or C_p). These changes increase the marginal benefit of acquiring more of the resource that they cannot acquire through trade.

Result 7—Specialization is more favored when individuals interact with fewer members of the other species, or when individuals of the other species interact with more trading partners. For example, decreasing the number of plants (n_p) or increasing the number of mycorrhizal fungi (n_m) increases the total quantity of phosphorus relative to the total quantity of carbon in the market. This increases the scarcity, and therefore value, of the carbon. This favors plants that invest relatively more in carbon acquisition, whether for their own use or to benefit from its increased value in trade.

These results demonstrate why mycorrhizal fungi are, in general, not favored to acquire carbon directly. Once the fungus is engaged in a stable mutualistic relationship where it is a specialized partner, it gains no fitness benefits from the ability to acquire carbon directly. Consequently, mycorrhizal fungi are likely to lose any adaptations related to direct (nonhost) carbon acquisition. The results in this section capture one of the central predictions of trade under comparative advantage: at least one class of trader will specialize completely, and individuals will be more likely to specialize the greater their relative disadvantage in acquiring one resource (Ricardo 1817). We highlight the generality of this principle, as it has also been recovered in other models where individuals are able to acquire two resources (Hoeksema and Schwartz 2003, Grman et al. 2012).

AGRICULTURAL CONSEQUENCES

We now explore three scenarios with relevance to agriculture. We consider how coevolutionary changes combine todetermine variation in agricultural yields (i.e., plant fitness, f_p) and mycorrhizal cooperativeness (which we define as the proportion

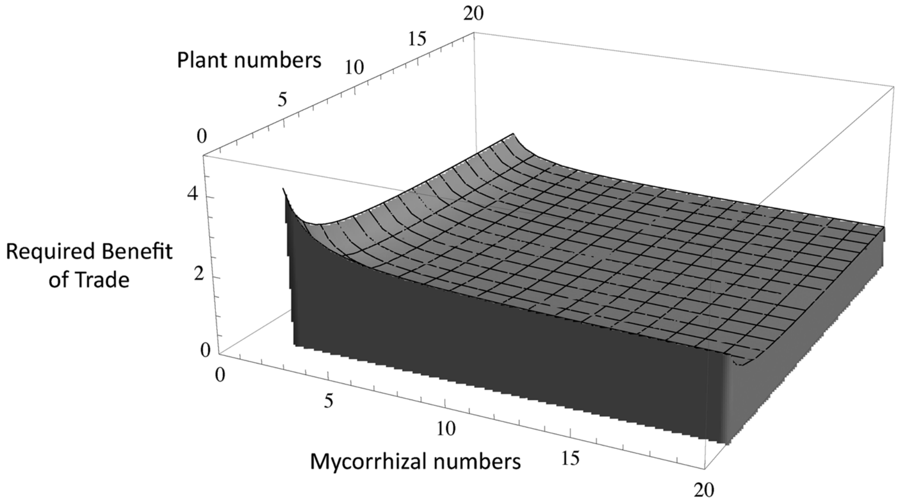


Figure 1. Condition for the stability of mutualistic trade. Above the threshold surface, $bC_pP_m/(P_p((1-b)I+bC_m)) = n_pn_m/((n_p-1)(n_m-1))$, the benefit of specialization and trade is large enough that individuals benefit from maintaining resource transfer. This condition becomes easier to satisfy as the number of individuals in each species, n_p or n_m, increases.

of their phosphorus that they send to plants, q_m) in response to: (i) changes in the number of mutualistic partners; (ii) the application of phosphorus fertilizers (higher P_m and/or P_p); (iii) an increase in atmospheric carbon (which is never available to mycorrhizae, $C_m = 0$).

Partner numbers

When host plants are grown as agricultural crops, this can alter plant density in a way that alters the number of available trading partners for each individual plant and mycorrhizal fungus. We assume that there is no initial cost to setting up a trading link. Such a cost might be important in the evolutionary origin of a de novo mutualism, but need not be if the mutualism arises from a preexisting association between plants and fungi. Moreover, we are not considering the origin of mutualism but its maintenance and elaboration, and the costs of setting up a trading link are likely negligible relative to the quantity of resources flowing through the network (Mikkelsen et al. 2008).

Result 8—An increase in the number of mycorrhizal partners per plant (n_m) increases both the cooperativeness of each mycorrhizal fungus (q_m) and the fitness of each plant (f_p). This is because the same plant carbon becomes shared between more mycorrhizal partners, increasing the marginal benefit of additional carbon for each mycorrhizal fungus. They are favored to transfer more phosphorus to compete for this carbon, thus increasing plant fitness. When plants acquire both resources before trade (condition 4a is not satisfied), the increase in fitness is slow because plants compete for phosphorus by increasing their investment in carbon acquisition and transferring that carbon to the fungal partner. When plants acquire only carbon directly, they cannot acquire any more of it to compete for mycorrhizal phosphorus. Therefore, plant fitness begins to increase rapidly, but at a diminishing rate (Fig. 4).

The increase in plant fitness caused by an increase in fungal numbers follows easily from the consequences of market supply and demand. The principle has been verbally applied to biological settings by Noe and Hammerstein (1994), but ours is the first model to quantify this effect. Grman et al. (2012) identify a similar trend that increased fungal biomass will lead to increased plant fitness because phosphorus becomes more readily available, but their model only considers one trader of each type, so the added impact on plant fitness of increased fungal cooperativeness is not captured. The predicted increase in fungal cooperativeness is also novel in the economic literature. Previous work suggests that less phosphorus may be supplied per fungus due to falling phosphorus prices because suppliers, in this case mycorrhizal fungi, increase in number (Amir and Lambson 2000).

Result 9—An increase in the number of plant partners per mycorrhiza (n_p) has a small positive effect on mycorrhizal cooperativeness, proportional to the size of the mycorrhizal carbon endowment (I). The impact on cooperativeness is small because two effects oppose. (i) The quantity of carbon that each mycorrhizal fungus receives, given the amount of phosphorus it sends, increases. This effect selects for more cooperative mycorrhizal fungi as trading away phosphorus yields a greater carbon return. (ii) Each mycorrhizal fungus receives more plant carbon, so the marginal value of an additional unit is lower, thus decreasing the quantity of phosphorus it trades. Overall, plant fitness decreases because more plants compete for a quantity of phosphorus that increases at a slow rate. This results in less phosphorus per

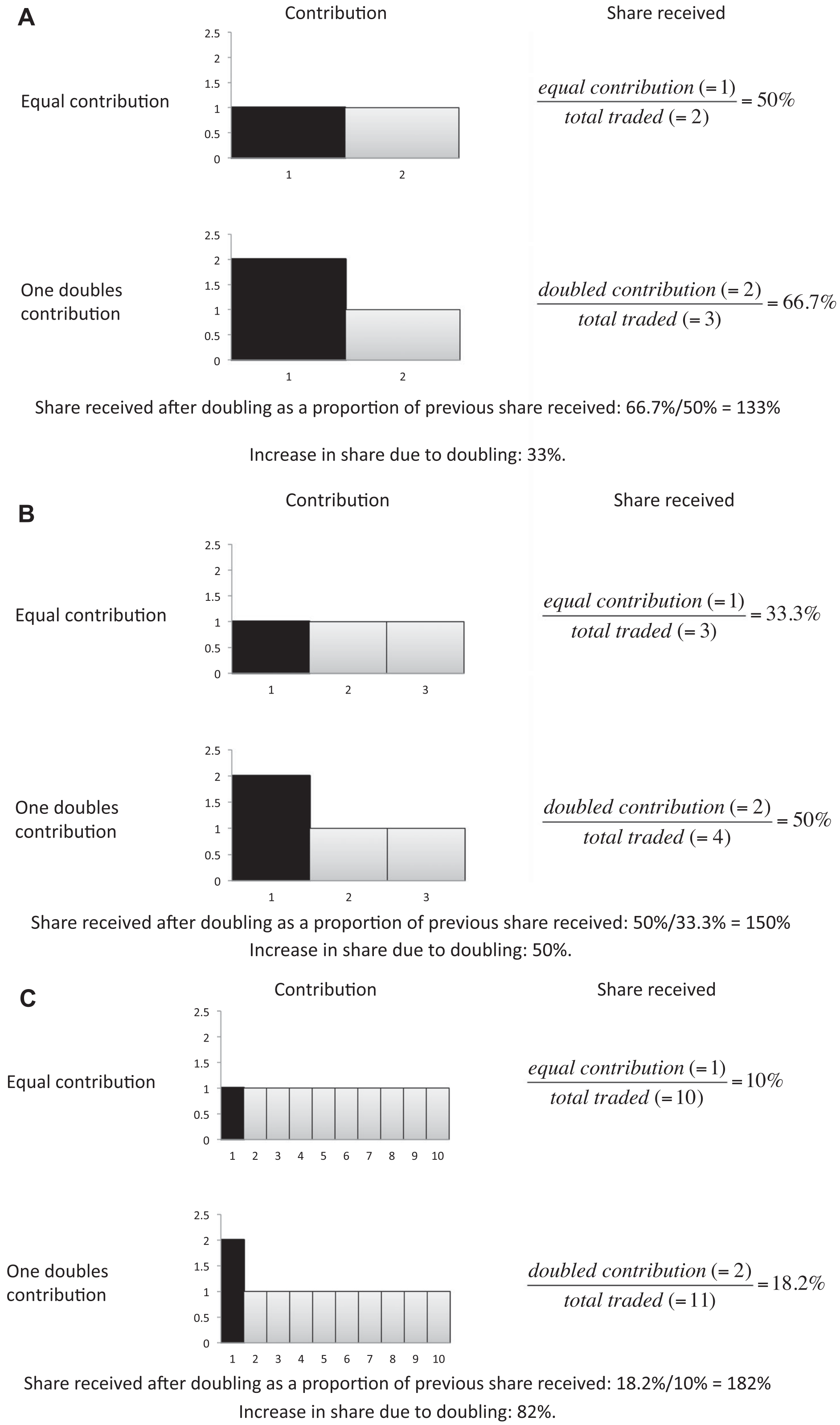


Figure 2. **Mutualistic trade and the number of trading partners. The proportional increase in resources returned to the black individual for doubling its contribution increases with the number of same species competitors, as illustrated by an increase from two (A), to three (B), to ten (C).**

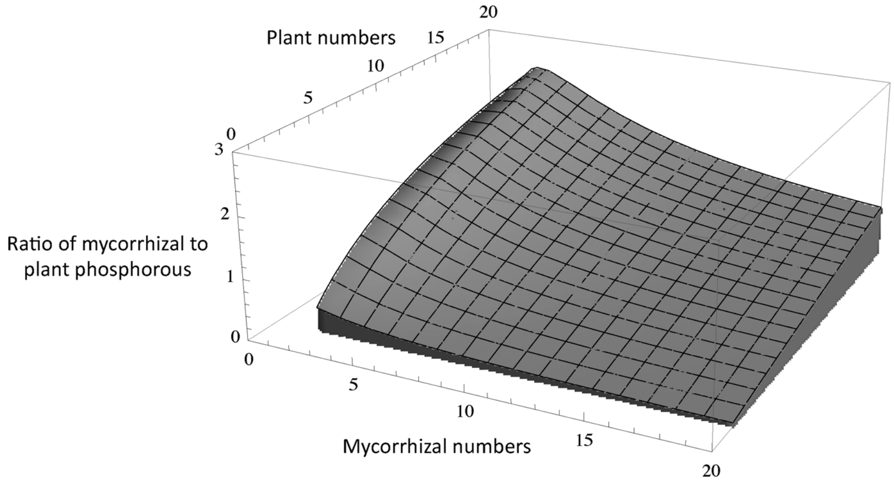


Figure 3. Specialisation and partner numbers. Above the surface, condition (3a) is satisfied. Plants acquire only carbon directly. Below it, plants acquire both resources directly. This surface is the critical ratio of mycorrhizal phosphorus to plant phosphorus, above which plants are favored to rely completely on mycorrhizal fungi for phosphorus (In graph, $a = 0.6$, $b = 0.4$, $C_p = 1$, $I = 0.1$).

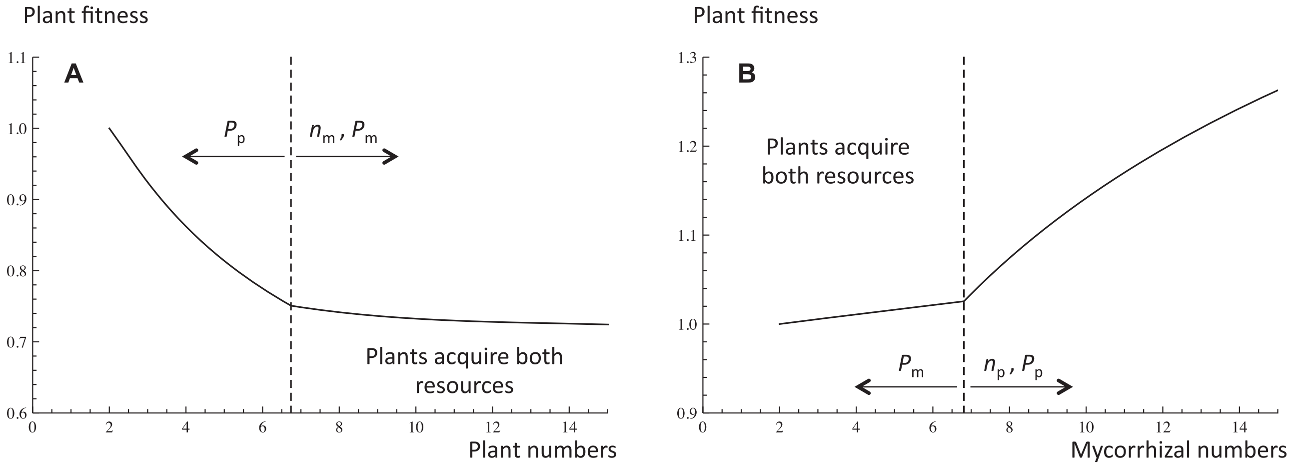


Figure 4. Effect of number of partners on plant fitness. (A) Plant fitness decreases with the number of plants. When plants acquire both resources directly (left of dashed line), the rate of fitness decrease slows dramatically as plants are no longer reliant on mycorrhizae for phosphorus. (In graph, $n_p = 10$, $C_p = 1$, $P_p = 0.5$, $P_m = 1$, $a = 0.7$, $b = 0.3$, $I = 0.1$). (B) Plant fitness increases with the number of mycorrhizal partners, n_m. When plants acquire only carbon directly (right of dashed line), fitness increases more rapidly as plants can no longer compete with each other by increasing the resources they allocate to acquiring carbon directly. (In graph, $n_m = 5$, $C_p = 1$, $P_p = 0.5$, $P_m = 1$, $a = 0.7$, $b = 0.3$, $I = 0.1$).

individual plant. When there are few plants, the decrease in fitness is rapid. However, the plants become self-reliant on phosphorus when there are many (condition 4a is not satisfied). Hence, further decreases in plant fitness are small (Fig. 5).

While the loss in fitness per plant with an increase in plant numbers follows directly from supply and demand predictions, the increase in fungal cooperativeness is again a novel and unexpected result.

Results 8 and 9 predict opposite effects on plant fitness because, all else being equal, having more competitors is bad for a focal individual's fitness. In contrast, having more trading partners competing against each other is good for the focal individual's fitness. Overall, extending plant-mycorrhizal networks (adding both plant and mycorrhizal partners) can have conflicting effects on agricultural yields: plants lose fitness when mycorrhizae make connections with more plant partners, but gain fitness as they make connections with more mycorrhizal partners (Fig. 4, Weremijewicz and Janos 2013). In addition, our model highlights potential for conflict over network size and composition as mycorrhizal fungi can benefit from increases in the number of both mycorrhizal fungi and plants, leading to different fitness optima in the two species (Fig. 6).

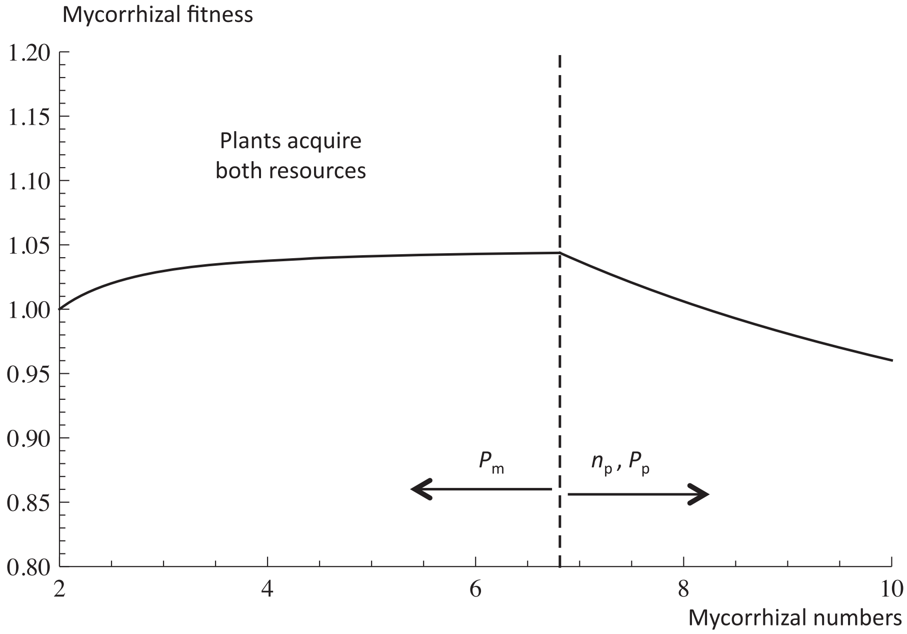


Figure 5. Effect of mycorrhizal numbers on mycorrhizal fitness. When there are few mycorrhizal fungi, their fitness increases as with their numbers. This occurs because they can induce plants to acquire more carbon and less phosphorus directly, thus lowering the phosphorus price of carbon. However, once plants acquire only carbon directly (right of dashed line), mycorrhizae lose fitness as their numbers increase. (In graph, $n_p = 10$, $C_p = 1$, $P_p = 0.5$, $P_m = 1$, $a = 0.7$, $b = 0.3$, $I = 0.1$).

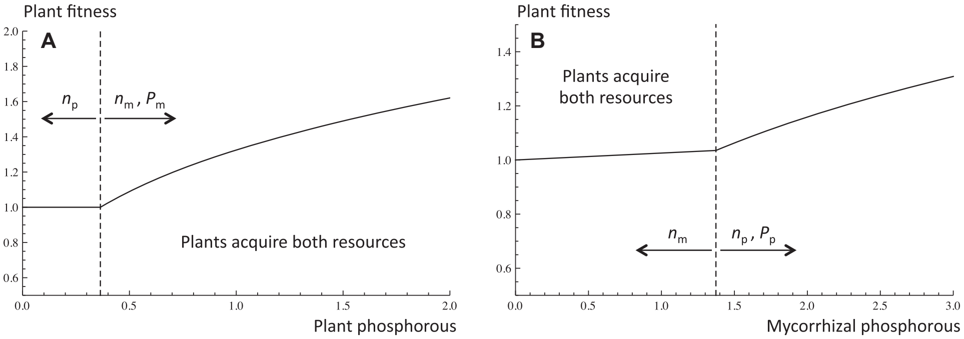


Figure 6. Effect of phosphorus availability on plant fitness. (A) Plants only benefit from an increase in phosphorus they can acquire directly once they start acquiring it (right of dashed line). (In graph, $n_p = 10$, $n_m = 5$, $C_p = 1$, $P_m = 1$, $a = 0.7$, $b = 0.3$, $I = 0.1$). (B) Plant fitness always increases with the quantity of phosphorus available to mycorrhizae. Fitness increases much more rapidly once plants acquire only carbon directly (right of dashed line, condition (6a) is satisfied) and therefore cannot compete with each other for phosphorus by acquiring more carbon directly. (In graph, $n_p = 10$, $n_m = 5$, $C_p = 1$, $P_p = 0.5$, $a = 0.7$, $b = 0.3$, $I = 0.1$).

Phosphorus fertilizer availability

An increase in phosphorus fertilizer availability will increase the amount of phosphorus available to plants (P_p), the amount of phosphorus available to mycorrhizal fungi (P_m), or both. In practice, scenarios where phosphorus availability increases to each plant (but not to each mycorrhizal fungus) are likely only when the quantity of mycorrhizal fungi increases as well, thus forcing the fungi to compete amongst each other for the increased phosphorus. However, our model can tease apart the separate effects of increase in phosphorus available to plants and mycorrhizal fungi. The effect of a simultaneous increase in both is a combination of the two separate effects that can be determined through empirical parametrization of our model.

Result 10—An increase in phosphorus available exclusively to plants decreases mycorrhizal cooperativeness, whereas an increase in phosphorus availability to mycorrhizae increases their cooperativeness. Again, these effects will be small, proportional to the fungi's initial carbon endowment *I*, because two effects oppose: (i) if additional phosphorus is available, it is relatively less valuable in trade than if consumed by the mycorrhizal fungi. This selects mycorrhizal fungi to transfer less phosphorus; (ii) the increased levels of phosphorus increase the marginal benefit of a unit of carbon, so mycorrhizal fungi are selected to transfer more phosphorus in exchange for this carbon.

Result 11—Increases in phosphorus availability, whether to plants or mycorrhizal fungi, increase plant fitness. However, this effect is threshold dependent. When plants acquire only carbon directly, they do not benefit from an increase in the phosphorus directly available to them (P_p), as they do not use this source. Plants benefit from an increase in either phosphorus source when they acquire both resources directly, as is most biologically realistic (Fig. 7). However, in this scenario, they benefit very little from an increase in phosphorus available to mycorrhizal fungi (P_m). They compete for this additional phosphorus by acquiring more carbon directly and transferring it to the fungal partner. Plants benefit more from an increase in phosphorus available to mycorrhizal fungi when they are fully reliant on mycorrhizal phosphorus (Fig. 8).

Result 10 analyses how strategies change with changes in phosphorus availability. Here, our model differs significantly from the model of Grman et al. (2012). Their model predicts a significantly less cooperative symbiont at high phosphorus availability to fungi because their single mycorrhizal fungus exploits monopoly power. In our model that allows multiple mycorrhizal individuals, as is most likely in the natural world, competition prevents this outcome. Result 11 analyses changes in plant fitness with phosphorus availability and highlights the same expected threshold dependencies found previously (Grman et al. 2012).

While the plants gain fitness even when additional phosphorus is not available to them except through trade, mycorrhizae lose fitness when plants can acquire more phosphorus directly. This is because plants become less reliant on them.

Result 12—When phosphorus availability to plants, P_p, reaches sufficiently high levels, trade between plants and mycorrhizae ceases. However, plant fitness does not suffer once this happens. When phosphorus is so easily available to plants, it is cheaper for the plants to acquire it directly than to acquire it through trade.

Hoeksema and Schwarz (2003) provide a more comprehensive analysis of conditions when mutualistic trade is not beneficial, although our model extends this by also showing when mutually beneficial trade fails to evolve due to public goods dilemmas. This outcome has already been shown in the economics literature (Bacchiega 2013).

Atmospheric carbon concentrations

How will rising CO_2 levels influence trade between plants and their mycorrhizae?

Result 13—Rising CO_2 concentrations increase plant fitness because plants are able to acquire more carbon directly (C increases). In addition, rising CO_2 levels increase mycorrhizal cooperativeness, although the effect will again be proportion to the mycorrhizal carbon endowment I, and hence small, because two effects oppose: (i) mycorrhizae are selected to transfer more phosphorus because plants can transfer more carbon in return; (ii) more carbon is available, which decreases its marginal value, and selects for mycorrhizae to transfer less phosphorus.

The diminishing marginal returns for an increase in availability limiting resource found in Result 13 are the default prediction in both economics and biology.

Discussion

Our work builds on previous research in biological market theory and its predictions. We demonstrate the validity of the market analogy and extend predictions on specialization and trade in mutualisms. We then use the biological market framework to make predictions about the agricultural consequences of ecological change.

BIOLOGICAL MARKETS

The plant-mycorrhizal mutualism consists of two-way trading connections between individuals. We have shown that this system can lead to the equivalent outcome as a central marketplace to which all individuals must bring the goods they trade. Specifically, we found that natural selection can lead to all individuals receiving the same market exchange rate for their goods and maintain trade. We derived our results using preexisting frameworks in the economics literature used for analyzing trade, termed "noncooperative trading games" (see Online Supplementary Material 1). Within species interactions were analyzed using frameworks for competition between suppliers of a particular good, where these suppliers must compete by adjusting quantities they bring to markets. This competitive structure is termed "Cournot competition" (Cournot 1838, see Online Supplementary Material 1).

Our results depend on linear proportional discrimination being an evolutionarily stable strategy for sharing resources. This is not a problem in economics, where it is typically assumed that individuals receive goods in proportion to the amount of money they pay, but it was not obvious that natural selection could lead to the same outcome. Linear proportional discrimination is stable when the ratio of benefits traded to benefits received is the same for any individual in each species. The ratio of exchange need not be 1:1 for the resources, but it must remain consistent across trades in that particular population. The optimal foraging theory literature on Ideal Free Distributions suggests that this ratio is often consistent, especially whenever individuals differ only in their competitive ability to acquire resources and are free to engage with whatever mutualistic partners they choose or whenever individuals acquiring more resources grow faster (Whitham 1980; Harper 1982; Sutherland and Parker 1985; Parker and Sutherland 1986; Houston and McNamara 1988; Sutherland et al. 1988; Inman 1990; Kacelnik et al. 1992; Krivan 1997). While plants and arbuscular mycorrhizal fungi have been shown to allocate more carbon resources to individuals offering more phosphorus in return (Bücking and Shachar-Hill 2005; Bever et al. 2009; Kiers et al. 2011), it is not known if they actually use a linear proportional discrimination rule. One confounding factor is that while plants trade only carbon with fungal partners, the fungal partners can trade additional resources, such as nitrogen and trace elements (Chen et al. 2003; Tanaka and Yano 2005). How this asymmetry in the diversity of goods offered by the two species affects proportional discrimination is unknown. Tracking and quantifying the exchange of multiple resources in mycorrhizal networks remains empirically difficult.

We have also shown that trade can only be maintained by linear proportional discrimination when individuals are exposed to enough potential competitors of the same species. As the number of competitors goes up, this increases competition for the resources provided by the mutualistic partner, and hence favors transferring more resources to the other species to earn a greater share of trade. If there are too few competitors, then a decrease in resources transferred can always be favored, and trade can even collapse altogether (Fig. 1). Empirical work in the mycorrhizal symbiosis suggests that individuals most often trade in large networks of partners (Giovannetti et al. 2004; Montesinos-Navarro et al. 2012), and so discriminating between individuals (and allocating resources accordingly) is likely to be a useful mechanism for maintaining cooperation (Fig. 2). The exact physiology of how this discrimination could take place is the focus of on-going work. It has been shown, for example, that an increase in host plant carbon can trigger the uptake of nutrients, such as nitrogen, by the fungal partner (Fellbaum et al. 2012). Vice versa, fungal partners can discriminate among adjacent roots differing in carbon resources (Bücking and Shachar-Hill 2005; Kiers et al. 2011), even allocating more nutrients to plants grown under sun rather than shade conditions (Fellbaum et al. 2014). However, such examples of fair-trade are not always the norm (e.g., Merckx and Bidartondo 2008; Walder et al. 2012).

Trade and specialization

A link between trade and specialization has long been recognized in economics (Ricardo 1817), and the tendency for specialization to drive trade has been explored in the biological market literature (Schwartz and Hoeksema 1998; Hoeksema and Schwartz 2001; Grman et al. 2012). Indeed, mutualisms tend to evolve more easily when species are highly specialized on a partner, as the benefits of trade are greater (Poisot et al. 2011). In our model, we recover and extend these results, suggesting that trade and specialization will go hand in hand: specialization evolves when mutualistic trade is present, and vice versa. In biological settings, it was unclear whether or not trade would drive specialization. Mycorrhizal fungi could have potentially benefited from retaining the ability to acquire carbon directly (rather than being dependent on the host), thus retaining bargaining power with plants (Bergmüller et al. 2007). However, physiological evidence suggests that whilst mycorrhizal fungi have not lost all of their saprophytic abilities, they do not possess the key genes to obtain carbon directly (e.g., genes to degrade plant cell walls, Tisserant et al. 2014). Instead, they have clearly evolved a dependence on host plant carbon, only expressing their full genetic potential when in symbiosis (Corradi and Bonfante 2012). An explanation suggested by our model is that mycorrhizal fungi compete most fiercely with other mycorrhizal fungi for plant carbon. As a result, only adaptations that will help them acquire more of the host carbon can be favored by natural selection even if these adaptations entail greater dependence on the host. This feedback loop may help explain how the mycorrhizal symbiosis and other mutualisms evolve from facultative to obligate (Aanen and Hoekstra 2007).

Ecological change and agricultural consequences

We have found that the impact of the number of social partners on plant fitness (and thus potentially crop yields) is threshold dependent (Fig. 4). Initially, increasing the number of mycorrhizal fungi per plant has only a small beneficial effect on per plant fitness. However, once plants start relying entirely on trade for phosphorus, per plant fitness increases rapidly, even though mycorrhizal cooperativeness increases at a diminishing rate throughout. In contrast, as plant number per fungal partner rises, per plant fitness falls rapidly but then levels off, even though mycorrhizal cooperativeness remains constant. Therefore our model suggests that large networks are likely to be better for plants, as the variety of suppliers means that plants can rely on mycorrhizae for phosphorus and enjoy the fitness gains associated with specializing on acquiring carbon.

The benefits of an increase in phosphorus availability are similarly threshold dependent (Fig. 6). When plants do not acquire phosphorus from the soil, only an increase in phosphorus available to mycorrhizae (P_{m}) increases plant fitness. On the other hand, when plants acquire both carbon and phosphorus directly, only an increase in phosphorus available directly to plants (P_{p}) significantly increases plant fitness. We also predict that mycorrhizal fungi lose fitness when plants can acquire more phosphorus directly, as plants become less reliant on them. This effect has the potential to select for mycorrhizal fungi that prevent, whether partially or completely, plants from acquiring phosphorus directly. There is some evidence that mycorrhizal fungi have evolved ways to suppress the direct nutrient uptake pathway of their host plants. The apparent deactivation of the direct pathway in plants colonized by mycorrhizal fungi is hypothesized to be a result of downregulation of the plant phosphorus transporters in root epidermis and root hairs (Smith et al. 2011). While our model shows that changing phosphorus conditions do not necessarily have a major effect on cooperativeness (i.e., the proportion of fungal phosphorus allocated to trade), it does suggest that there is room for the fungal partner to evolve greater control of soil resources.

Predicting the effects of increasing atmospheric CO_2 concentration on crop yields is difficult, and remains a hotly debated topic (Jaggard et al. 2010). While carbon becomes more readily available to plants, the increase in fitness directly attributable to increased carbon is likely to show diminishing returns, as other resources become more limiting. Our model suggests that this benefit is enhanced by interactions with symbionts. Mycorrhizal fungi will be competing for a larger pool of plant carbon, which encourages them to transfer more phosphorus, although this will be moderated by the increasingly limiting role of phosphorus throughout the system. Consistent with these predictions, long-term studies, such as the free air CO_2 enrichment (FACE) experiment in Switzerland suggest that increasing CO_2 can drive strong selection pressures in mycorrhizal fungi (Staddon et al. 2004). Within 8 years, mycorrhizal fungal isolates (e.g., *Glomus* sp.) from plots treated with elevated CO_2 improved the nitrogen nutrition of their host plants significantly more than those in plots treated with ambient CO_2 (Gamper et al. 2005). These experiments demonstrate the potential for harnessing evolved mutualistic strategies in order to increase crop yields. An improved understanding of the coevolutionary dynamics, with a particular emphasis on identifying thresholds beyond which plant growth increases rapidly, is a key part of a "Darwinian Agricultural" strategy to increase crop yields in a more sustainable manner (Denison et al. 2003; Denison 2013).

ACKNOWLEDGMENTS

We are grateful to G.D.A Werner, P. Bonfante, T. Cordella, J. F. Wilkins, and two anonymous referees for useful input and constructive comments. This research was supported by the BBSRC (GAKW), the European Research Council (SAW, ETK), the Dutch Science Foundation (NWO: Meervoud 836.10.001 and Vidi 864.10.005 grants, ETK), the Natural Environment Research Council (AG), and the Royal Society of London (AG).

LITERATURE CITED

Aanen, D. K., and R. F. Hoekstra. 2007. The evolution of obligate mutualism: if you can't beat 'em, join 'em. Trends Ecol. Evol. 22:506–509.

Agrawal, A. A., and R. Karban. 1997. Domatia mediate plant-arthropod mutualism. Nature 387:562–563.

Akçay, E., and J. Roughgarden. 2007. Negotiation of mutualism: rhizobia and legumes. Proc. R. Soc. Lond. B 274:25–32.

Akçay, E., and E. L. Simms. 2011. Negotiation, sanctions, and context dependency in the legume-rhizobium mutualism. Am. Nat. 178:1–14.

Amir, R., and V. E. Lambson. 2000. On the effects of entry in cournot markets. Rev. Econ. Stud. 67:235–254.

Archetti, M., I. Scheuring, M. Hoffman, M. E. Frederickson, N. E. Pierce, and D. W. Yu. 2011. Economic game theory for mutualism and cooperation. Ecol. Lett. 14:1300–1312.

Axelrod, R., and W. D. Hamilton. 1981. The evolution of cooperation. Science 27:1390–1396.

Bacchiega, E. 2013. A note on the effect of market power in Ricardian economies. Res. Econ. 67:111–116.

Baldwin, R. E. 1948. Equilbrium in international trade: a diagrammatic analysis. Q. J. Econ. 62:748–762.

Bergmüller, R., R. A. Johnstone, A. F. Russell, and R. Bshary. 2007. Integrating cooperative breeding into theoretical concepts of cooperation. Behav. Process 76:61–72.

Bever, J. D., S. Richardson, B. M. Lawrence, J. Holmes, and M. Watson. 2009. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. Ecol. Lett. 12:13–21.

Bücking, H., and Y. Shachar-Hill. 2005. Phosphorous uptake, transport, and transfer by the arbuscular mycorrhizal fungus *Glomus intraradices* is stimulated by increased carbohydrate availability. New Phytol. 165:899–911.

Bull, J. J., and W. R. Rice. 1991. Distinguishing mechanisms for the evolution of co-operation. J. Theor. Biol. 149:63–74.

Chen, B. D., X. L. Li, H. Q. Tao, P. Christie, and M. H. Wong. 2003. The role of arbuscular mycorrhiza in zinc uptake by red clover growing in a calcareous soil spike with various quantities of zinc. Chemosphere 50:839–846.

Cobb, C. W., and P. H. Douglas. 1928. A theory of production. Am. Econ. Rev. 18:139–165.

Cordella, T., & J. J. Gabszewicz. 1997. Comparative advantage under oligopoly. J. Int. Econ. 43:333–346.

———. 1998. "Nice" trivial equilibria in strategic market games. Game. Econ. Behav. 22:162–169.

Corradi, N., and P. Bonfante. 2012. The arbuscular mycorrhizal symbiosis: origin and evolution of a beneficial plant infection. PLoS Pathog. 8:e1002600.

Cournot, A. A. 1838. Recherches sur les principes mathematiques de la theorie des richesses. Imprimerie d'Amedee, Paris. de Mazancourt, C. & M. W. Schwartz. 2010. A resource ratio theory of cooperation. Ecol. Lett. 13: 349–359.

de Mazancourt, C., and M. W. Schwarz. 2010. A resource ratio theory of cooperation. Ecol. Lett. 13:349–359.

Denison, R. F. 2013. Darwinian agriculture—how understanding evolution can improve agriculture. Princeton Univ. Press, Princeton, NJ.

Denison, R. F., E. T. Kiers, and S. A. West. 2003. Darwinian agriculture: when can humans find solutions beyond the reach of natural selection? Q. Rev. Biol. 78:145–168.

Eddington, A. S. 1928. The nature of the physical world. Cambridge Univ. Press, Cambridge.

Edwards, D. P., M. Hassall, W. J. Sutherland, and D. W. Yu. 2006. Selection for protection in an ant-plant mutualism: host sanctions, host modularity, and the principal-agent game. Proc. R. Soc. Lond. B 273:595–602.

Fellbaum, C. R., E. W. Gachomo, Y. Beessetty, S. Choudhari, G. D. Strahan, P. E. Pfeffer, E. T. Kiers, and H. Bücking. 2012. Carbon availability triggers fungal nitrogen uptake and transport in arbuscular mycorrhizal symbiosis. Proc. Natl. Acad. Sci. USA 109:2666–2671.

Fellbaum, C. R., J. Mensah, A. Cloos, P. Pfeffer, G. Strahan, E. T. Kiers, and H. Bücking. 2014. Fungal nutrient allocation in common mycorrhizal networks is regulated by the carbon source strength of individual host plants. New Phytol. 2:646–656.

Foster, K., and T. Wenseleers. 2006. A general model for the evolution of mutualisms. J. Evol. Biol. 19:1283–1293.

Frank, S. A. 1994. Genetics of mutualism: the evolution of altruism between species. J. Theor. Biol. 170:393–400.

Frean, M. R., and E. R. Abraham. 2004. Adaptation and enslavement in endosymbiont-host associations. Phys. Rev. E 69:051913.

Gamper, H. A., U. A. Hartwig, and A. Leuchtmann. 2005. Mycorrhizas improve nitrogen nutrition of *Trifolium repens* after 8 yr of selection under elevated atmospheric CO_2 partial pressure. New Phytol. 167:531–542.

Ghoul, M., A. S. Griffin, and S. A. West. 2014. Towards an evolutionary definition of cheating. Evolution 68:318–331.

Giovannetti, M., C. Sbrana, L. Avio, and P. Strani. 2004. Patterns of below-ground plant interconnections established by means of arbuscular mycorrhizal networks. New Phytol. 164:175–181.

Goto, R., T. Okamoto, E. T. Kiers, A. Kawakita, and M. Kato. 2010. Selective flower abortion maintains moth cooperation in a newly discovered pollination mutualism. Ecol. Lett. 13:321–329.

Grman, E., T. M. P. Robinson, and C. A. Klausmeier. 2012. Ecological specialization and trade affect the outcome of negotiations in mutualism. Am. Nat. 179:567–581.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I & II. J. Theor. Biol. 7:1–52.

Hammer, E. C., J. Pallon, H. Wallander, and P. A. Olsson. 2011. Tit for tat? A mycorrhizal fungus accumulates P under low plant C availability. Proc. Natl. Acad. Sci. USA 76:236–244.

Harper, D. G. C. 1982. Competitive foraging in mallards: 'Ideal Free' ducks. Anim. Behav. 31:575–584.

Hoeksema, J. D., and M. W. Schwartz. 2001. Modeling interspecific mutualisms as biological markets. Pp. 173–183 *in* R. Noë, J. A. R. A. M. van Hooff, and P. Hammerstein, eds. Economics in nature. Cambridge Univ. Press, Cambridge.

———. 2003. Expanding comparative-advantage biological market models: contingency of mutualism on partners' resource requirements and acquisition trade-offs. Proc. R. Soc. Lond. B 270:913–919.

Houston, A. I., and J. M. McNamara. 1988. The ideal free distribution when competitive abilities differ: an approach based on statistical mechanics. Anim. Behav. 36:166–174.

Inman, A. J. 1990. Group foraging in starlings: distribution of unequal competitors. Anim. Behav. 40:801–810.

Jaggard, K. W., A. Qi, and E. S. Ober. 2010. Possible changes to arable crop yields by 2050. Phil. Trans. R. Soc. B 365:2835–2851.

Jander, K. C., and E. A. Herre. 2010. Host sanctions and pollinator cheating in the fig tree-fig wasp mutualism. Proc. R. Soc. Lond. B 277:1481–1488.

Johnson, D., F. Martin, J. W. G. Cairney, and I. C. Anderson. 2012. The importance of individuals: intraspecific diversity of mycorrhizal plants and fungi in ecosystems. New Phytol. 194:614–628.

Johnstone R. A., and R. Bshary. 2008. Mutualism, market effects and partner control. J. Evol. Biol. 21:879–888.

Kacelnik, A., J. R. Krebs, and C. Bernstein. 1992. The ideal free distribution and predator-prey populations. Trends Ecol. Evol. 7:50–55.

Kiers, E. T., and R. F. Denison. 2008. Sanctions, cooperation, and the stability of plant-rhizosphere mutualisms. Annu. Rev. Ecol. Evol. Syst. 39:215–236.

Kiers, E. T., M. Duhamel, Y. Beesetty, J. A. Mensah, O. Franken, E. Verbruggen, C. R. Fellbaum, G. A. Kowalchuk, M. M. Hart, A. Bago, et al. 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. Science 333:880–882.

Kiers, E. T., R. A. Rousseau, S. A. West, and R. F. Denison. 2003. Host sanctions and the legume-rhizobia mutualism. Nature 425:78–81.

Krivan, V. 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. Am. Nat. 149:164–178.

Korb, J., and D. K. Aanen. 2003. The evolution of uniparental transmission of fungal symbionts in fungus-growing termites (Macrotermitinae). Behav. Ecol. Sociobiol. 53:65–71.

Kummel, M., and S. W. Salant. 2006. The economics of mutualisms: optimal utilization of mycorrhizal mutualistic partners by plants. Ecology 87:892–902.

Leigh, E. G. Jr. 2010. The group selection controversy. J. Evol. Biol. 23:6–19.

Maynard Smith, J., and G. R. Price. 1973. The logic of animal conflict. Nature 246:15–18.

McFall-Ngai, M. 2008. Hawaiian bobtail squid. Curr. Biol. 18:R1043–R1044.

Merckx, V., and M. I. Bidartondo. 2008. Breakdown and delayed cospeciation in the arbuscular mycorrhizal mutualism. Proc. R. Soc. Lond. B 275:1029–1035.

Mikkelsen, T. N., C. Beier, S. Jonasson, M. Holmstrup, I. K. Schmidt, P. Ambus, K. Pilegaard, A. Michelsen, K. Albert, L. C. Andresen, et al. 2008. Experimental design of multifactor climate change experiments with elevated CO_2, warming and drought: the CLIMAITE project. Funct. Ecol. 22:185–195.

Montesinos-Navarro, A., J. G. Segarra-Moragues, A. Valiente-Banuet, and M. Verdu. 2012. The network structure of plant-arbuscular mycorrhizal fungi. New Phytol. 194:536–547.

Noë, R. 1990. A veto game played by baboons: a challenge to the use of the Prisoner's Dilemma as a paradigm for reciprocity and cooperation. Anim. Behav. 39:78–90.

Noë, R., C. P. V. Schaik, and J. A. R. A. M. van Hooff. 1991. The market effect: an explanation for pay-off asymmetries among collaborating animals. Ethology 87:97–118.

Noë, R. 1992. Alliance formation among male baboons: shopping for profitable partners. Pp. 285–321 *in* A. H. Harcourt and F. B. M. de Waal, eds. Coalitions and alliances in humans and animals. Oxford Univ. Press, Oxford, U.K.

Noë, R., and P. Hammerstein. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. Behav. Ecol. Sociobiol. 35:1–11.

———. 1995. Biological markets. Trends. Ecol. Evol. 10:336–339.

Noë, R., J. A. R. A. M. van Hooff, and P. Hammerstein. 2001. Economics in nature. Cambridge Univ. Press, Cambridge.

Oono, R., C. G. Anderson, and R. F. Denison. 2011. Failure to fix nitrogen (N_2) by nonreproductive symbiotic rhizobia triggers sanctions that reduce fitness of their reproductive clonemates. Proc. R. Soc. Lond. B 278:2698–2703.

Oono, R., R. F. Denison, and E. T. Kiers. 2009. Tansley review: controlling the reproductive fate of rhizobia: how universal are legume sanctions? New Phytol. 183:967–979.

Parniske, M. 2008. Arbuscular mycorrhiza: the mother of plant root endosymbiosis. Nat. Rev. Microbiol. 6:763–775.

Parker, G. A., and W. J. Sutherland. 1986. Ideal free distributions when individuals differ in competitive ability. Anim. Behav. 34:1222–1242.

Peleg, B., and A. Shmida. 1992. Short-run stable matchings between bees and flowers. Games Econ. Behav. 4:232–251.

Peleg, B., A. Shmida, and S. Ellner. 1992. Foraging graphs: constraint rules on matching between bees and flowers in a two-sided pollination market. J. Theor. Biol. 157:191–201.

Pellmyr, O., and C. J. Huth. 1994. Evolutionary stability of mutualism between yuccas and mucca moths. Nature 372:257–260.

Poisot, T., J. D. Bever, A. Nemri, P. H. Thrall, and M. E. Hochberg. 2011. A conceptual framework for the evolution of ecological specialisation. Ecol. Lett. 14:841–851.

Regus, J. U., K. A. Gano, A. C. Hollowell, and J. L. Sachs. 2014. Efficiency of partner choice and sanctions in Lotus is not altered by nitrogen fertilization. Proc. R. Soc. Lond. B 281:20132587.

Ricardo, D. 1817. On the principles of political economy and taxation. John Murray, London.

Rieber, W. J. 1982. Discriminating monopoly and international trade. Econ. J. 92:365–376.

Sachs, J. L., U. G. Mueller, T. P. Wilcox, and J. J. Bull. 2004. The evolution of cooperation. Q. Rev. Biol. 79:135–160.

Sbrana, C., P. Fortuna, and M. Giovannetti. 2011. Plugging into the network: belowground connections between germlings and extraradical mycelium of arbuscular mycorrhizal fungi. Mycologia 103:307–316.

Schwartz, M. W., and J. D. Hoeksema. 1998. Specialization and resource trade: biological markets as a model of mutualisms. Ecology 79:1029–1038.

Selosse, M. A., F. Richard, X. H. He, and S. W. Simard. 2006. Mycorrhizal networks: des liaisons dangereuses? Trends Ecol. Evol. 21:621–628.

Selten, R., and A. Shmida. 1991. Pollinator foraging and flower competition in a game equilibrium model. Pp. 195–256 *in* R. Selten, ed. Game equilibrium models Vol. I. Springer-Verlag, Berlin.

Simms, E. L., D. L. Taylor, J. Povich, R. P. Shefferson, M. Urbina, and Y. Tauszick. 2006. An empirical test of partner choice mechanisms in a legume-rhizobium interaction. Proc. R. Soc. Lond. B 273: 77–81.

Smith, S. E., I. Jakobsen, M. Gronlund, and F. A. Smith. 2011. Roles of arbuscular mycorrhizas in plant phosphorus nutrition: interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorous acquisition. Plant Physiol. 156:1050–1057.

Staddon, P. L., I. Jakobsen, and H. Blum. 2004. Nitrogen input mediates the effect of free-air enrichment on mycorrhizal fungal abundance. Glob. Change Biol. 10:1678–1688.

Sutherland, W. J., and G. A. Parker. 1985. The distribution of unequal competitors. Pp. 255–273 *in* R. M. Sibly and R. H. Smith, eds. Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell, Oxford, U.K.

Sutherland, W. J., C. R. Townsend, and J. M. Patmore. 1988. A test of the ideal free distribution with unequal competitors. Behav. Ecol. Sociobiol. 23:51–53.

Tanaka, Y., and K. Yano. 2005. Nitrogen delivery to maize via mycorrhizal hyphae depends on the form of N supplied. Plant Cell Environ. 28:1247–1254.

Tang-Martinez, Z. 2001. The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: a critical re-evaluation. Behav. Proc. 53:21–40.

Tisserant, E., M. Malbreil, A. Kuo, A. Kohler, A. Symeonidi, R. Balestrini, P. Charron, N. Duensing, N. Frei, V. Gianinazzi-Pearson, et al. 2014. The genome of an arbuscular mycorrhizal fungus provides insights into the oldest plant symbiosis. Proc. Natl. Acad. Sci. USA 110:20117–20122.

Walder, F., H. Niemann, M. Natarajan, M. F. Lehmann, T. Boller, and A. Wiemken. 2012. Mycorrhizal networks: common goods of plants shared under unequal terms of trade. Plant Physiol. 159:789–797.

Weremijewicz, J., and D. P. Janos. 2013. Common mycorrhizal networks amplify size inequality in *Andropogon gerardii* monocultures. New Phytol. 198:203–213.

Werner, G. D. A., J. E. Strassman, A. B. H. Ivens, D. J. P. Engelmoer, E. Verbruggen, D. C. Queller, R. Noë, N. C. Johnson, P. Hammerstein, and E. T. Kiers. 2014. Evolution of microbial markets. Proc. Natl. Acad. Sci. USA 111:1237–1244.

West, S. A., and E. A. Herre. 1994. The ecology of the New World fig-parasitising wasps Idarnes and implications for the evolution of the fig-pollinator mutualism. Proc. R. Soc. Lond. B 258:67–72.

West, S. A., A. S. Griffin, and A. Gardner. 2007. Evolutionary explanations for cooperation. Curr. Biol. 17:R661–R672.

West, S. A., E. T. Kiers, I. Pen, and R. F. Denison. 2002a. Sanctions and mutualism stability: when should less beneficial mutualists be tolerated? J. Evol. Biol. 15:830–837.

West, S. A., E. T. Kiers, E. L. Simms, and R. F. Denison. 2002b. Sanctions and mutualism stability: why do rhizobia fix Nitrogen? Proc. R. Soc. Lond. B 269: 685–694.

Whitham, T. G. 1980. The theory of habitat selection: examined and extended using pemphigus aphids. Am. Nat. 115:449–466.

Wyatt, G. A. K., S. A. West, A. Gardner. 2013. Can natural selection favour altruism between species? J. Evol. Biol. 26:1854–1865.

Associate Editor: J. Wilkins

Appendix A: Linear proportional discrimination

Here, we prove that linear proportional discrimination is an evolutionarily stable strategy. Assume that a focal plant interacts with two mycorrhizae using linear proportional discrimination, m_1 and m_2. The amount of phosphorus that m_1 allocates for trade is $P_{\mathrm{t1,}}$ while the amount that partner m_2 allocates is P_{t2}. These mycorrhizae receive total amounts of carbon C_{re1} and C_{re2} respectively from all of their other plant trading partners (i.e., not including the focal plant). The focal plant then shares an amount of carbon allocated for trade, C_{t}, between the two mycorrhizae, giving a proportion $C_{\mathrm{t}}f_1$ and a proportion $C_{\mathrm{t}}(1\text{-}f_1)$ of that amount to m_1 and m_2, respectively. In return, the plant receives a total amount of phosphorus P_{r}, as determined by the linear proportional discrimination functions of the two mycorrhizae:

$$P_{\mathrm{r}} = \frac{C_{\mathrm{t}} f_1}{C_{\mathrm{t}} f_1 + C_{\mathrm{re1}}} P_{\mathrm{t1}} + \frac{C_{\mathrm{t}}(1 - f_1)}{C_{\mathrm{t}}(1 - f_1) + C_{\mathrm{re2}}} P_{\mathrm{t2}}. \tag{4}$$

We denote the shares of phosphorus $C_{\mathrm{t}} f_{\mathrm{p1}}/(C_{\mathrm{t}} f_{\mathrm{p1}} + C_{\mathrm{r1}})$ and $C_{\mathrm{t}}(1 - f_1)/\,(C_{\mathrm{t}}(1 - f_1) + C_{\mathrm{re2}})$ received by the plant as s_1 and s_2. We now calculate $\partial P_{\mathrm{r}}/\partial f_1$ and $\partial^2 P_{\mathrm{r}}/\partial f_1^2$ from equation 4. We then evaluate these derivatives at the value of f_1 determined by linear proportional discrimination, which must satisfy

$$\frac{f_1}{1 - f_1} = \frac{s_1 P_{\mathrm{t1}}}{s_2 P_{\mathrm{t2}}}. \tag{5}$$

We simplify the resulting expressions and find that phosphorus received is maximized when

$$\frac{C_{\mathrm{re1}}}{P_{\mathrm{t1}}} = \frac{C_{\mathrm{re2}}}{P_{\mathrm{t2}}}. \tag{6}$$

Hence, linear proportional discrimination maximizes phosphorus received, and allocating amongst partners according to this rule is therefore an ESS when equation 6 is satisfied. This is always true in our model, where all individuals in a species are identical. Note that we have not demonstrated that linear proportional discrimination is the only ESS of our model, but we do demonstrate that allocating all resources to the best trading partner or sharing equally between all partners are not evolutionarily stable in the mutualistic system (see Online Supplementary Material 2).

We also note that across the population, equation 6 will be satisfied on average. That is, the expected ratio of carbon sent to phosphorus received is the same for any individual. Hence, if the resource sharing strategy is genetically encoded, or if individuals cannot measure whether or not an alternative sharing strategy yields an increase in resources returned, they cannot do better than also adopt linear proportional discrimination.

Appendix B: Conditions for existence of trading ESS and equilibrium allocations

We take plant fitness from equation (1a), and substitute model parameters and evolved strategies for the proportion of traded phosphorus acquired by the focal plant, s_{p}, which is equal to the share of total traded carbon that the plant acquires which we now write down in terms of model parameters. The numerator of s_{p} is the total amount of carbon that the focal plant provides in trade that is the proportion of acquired carbon that the focal plant allocates to trade, $C_{\mathrm{t}} = x_{\mathrm{p}} C_{\mathrm{p}} q_{\mathrm{p}}$. The denominator of s_{p} is the total amount of carbon traded by all competing plants, including the focal individual. There are n_{p}-1 competitors, and the average amount of carbon each trades is the average proportion of the average total amount of carbon that each plant acquires, $x'_{\mathrm{p}} C_{\mathrm{p}} q'_{\mathrm{p}}$. We add this across all of the competitors and add the amount of carbon provided by the focal individual, so the denominator is $((n_{\mathrm{p}} - 1) x'_{\mathrm{p}} C_{\mathrm{p}} q'_{\mathrm{p}} + x_{\mathrm{p}} C_{\mathrm{p}} q_{\mathrm{p}})$. Hence, the proportion of total traded phosphorus that the plant acquires is $s_{\mathrm{p}} = (x_{\mathrm{p}} C_{\mathrm{p}} q_{\mathrm{p}})/((n_{\mathrm{p}} - 1) x'_{\mathrm{p}} C_{\mathrm{p}} q'_{\mathrm{p}} + x_{\mathrm{p}} C_{\mathrm{p}} q_{\mathrm{p}})$. This means that equation (1a) is now entirely expressed in terms of model parameters and evolved strategies. The same approach allows us to express equation (1b) in the same way.

We now calculate the fixed points with respect to allocation to direct carbon acquisition and trade, $\partial w_{\mathrm{p}}/\partial x_{\mathrm{p}} = \partial w_{\mathrm{p}}/\partial q_{\mathrm{p}} = 0$. At an ESS, any focal plant receives population mean fitness to first order, so we take its strategy to be the population average ($q_{\mathrm{p}} = q'_{\mathrm{p}}$, $x_{\mathrm{p}} = x'_{\mathrm{p}}$). Substituting, we find that at a fixed point

$$q'_{\mathrm{p}} = \frac{(1-a) q'_{\mathrm{m}} (1 - x'_{\mathrm{m}})(n_{\mathrm{p}} - 1) n_{\mathrm{m}} P_{\mathrm{m}}}{a(1 - x'_{\mathrm{p}}) n_{\mathrm{p}}^2 P_{\mathrm{p}} + q'_{\mathrm{m}} (1 - x'_{\mathrm{m}})(n_{\mathrm{p}} - 1 + a) n_{\mathrm{m}} P_{\mathrm{m}}} \tag{7a}$$

$$x'_{\mathrm{p}} = a + \frac{q'_{\mathrm{m}} (1 - x'_{\mathrm{m}})(n_{\mathrm{p}} - 1 + a) n_{\mathrm{m}} P_{\mathrm{m}}}{n_{\mathrm{p}}^2 P_{\mathrm{p}}}. \tag{7b}$$

Similarly, we find that the fixed-point values of trade and direct carbon acquisition for mycorrhizae are

$$q'_{\mathrm{m}} = \frac{b C_{\mathrm{p}} x'_{\mathrm{p}} q'_{\mathrm{p}} n_{\mathrm{p}} (n_{\mathrm{m}} - 1)}{(n_{\mathrm{m}} - b) C_{\mathrm{p}} x'_{\mathrm{p}} q'_{\mathrm{p}} n_{\mathrm{p}} + (1 - b)(I + C_{\mathrm{m}} x'_{\mathrm{m}}) n_{\mathrm{m}}^2} \tag{7c}$$

$$x'_{\mathrm{m}} = \frac{b C_{\mathrm{p}} x'_{\mathrm{p}} q'_{\mathrm{p}} n_{\mathrm{p}} - (C_{\mathrm{p}} x'_{\mathrm{p}} q'_{\mathrm{p}} n_{\mathrm{p}} + I n_{\mathrm{m}}) n_{\mathrm{m}} + b(I + C_{\mathrm{m}}) n_{\mathrm{m}}^2}{C_{\mathrm{m}} n_{\mathrm{m}}^2}. \tag{7d}$$

We find that there is a unique solution that satisfies equation (7a–d)

$$(x'_{\mathrm{p}}, q'_{\mathrm{p}}, x'_{\mathrm{m}}, q'_{\mathrm{m}}) = \left(a, 0, b + \frac{I(1-b)}{C_{\mathrm{m}}}, 0\right). \tag{8}$$

Any mutant in either species that uses a different strategy to the one specified in equation (8) has lower fitness as long as individuals in both species can acquire both resources directly, hence equation (8) defines a pair of ESSs when C_{p}, C_{m} or I, P_{p}, and P_{m} are positive.

In addition, plants and mycorrhizae are constrained to allocations to direct carbon acquisition and trade between 0 and 1. We look for other pairs of ESSs that are constrained maxima on this boundary. We eliminate $x'_{\mathrm{p}} = 0$ and $q'_{\mathrm{p}} = 1$ as this would leave plants without carbon, and $x'_{\mathrm{m}} = 1$ and $q'_{\mathrm{m}} = 1$ as this would leave mycorrhizae without phosphorus. We first set $x'_{\mathrm{p}} = 1$ and work out the evolved best response values for the other variables if all other individuals use the same strategy:

$$(x'_{\mathrm{p}}, q'_{\mathrm{p}}, x'_{\mathrm{m}}, q'_{\mathrm{m}}) = \left(1, \quad \frac{(1-a)(n_{\mathrm{p}} - 1)}{n_{\mathrm{p}} - 1 + a}, \quad \frac{(b C_{\mathrm{m}} - (1-b) I)(n_{\mathrm{p}} - 1 + a) n_{\mathrm{m}}^2 - (1-a) C_{\mathrm{p}} (n_{\mathrm{p}} - 1) n_{\mathrm{p}} (n_{\mathrm{m}} - b)}{C_{\mathrm{m}} (n_{\mathrm{p}} - 1 + a) n_{\mathrm{m}}^2}, \right.$$
$$\left. \frac{(1-a) C_{\mathrm{p}} (n_{\mathrm{p}} - 1) n_{\mathrm{p}} (n_{\mathrm{m}} - 1)}{(1-b)(I + C_{\mathrm{m}})(n_{\mathrm{p}} - 1 + a) n_{\mathrm{m}}^2 + (1-a) C_{\mathrm{p}} (n_{\mathrm{p}} - 1) n_{\mathrm{p}} (n_{\mathrm{m}} - b)} \right). \tag{9}$$

We verify whether fitness at $x_{\mathrm{p}} = 1$ is greater than at $x_{\mathrm{p}} < 1$, given the corresponding values of q'_{p}, x'_{m}, and q'_{m}:

$$\frac{\partial w_{\mathrm{p}}}{\partial x_{\mathrm{p}}}\Big|_{x'_{\mathrm{p}}=1} > 0 \Leftrightarrow \frac{C_{\mathrm{p}} P_{\mathrm{m}}}{P_{\mathrm{p}}((1-b) I + b C_{\mathrm{m}}} > \frac{n_{\mathrm{p}} n_{\mathrm{m}}}{(n_{\mathrm{p}} - 1)(n_{\mathrm{m}} - 1)}. \tag{10}$$

In the parameter region from equation (10), the best response values in equation (9) are feasible (and eq. 9 is thus a pair of ESSs) if

$$C_p \geq \frac{(bC_m - I(1-b))(n_p - 1 + a)n_m^2}{(1-a)(n_p-1)n_p(n_m-b)}. \tag{11}$$

We can also set $x_m' = 0$ and find a pair of ESSs by the same method with

where expression

$$e = n_p \left(a\,(n_m - b)\,C_p\,(n_p-1)\,n_p - I\,(1-b)\,(n_p - 1 + a)\,n_m^2\right) P_p + bC_p\,(n_p-1)\,(n_p-1+a)\,(n_m-1)\,n_m P_m.$$

Fitness is also maximized at $x_m' = 0$ in the parameter region defined by equation (10), given the best response values in equation (12). These are feasible when

$$(x_p', q_p', x_m', q_m') = \left(\frac{e}{C_p(n_p-1)n_p^2(n_m-b)P_p},\quad \frac{(n_p-1)n_m(bC_p(n_p-1)(n_m-1)P_m - I(1-b)n_pn_mP_p)}{e},\quad 0,\quad \frac{(n_pn_m - n_p - n_m + 1)P_mC_pb - I(1-b)n_pn_mP_p}{C_p(n_p-1)(n_m-b)P_m}\right) \tag{12}$$

$$P_p \leq \frac{bC_p(n_p-1)(n_p-1+a)(n_m-1)n_mP_m}{n_p((1-a)C_p(n_p-1)n_pn_m + I(1-b)(n_p-1+a)n_m^2 - (1-a)bC_p(n_p-1)n_p)}. \tag{13}$$

Finally, we set $x_p' = 1$ and $x_m' = 0$. We find that

$$(x_p', q_p', x_m', q_m') = \left(1,\quad \frac{(1-a)(n_p-1)}{n_p-1+a},\quad 0,\quad \frac{(1-a)bC_p(n_p-1)n_p(n_m-1)}{(1-a)C_p(n_p-1)n_p(n_m-b) + I(1-b)(n_p-1+a)n_m^2}\right). \tag{14}$$

These strategies are a pair of ESSs when both inequality (11) and inequality (13) are satisfied.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Supporting information 1. Economic Background and Future Avenues.
Supporting information 2. Alternative Resource Sharing Rules.
Figure S1. Probability distribution of C_{t1} and C_{t2}.

JOURNAL OF Evolutionary Biology eseb European Society for Evolutionary Biology

doi: 10.1111/jeb.12195

Can natural selection favour altruism between species?

G. A. K. WYATT*, S. A. WEST* & A. GARDNER*†

*Department of Zoology, University of Oxford, Oxford, UK
†Balliol College, University of Oxford, Oxford, UK

Keywords:

evolutionary graph theory;
Hamilton's rule;
inclusive fitness;
kin selection;
mutualism;
relatedness.

Abstract

Darwin suggested that the discovery of altruism between species would annihilate his theory of natural selection. However, it has not been formally shown whether between-species altruism can evolve by natural selection, or why this could never happen. Here, we develop a spatial population genetic model of two interacting species, showing that indiscriminate between species helping can be favoured by natural selection. We then ask if this helping behaviour constitutes altruism between species, using a linear-regression analysis to separate the total action of natural selection into its direct and indirect (kin selected) components. We show that our model can be interpreted in two ways, as either altruism within species, or altruism between species. This ambiguity arises depending on whether or not we treat genes in the other species as predictors of an individual's fitness, which is equivalent to treating these individuals as agents (actors or recipients). Our formal analysis, which focuses upon evolutionary dynamics rather than agents and their agendas, cannot resolve which is the better approach. Nonetheless, because a within-species altruism interpretation is always possible, our analysis supports Darwin's suggestion that natural selection does not favour traits that provide benefits exclusively to individuals of other species.

Introduction

> 'If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection'.
>
> Darwin (1859, p. 201)

Darwin's (1859) theory of natural selection explains the process and purpose of organismal adaptation. Specifically, those heritable characters that are associated with higher individual reproductive success will tend to accumulate in biological populations under the action of natural selection. Hence, Darwin argued, individual organisms will appear increasingly well designed to maximize their reproductive success. Darwin (1859) also recognized that natural selection can work indirectly, through the reproductive success of family members, so as to favour characters that promote the reproductive success of an individual's close kin. Hamilton's (1963, 1964, 1970) theory of inclusive fitness expanded on this principle, showing that natural selection can favour the evolution of altruistic behaviour that reduces the actor's reproductive success provided that sufficient benefits accrue to the actor's kin.

Darwin (1859) suggested that natural selection would never favour altruism between individuals of different species. This appears to be borne out by empirical observation: although cooperative interactions between different species (mutualisms) are widespread in the natural world, these typically involve mechanisms that ensure return benefits accrue either to the actor or to her close kin (Foster & Wenseleers, 2006; Leigh, 2010; Bourke, 2011). For example, plants that form symbioses with mycorrhizae provide more carbohydrates to mutualistic partners that supply more nutrients, giving the mycorrhizae an incentive to cooperate (Kiers *et al.*, 2011). This mutualism may involve mutually beneficial helping if sufficient return benefits accrue to the helpful mycorrhiza. Alternatively, it may involve altruistic

Correspondence: Gregory A. K. Wyatt, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK.
Tel.: +44 (0) 7792 480 455; fax: +44 (0) 1865 310 447;
e-mail: gregory.wyatt@sjc.ox.ac.uk

helping, favoured owing to return benefits that accrue to the mycorrhiza's close kin forming symbioses with the same root. Hence, although altruism may occur in the context of mutualisms, it appears that this altruism is occurring within rather than between species.

From a theoretical perspective, although some authors have argued that natural selection cannot favour altruism between species (Foster *et al.*, 2006; Bourke, 2011), others have argued that it can (Frank, 1994; Fletcher & Zwick, 2006; Fletcher & Doebeli, 2009). Hamilton's (1963, 1964, 1970) theory of inclusive fitness highlights that it is not kinship (i.e. genealogical relationship) per se that is needed in order for altruism to be favoured, but rather that the actor and recipient are genetically similar (i.e. genetic relatedness). Frank (1994) suggested that genetic relatedness could arise between species due to the action of selection in viscous populations in a way that could favour the evolution of altruism between species (see also Gardner *et al.*, 2007). However, a formal analysis of when such genetic associations arise, when they will favour indiscriminate helping between species, and whether this helping fits the criteria for altruism between species remains to be undertaken.

Here, we first develop an infinite stepping stone population genetic model to provide a concrete illustration of whether and how indiscriminate helping can evolve between species. Previous theory has shown that: (i) population viscosity alone can favour the evolution of indiscriminate helping within a single species because it leads to a positive genetic relatedness between interacting individuals (Hamilton, 1964; Ohtsuki & Nowak, 2006; Ohtsuki *et al.*, 2006; Grafen, 2007; Lehmann *et al.*, 2007a; Taylor *et al.*, 2007), (ii) the evolution of reciprocal helping between species can be facilitated by population structuring (Doebeli & Knowlton, 1998), (iii) the evolution of indiscriminate helping between species can be favoured by transmission mechanisms that systematically force pairs of helpers together across generations (Yamamura *et al.*, 2004; Gardner *et al.*, 2007; Fletcher & Doebeli, 2009). Our aim here is to extend this previous theory, by examining whether population viscosity alone can favour indiscriminate helping between species.

We then examine whether such helping can be classified as between-species altruism using an inclusive fitness analysis. This requires dissecting the analytical conditions calculated for natural selection to favour indiscriminate between species helping in our model into separate inclusive fitness costs and benefits. In their most general sense, the costs and benefits of an inclusive fitness analysis are defined as least-squares regressions of fitness against genetic predictors (Queller, 1992; Gardner *et al.*, 2011). We explore the consequences of allowing or disallowing the genes of other species to feature in this regression analysis, both in general and also using our stepping stone model as a concrete illustration. Our aim here is to determine both whether indiscriminate helping between species can qualify as altruism between species and whether it must be considered altruism between species.

Indiscriminate helping between species?

In this section, we ask whether indiscriminate helping between species can be favoured by natural selection despite fecundity costs to the helper. We develop an infinite stepping stone population model, derive analytical conditions for helping to be favoured in this model, and then check the robustness of these results using individual-based numerical simulations of finite populations.

Model

We consider two identical asexual haploid species – A and B – in a one-dimensional stepping stone model (Kimura & Weiss, 1964) with infinitely many consecutively numbered patches, each containing one individual of each species. Individuals vary only at a locus controlling social behaviour and may carry either an allele for helping (H) or carry a null allele and are nonhelpers (N; Ohtsuki & Nowak, 2006; Taylor *et al.*, 2007; Taylor, 2010; Grafen & Archetti, 2008). The fecundity of an individual in patch i is given by $F_i = 1 - cx + by$, where x is her own helping genotype ($x = 1$ if H, $x = 0$ if N) and y is the helping genotype of her social partner ($y = 1$ if H, $y = 0$ if N; as illustrated in Fig. 1). Thus, $0 < c < 1$ is the marginal fecundity cost of cooperation and $b > 0$ is the marginal fecundity benefit of cooperation.

In every generation, we assume that all individuals die and that most are replaced by their clonal offspring, resulting in no genetic change within the patch. However, a small fraction of individuals are chosen at random to die without reproducing in this way, in which case their two conspecific neighbours in adjacent patches compete to fill the vacant breeding spot with one of their own offspring. If the fecundity of the neighbour in patch $i{-}1$ is F_{i-1} and the fecundity of the neighbour in patch $i{+}1$ is F_{i+1}, then the probability that a vacant spot in patch i is filled with an offspring of the neighbour in patch $i{-}1$ is $F_{i-1}/(F_{i-1} + F_{i+1})$ and the probability that it is filled with an offspring of the neighbour in patch $i{+}1$ is $F_{i+1}/(F_{i-1}+F_{i+1})$.

Evolution of helping

We consider a resident population of nonhelpers into which we introduce helpers of both species at random and at low frequency. Most helpers will leave no descendants in the long term, owing to them never meeting helpers of the other species, and hence, being outcompeted by their nonhelping conspecific neighbours. However, there is a nonzero probability that any helper of species A will eventually meet a helper of species B. If this happens, then there may be a nonzero

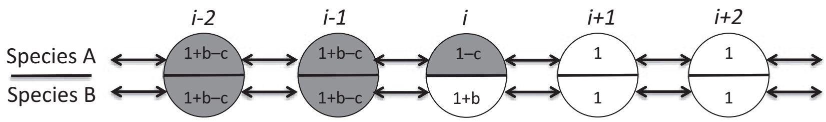


Fig. 1 Population structure. This figure shows a section of five patches in the population. The fecundity rate of individuals is affected by the individual of the other species with which they share a patch and they compete with individuals that reside two patches away. Shaded patches are inhabited by helpers, whereas white patches are inhabited by nonhelpers.

probability that these helpers will give rise to an expanding chain of patches that contain a helper of each species, leading the local frequency of helpers to increase when:

$$b > 2 + \sqrt{8 - 4c + c^2} \tag{1}$$

(see Appendix for derivation).

More realistically, we should take into account the effects of interactions between chains of patches that contain a helper of each species, and also the effect of mutation, which is the ultimate source of genetic variation. We assume that nonhelpers transform into helpers, and vice versa, at a low rate in each generation. The evolutionary dynamics are consequently complicated by the fact that nonhelpers may appear within expanding chains of patches containing a helper of each species, whether due to the junction of two pre-existing chains or fresh mutational input. Thus, it is not sufficient that chains of helpers tend to increase in length (i.e. inequality (1)), but also these chains must expand faster than the subpopulations of nonhelpers that appear within them. This gives rise to a more stringent condition for natural selection to favour helping:

$$\frac{(b-4)b-(c-2)^2}{(4b+(c-2)^2)(2+b-c)} > \frac{1}{2+2b-c} \tag{2}$$

We obtain this result irrespective of the relative rates of mutation in each direction (see Appendix for derivation), although the derivation requires low absolute rates. These analytical results are readily confirmed by numerical simulation with higher mutation rates, also revealing the robustness of the results to relaxation of the assumption of infinite population size (Figs 2 and 3, see Appendix for details). Natural selection favours helping when the benefit is greater than approximately 7.13 for a cost near 0 and when the benefit is greater than approximately 6.39 for a cost near 1. The required level of benefit changes almost linearly with cost. We notice that the cost has a relatively small effect on whether or not natural selection favours helping.

Paradoxically, we find that between species helping is promoted when the fecundity cost of helping is higher, as higher values of *c* make conditions (1) and (2) less stringent. This is because a larger cost is associated with stronger selection, and selection is responsible for generating a statistical association between species, such that helpers of one species are more likely to be associated with helpers of the other species (see Appendix; Gardner *et al.*, 2007). Natural selection can even favour helping when the fecundity cost is 1, meaning that helpers who do not share patches with other helpers cannot successfully place offspring into adjacent

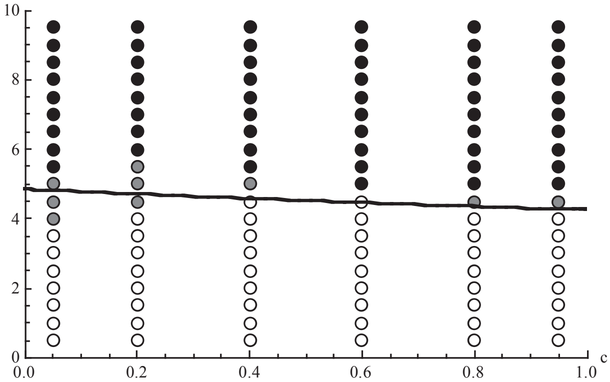


Fig. 2 Condition for expected local frequency of helpers to be expected to increase under natural selection. The line indicates the analytically derived condition for the expected local frequency of helpers to increase under natural selection (inequality (2) is satisfied above the line). Black dots indicate parameter values where helpers are significantly fitter than a neutral allele, white where they are significantly less fit and grey where there is no significant difference in fitness at a 95% confidence level (see Appendix for details).

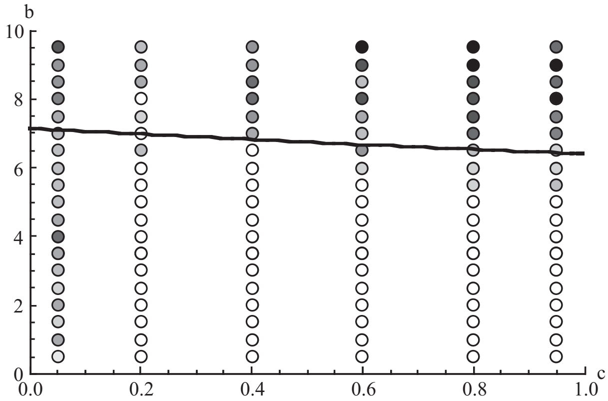


Fig. 3 Condition for natural selection to favour helpers. The line indicates the analytically derived condition for natural selection to favour helpers (inequality (1) is satisfied above the line). Dots indicate parameter values tested by simulation and darker dots indicate greater evolutionary success of helpers (see Appendix for details).

patches. This maximizes the association between helpers in the two species.

Altruism between species?

We have determined that indiscriminate helping between species can be selectively favoured in the face of fecundity costs. But can this helping be considered as altruism between species? To address this problem, we need to calculate the cost and benefit terms of Hamilton's rule. In empirical studies, fecundity and survival effects are often used as readily measured proxies for these costs and benefits. However, from a theoretical perspective, the benefit and cost terms of Hamilton's rule are not just the fecundity and/or survival effects (Rousset, 2004; Gardner *et al.*, 2011). Most generally, the benefit and cost terms of Hamilton's rule are defined as marginal fitness effects, which are computed by means of least-squares regression of fitness against genetic predictors (Queller, 1992; Gardner *et al.*, 2007, 2011).

Here, we briefly review: (i) how least-squares regression methodology can be used to formally separate individual fitness into its direct versus indirect (kin selected) effects (Queller, 1992; Frank, 1997a,b, 1998; Gardner *et al.*, 2007, 2011), (ii) how these fitness effects are used to classify social behaviours as altruistic, selfish, mutually beneficial or spiteful (Hamilton, 1964; West *et al.*, 2007), and (iii) how these fitness effects are weighted by coefficients of relatedness to yield Hamilton's rule of kin selection (Hamilton, 1963, 1964, 1970; Queller, 1992; Gardner *et al.*, 2011). We then: (iv) describe an ambiguity that arises in the application of these methods to our evolutionary model of helping between species, and (v) show that this ambiguity has a bearing upon whether or not such helping is classified as altruism between species.

Direct fitness versus indirect fitness

An individual's fitness w is her expected lifetime number of offspring that survive to breed in the next generation. Fitness depends not only on an individual's own genotype but also on the genotypes of her social partners. We may calculate the separate fitness effects by fitting an equation of the following form to population data by the method of least squares:

$$\begin{aligned} w = {} & 1 + \beta_{w,x|x_1,\ldots,x_n}(x - E(x)) \\ & + \sum_{j=1}^{n} \beta_{w,x_j|x,x_1,\ldots,x_{j-1},x_{j+1},\ldots,x_n}(x_j - E(x_j)) + \varepsilon \end{aligned} \qquad (3)$$

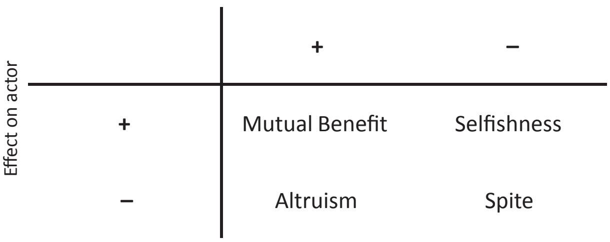
where the predictor x is the focal individual's genic value for helping, and the predictors $x_1,\ldots,x_n$ are the genic values of the individual's n social partners, that is, those individuals whose genotypes mediate the focal individual's fitness (e.g. Gardner *et al.*, 2011). The partial regression coefficient $\beta_{w,x|x_1,\ldots,x_n}$ describes the effect of the individual's own genic value on her fitness, holding fixed the genic values of her n social partners, and defines the direct fitness effect $-C$. The partial regression coefficient $\beta_{w,x|x_1,\ldots,x_{j-1},x_{j+1},\ldots,x_n}$ describes the effect of the individual's j^{th} social partner's genic value on her fitness, holding fixed the genic value of the focal individual and the genic values of her $n-1$ other social partners, and defines an indirect fitness effect B_j. We note that any partition of fitness that includes the focal individual's genic value for helping allows us to recover the total fitness effect of helping. The effects of genic values that mediate the focal individual's fitness but are not used in the partition will be redistributed into the fitness effects of the other predictors included in the analysis.

Classification of social behaviours

The signs of the direct and indirect fitness effects yielded by the above regression analysis are used to formally classify social behaviours. According to Hamilton's (1964) two-by-two matrix (Fig. 4), those behaviours involving $B > 0$ and $C > 0$ are 'altruistic', those involving $B > 0$ and $C < 0$ are 'mutually beneficial', those involving $B < 0$ and $C > 0$ are 'spiteful' and those involving $B < 0$ and $C < 0$ are 'selfish' (see West *et al.*, 2007 for a review of the history of this terminology). Importantly, these fitness costs and benefits derived from the statistical model must not be confused with the fecundity cost and benefit c and b of the evolutionary model (Rousset & Ronce, 2004; Grafen, 2007; Lehmann *et al.*, 2007a,b; West *et al.*, 2007; Gardner *et al.*, 2011).

Hamilton's rule

We can weigh the direct and indirect fitness effects ($-C$ and B_j) yielded by the above regression analysis by appropriate coefficients of genetic relatedness (r_j) to give a condition for natural selection to favour an increase in the trait of interest. This is Hamilton's (1963, 1964, 1970) rule: $-C + \sum_j B_j\, r_j > 0$. This can easily be seen to emerge from application of the least-squares regression model of individual fitness to Price's (1970) equation of



		Effect on recipient	
		+	−
Effect on actor	+	Mutual Benefit	Selfishness
	−	Altruism	Spite

Fig. 4 Hamilton's classification of social behaviours. A classification of social behaviours based on their effect on the reproductive fitness of actors and recipients.

natural selection. Price's equation states that the change in average genic value is given by:

$$\Delta E(x) = \mathrm{cov}(w, x), \tag{4}$$

noting that $\mathrm{E}(w) = 1$, since the population is of fixed size across generations. Substituting the expression for fitness in eqn (3) into eqn (4) yields:

$$\Delta E(x) = \left(\beta_{w,x|x_1,\ldots,x_n} + \sum_{j=1}^{n} \beta_{w,x_j|x,x_1,\ldots,x_{j-1},x_{j+1},\ldots,x_n}\beta_{x_j,x}\right)\mathrm{var}(x), \tag{5}$$

noting that $\mathrm{cov}(x,x) = \mathrm{var}(x)$, $\mathrm{cov}(x_j,x)/\mathrm{cov}(x,x) = \beta_{xj,x}$, $\mathrm{cov}(\varepsilon,x) = 0$ and $\mathrm{cov}(\varepsilon,x_j) = 0$ for all j. Replacing the complicated regression terms with the $-C$ and B_j symbols defined above (Queller, 1992), and noting that $r_j = \beta_{xj,x}$ is the regression form of genetic relatedness between a focal individual and her j^{th} social partner (Orlove & Wood, 1978), the condition for the genetical trait to be favoured by natural selection $\Delta\mathrm{E}(x) > 0$ is Hamilton's (1963, 1964, 1970) rule: $-C + \sum_j B_j\, r_j > 0$.

Which predictors to use?

Here, we have used purely genetic predictors of fitness (Queller, 1992; Gardner *et al.*, 2011). Frank (1997a,b, 1998, 2013a,b) has clarified that any set of predictors – including, for example, phenotypes – can be used. However, we are following Fisher's (1918, 1930) genetical paradigm that partitions the action of natural selection into purely genetic effects, as this reduces ambiguity over the definition of direct versus indirect fitness effects and consequent classification of social behaviours. For example, in a scenario involving reciprocated cooperation among nonrelatives, the direct fitness effect of a gene for cooperation can be positive, because it is associated with greater levels of cooperation among one's social partners, independently of the genes that they carry. Thus, cooperation, in the context of reciprocity, is a mutually beneficial behaviour (West *et al.*, 2007). But, if cooperation phenotypes had been used as explicit predictors of individual fitness, then because the partial effect of the individual's own phenotype is negative and the partial effect of the phenotype of a social partner is positive, the reciprocated cooperation would be incorrectly diagnosed as altruistic.

Nevertheless, even restricting ourselves to purely genetical predictors of fitness, an ambiguity arises as to which set of genes we should use in our regression analysis. Specifically, should we only consider those genes belonging to social partners of the individual's own species, or should we also consider those genes belonging to heterospecific social partners? Below, we show that the genes of conspecific and heterospecific social partners both mediate the focal individual's fitness. We then investigate the consequences of taking alternative approaches to resolving the ambiguity over the use of statistical predictors of fitness.

Causal relationship between genes and fitness

Genes in both species mediate the focal individual's fitness (Fig. 5a). First, her fitness is mediated by her own gene at the locus for helping as, all else being equal, she has fewer offspring if she helps more. Second, her fitness is mediated by the gene at the locus for helping carried by her heterospecific patch mate as, all else being equal, she has more offspring if her patch mate helps more. Third, her fitness is mediated by the genes carried by the conspecific individuals residing two patches away on either side, because she competes with these individuals to leave offspring whenever the patches immediately adjacent to her own become vacant. All else being equal, she has more offspring if these conspecific individuals help more. Fourth, her fitness is mediated by the genes carried by the heterospecific individuals residing two patches away on either side, because their help enhances the fitness of her competitors. All else being equal, she has fewer offspring if these heterospecific individuals help more.

This suggests that six genes mediate the individual's fitness: three belonging to her own species and three belonging to the other species. However, the causality can be traced further back in time, to other genes. The local genetic composition of the other species owes, in part, to the local genetic composition of the individual's own species in the previous generation. It also owes, in part, to the genetic composition of the individual's own species in each generation prior to that. In fact, the presence of any helper in the other species after a sufficiently long time owes entirely to the action of the individual's conspecific helpers in previous generations, as without these natural selection would eliminate helpers in the other species. This flow of causation is illustrated in Fig. 5a.

Conspecific genetic predictors only

If we consider that only genes from the individual's own species may be used as predictors of her fitness, then the effects of heterospecific genes are subsumed into the effects of conspecific genes from past generations. The resulting path diagram is illustrated in Fig. 5b. In the context of this statistical model, the partial effect of increasing the focal individual's genetic value for helping (that is, keeping all other predictors constant) is to decrease her own fitness. Hence, the direct fitness effect of helping is negative ($-C < 0$) and helping is altruistic. However, the indirect fitness effects of helping are all within species according to this statistical model, and so although the trait is altruistic, it is altruism within species. The inclusive fitness interpretation of this view is that, by helping, the actor suffers a

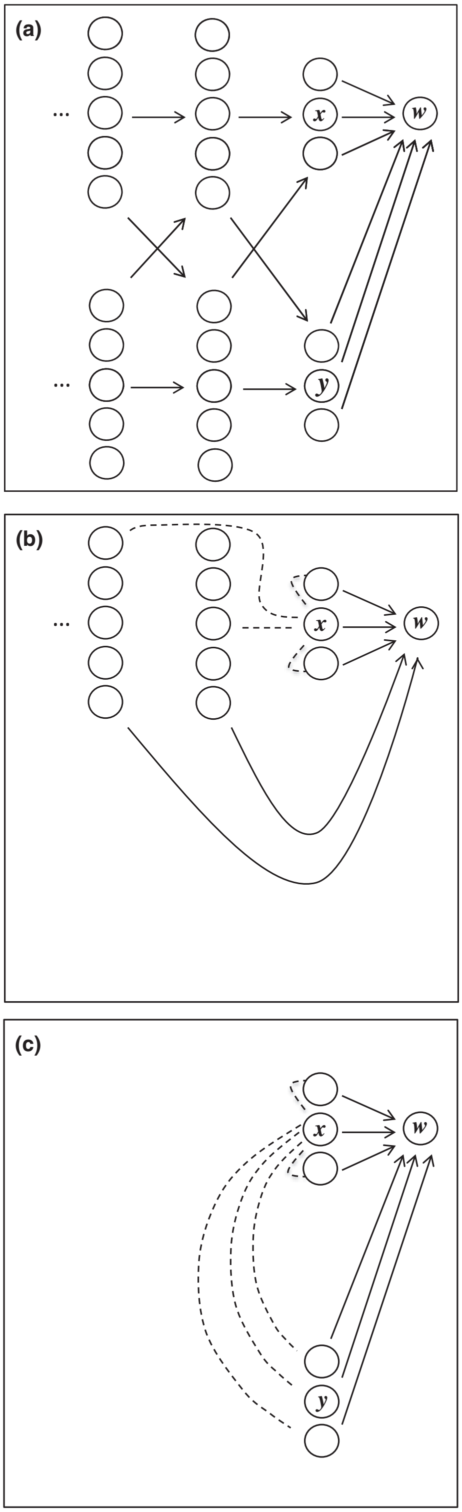


Fig. 5 Genetic mediators of fitness. (a) The genetic composition of past generations of both species causally impacts upon the genetic composition of the present generation of both species, and the genetic composition of the present generation of both species causally impacts upon the focal individual's fitness, *w*. A larger number of individual affect the fitness of a focal individual in each previous generation. (b) A path diagram illustrating the statistical model of fitness that uses genetic predictors from the focal individual's species only. The causal impact of genes in the other species is subsumed into the causal impact of genes in the focal individual's species from previous generations. A larger number of conspecifics affect the fitness of a focal individual in each previous generation. (c) A path diagram illustrating the statistical model of fitness that uses genetic predictors from the focal individual's species and also from the other species. The causal impact of genes in past generations of the individual's own species is subsumed into the causal impact of genes in the present generation of the focal individual's own species and in the present generation of the other species. Genetic correlations are shown as dashed lines.

direct fitness loss, but enjoys an indirect fitness benefit by increasing the local abundance of heterospecific helpers whose help will improve the reproductive success of future generations of the actor's conspecific kin.

In this statistical model, the help provided by heterospecific helpers to a focal individual is interpreted as caused by previous generations of conspecifics. It cannot be interpreted as caused by the focal individual, as she cannot impact the help provided by heterospecifics in her lifetime.

Conspecific and heterospecific genetic predictors

Alternatively, if we consider that genes from both conspecifics and heterospecifics may be used as predictors, then we need only to employ the six genes that determine a focal individual's fitness described above, as no other genes have an impact upon the individual's fitness except through those six. The resulting path diagram is illustrated in Fig. 5c. Again, the partial effect of increasing the focal individual's genetic value for helping is to decrease her own fitness, and hence, the direct fitness effect of helping is negative ($-C < 0$) and altruistic. Whenever helping is favoured, we have $-C + \sum_K B_k r_k + \sum_L B_l r_l > 0$, where K is the set of all conspecific genes that mediate fitness, and L is the set of all heterospecific genes that mediate fitness, and in particular $-C + \sum_K B_k r_k < 0$ (see Appendix for details). That is, the selective benefit of helping is dependent on the help that is directed to heterospecifics, and this diagnoses the helping trait as true altruism between species. The inclusive fitness interpretation here is that the coefficient of relatedness describes how the reproductive success of a social partner correlates with the transmission of copies of the actor's genes to future generations, and so – because the continued success of helper heterospecifics is important to the reproductive success of future generations of the actor's conspecific kin – these heterospecific social partners can be considered 'relatives' and consequently afforded positive valuation by the actor.

Discussion

We have developed an infinite stepping stone population model to explore the evolution of indiscriminate helping between species. We have found that natural selection may build genetic associations between individuals in different species, such that helpers of one species tend to interact socially with helpers of another species, giving an indirect fitness benefit for helping. Moreover, we have found that the classification of this helping behaviour depends on the modeller's decision as to which set of genetic predictors are used in a statistical model of fitness. If genetic predictors are restricted to those genes of the individual's own species, then the helping behaviour represents within-species altruism. However, if genetic predictors are allowed to include genes from both the individual's own species and also the other species, then the helping behaviour is diagnosed as between-species altruism.

Indiscriminate helping between species

We have shown that natural selection can favour indiscriminate helping, even when the trait can only benefit members of another species and carries a fecundity cost to the actor. Discriminate helping, involving mechanisms such as partner choice or partner-fidelity feedback, readily evolves between species, owing to return benefits for the actor and/or her conspecific relatives (Doebeli & Knowlton, 1998; West *et al.*, 2002; Foster & Wenseleers, 2006). However, the evolution of indiscriminate helping between species has been more difficult to address. Frank's (1994) analysis suggests that indiscriminate helping between species can be favoured in principle, but his model was not fully dynamical, and so the robustness of this result is unclear. Fully explicit dynamical models that have considered indiscriminate between species helping are problematic in that they systematically force pairs of helpers together across generations through the transmission scheme (Yamamura *et al.*, 2004; Gardner *et al.*, 2007). In contrast, in the present model, we allow individuals to reproduce and disperse independently. A statistical association between helpers across species boundaries builds up purely by population viscosity and the action of natural selection.

We have focused upon a simple, infinite stepping stone model (Kimura & Weiss, 1964), for the purpose of illustration. Investigating the impact of more complex population structure on the evolution of helping between species represents an interesting avenue for future research. Perhaps most work on social evolution in genetically structured populations has focused upon the infinite island model (Wright, 1931). But the island model does not present any means for pairs of helpers from different species to retain associations whilst spreading into new territory. This is because every disperser moves to a new patch at random, independently of the destinations of the other individuals dispersing away from her natal patch. However, there is further scope for studying the evolution of helping between species on lattices, which have explicitly spatial structure in more than one dimension (Taylor, 1992).

Altruism between species

When is helping between species truly altruistic? Our analysis suggests that this classification issue hinges upon the set of fitness predictors that are employed in a regression analysis. Different sets of predictors lead to different partitions of fitness effects, including different estimates of the direct versus indirect components of an individual's fitness, and hence, differences in classification of social behaviour as altruistic, selfish, mutually beneficial or spiteful. We have focused on genetical predictors, because using phenotypes leads to ambiguity and misinterpretation. Moreover, the phenotype is not the inherited strategy upon which natural selection acts. For example, in the context of reciprocity between nonrelatives, if fitness is partitioned into the effects of own versus social partner's level of cooperation, then cooperation can appear altruistic (Fletcher & Doebeli, 2009), but if it is partitioned into the effects of own versus social partner's genes, then it appears mutually beneficial (West *et al.*, 2007). The genetical approach is preferable, because it highlights that the rationale for cooperating in this scenario is to elicit cooperation from one's social partners, in a purely self-interested manner.

However, we have also shown that even the strictly genetical approach is beset by ambiguity over which genes are to be included as explicit predictors of fitness. In particular, do we only include genes belonging to the focal individual's own species, or do we also include genes belonging to other species? We have found that the evolution of between species helping can be fully accounted for using either approach. If we use only conspecific genes as predictors, then we find that helping between species constitutes within-species altruism. That is, the focal actor helps cooperators of the other species in order to improve the social environment for future generations of her own kin. In contrast, if we use both conspecific and heterospecific genes as predictors, then we find that helping between species constitutes between-species altruism. That is, the focal actor aids helpers of the other species because their reproductive success – like that of conspecific relations – is associated with an increase in the population frequency of the actor's genes.

Actors and recipients

The decision as to which genetic predictors are to be used in the regression model of fitness amounts to deciding which individuals we are considering as the actors and the recipients of the helping behaviour (Fig. 5). Simply having an impact upon a social partner's reproductive success does not necessarily make an individual an actor, if they might alternatively be considered a mere instrument that is used by a different individual – the true actor – in order to bring about the fitness effect. And simply having one's reproductive success mediated by a social partner does not necessarily make an individual a recipient, if they might alternatively be considered a mere instrument that is used by the actor to bring about a fitness effect for a different individual – the true recipient. This notion of agency is already implicit in any discussion of altruism: an intentional term, the use of which in scientific discourse is justified on the basis of a mathematical relationship (isomorphism) between the dynamics of natural selection and an individual-as-maximizing-agent analogy (Grafen, 2002, 2006).

If we use only conspecific genes as predictors then we must consider only conspecific individuals in the roles of actor and recipient. That is, those heterospecific individuals who mediate a focal recipient's reproductive success must be considered mere instruments, and the causality underlying their behaviour (i.e. why they carry out the helping behaviour) must be traced back to previous generations of the focal individual's conspecific kin (the true actors). Similarly, the heterospecific individuals whose reproductive success is mediated by a focal actor must be considered mere instruments, having only instrumental value in ensuring a better social environment for future generations of the actor's conspecific kin (the true recipients). In contrast, if we use heterospecific as well as conspecific genes as predictors of fitness, then we must consider both conspecific and heterospecific individuals in the roles of actor and recipient. Note that few mutualisms admit the latter interpretation – it requires special circumstances, such as those considered in our mathematical model, where genetic correlations arise between species. Most mutualisms appear to function through phenotypic correlations, such as cooperator association, partner-fidelity feedback or partner choice (Foster & Wenseleers, 2006). Also note that we cannot use only heterospecific genes as predictors because, unless these fully screen-off the effects of the individual's own gene, the sum of partial effects will not generally be equal to the overall least-squares linear regression of the individual's fitness against her own genetic value, which determines the direction of natural selection.

Are these different interpretations equally valid? A possible justification for the conspecifics-only approach is to note that the dynamics of natural selection is framed in terms of within-species genetical change, so that it makes sense to also restrict corresponding notions of optimization and agency to conspecifics. We also suggest that whilst there may be appreciable genetic relatedness across species with regard to helping genes, this might not be the case across the rest of the genome. In contrast, co-ancestry of conspecifics leads to an approximately equal relatedness across the entire genome, allowing for the evolutionary elaboration of complex adaptations.

On the other hand, a possible justification for the conspecifics and heterospecifics approach is that real-world organisms do not cease to manifest the appearance of agency and intention when we are considering the evolution of traits in other species. Consequently, it makes sense to regard individuals in all species as having agency at all times. Our formal analysis cannot address this issue, as it is framed only in terms of the dynamics of gene frequency change and not in terms of optimization theory, which is the proper framework within which to develop notions of agency and intentionality (Grafen, 2002, 2006). Hence, we leave this puzzle as an open problem for future exploration.

Conclusion

To conclude, was Darwin correct to rule out the adaptive evolution of behaviours that provide benefits only for individuals of other species? We suggest that he was. Natural selection can favour the evolution of indiscriminate helping between species and, in certain circumstances such helping may justifiably be interpreted as altruism between species. However, the alternative interpretation that such helping behaviour represents mere within-species altruism is available, as restricting the set of predictors to conspecifics gives a full account of the fitness effects of the trait. Thus, benefits to individuals of other species would never provide an exclusive explanation for any behaviour that has evolved by natural selection.

Acknowledgments

We thank Kevin Foster, Alan Grafen and David Queller and three anonymous reviewers for helpful comments and discussion, and the BBSRC, ERC, Royal Society and Balliol College for funding.

References

Bourke, A.F.G. 2011. *Principles of Social Evolution*. Oxford University Press, Oxford.

Darwin, C.R. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.

Doebeli, M. & Knowlton, N. 1998. The evolution of interspecific mutualisms. *Proc. Natl. Acad. Sci. USA* **95**: 8676–8680.

Fisher, R.A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. *Trans. R. Soc. Ed.* **52**: 399–433.

Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.

Fletcher, J.A. & Doebeli, M. 2009. A simple and general explanation for the evolution of altruism. *Proc. R. Soc. Lond. B* **276**: 13–19.

Fletcher, J.A. & Zwick, M. 2006. Unifying the theories of inclusive fitness and reciprocal altruism. *Am. Nat.* **168**: 252–262.

Foster, K.R. & Wenseleers, T. 2006. A general model for the evolution of mutualisms. *J. Evol. Biol.* **19**: 1283–1293.

Foster, K.R., Wenseleers, T., Ratnieks, F.L.W. & Queller, D.C. 2006. There is nothing wrong with inclusive fitness. *Trends Ecol. Evol.* **21**: 57–60.

Frank, S.A. 1994. Genetics of mutualism: the evolution of altruism between species. *J. Theor. Biol.* **170**: 393–400.

Frank, S.A. 1997a. The Price equation, Fisher's fundamental theorem, kin selection, and causal analysis. *Evolution* **51**: 1712–1729.

Frank, S.A. 1997b. Multivariate analysis of correlated selection and kin selection, with an ESS maximization method. *J. Theor. Biol.* **189**: 307–316.

Frank, S.A. 1998. *Foundations of Social Evolution*. Princeton University Press, Princeton.

Frank, S.A. 2013a. Natural selection. VI. Partitioning the information in fitness and characters by path analysis. *J. Evol. Biol.* **26**. 457–471.

Frank, S.A. 2013b. Natural selection. VII. History and interpretation of kin selection theory. *J. Evol. Biol*. doi: 10.1111/jeb.12131.

Gardner, A., West, S.A. & Barton, N.H. 2007. The relation between multilocus population genetics and social evolution theory. *Am. Nat.* **169**: 207–226.

Gardner, A., West, S.A. & Wild, G. 2011. The genetical theory of kin selection. *J. Evol. Biol.* **24**: 1020–1043.

Grafen, A. 2002. A first formal link between the price equation and an optimization program. *J. Theor. Biol.* **217**: 75–91.

Grafen, A. 2006. Optimization of inclusive fitness. *J. Theor. Biol.* **238**: 541–563.

Grafen, A. 2007. An inclusive fitness analysis of altruism on a cyclical network. *J. Evol. Biol.* **20**: 2278–2283.

Grafen, A. & Archetti, M. 2008. Natural selection of altruism in inelastic viscous homogeneous populations. *J. Theor. Biol.* **252**: 694–710.

Hamilton, W.D. 1963. The evolution of altruistic behaviour. *Am. Nat.* **97**: 31–33.

Hamilton, W.D. 1964. The genetical evolution of social behaviour. *J. Theor. Biol.* **7**: 1–52.

Hamilton, W.D. 1970. Selfish and spiteful behaviour in an evolutionary model. *Nature* **228**: 1218–1220.

Kiers, E.T., Duhamel, M., Beesetty, Y., Mensah, J.A., Franken, O., Verbruggen, E. *et al.* 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* **333**: 880–882.

Kimura, M. & Weiss, G.H. 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics* **49**: 561–576.

Lehmann, L., Keller, L. & Sumpter, J.T. 2007a. The evolution of helping and harming on graphs: the return of the inclusive fitness effect. *J. Evol. Biol.* **20**: 2284–2295.

Lehmann, L., Rousset, F., Roze, D. & Keller, L. 2007b. Strong reciprocity or strong ferocity? A population genetic view of the evolution of altruistic punishment. *Am. Nat.* **170**: 21–36.

Leigh, E.G. Jr 2010. The evolution of mutualism. *J. Evol. Biol.* **23**: 2507–2528.

Ohtsuki, H. & Nowak, M. 2006. Evolutionary games on cycles. *Proc. R. Soc. Lond. B* **273**: 2249–2256.

Ohtsuki, H., Hauert, C., Lieberman, E. & Nowak, M. 2006. A simple rule for the evolution of cooperation on graphs and social networks. *Nature* **441**: 502–505.

Orlove, M.J. & Wood, C.L. 1978. Coefficients of relationship and coefficients of relatedness in kin selection: a covariance form for the Rho formula. *J. Theor. Biol.* **73**: 679–686.

Price, G.R. 1970. Selection and covariance. *Nature* **227**: 520–521.

Queller, D.C. 1992. A general model for kin selection. *Evolution* **46**: 376–380.

Rousset, F. 2004. *Genetic Structure and Selection in Subdivided Populations*. Monographs in Population Biology, Princeton University Press, Princeton.

Rousset, F. & Ronce, O. 2004. Inclusive fitness for traits affecting metapopulation demography. *Theor. Popul. Biol.* **65**: 127–141.

Taylor, P.D. 1992. Inclusive fitness in a homogeneous environment. *Proc. R. Soc. Lond. B* **249**: 299–302.

Taylor, P.D. 2010. Birth-death symmetry in the evolution of a social trait. *J. Evol. Biol.* **23**: 2569–2578.

Taylor, P.D., Day, T. & Wild, G. 2007. Evolution of cooperation in a finite homogeneous graph. *Nature* **447**: 469–472.

West, S.A., Kiers, E.T., Pen, I. & Denison, R.F. 2002. Sanctions and mutualism stability: when should less beneficial mutualists be tolerated? *J. Evol. Biol.* **15**: 830–837.

West, S.A., Griffin, A.S. & Gardner, A. 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* **20**: 415–432.

Wright, S. 1931. Evolution in Mendelian populations. *Genetics* **16**: 97–159.

Yamamura, N., Higashi, M., Behera, N. & Wakano, J.Y. 2004. Evolution of mutualism through spatial effects. *J. Theor. Biol.* **226**: 421–428.

Appendix

Evolution of Helping: condition for the expected local frequency of helpers to increase over time under natural selection

Here, we derive the condition on b and c for natural selection to favour a local population of helpers in both species. Helpers can gain offspring irrespective of whether they share patches with other helpers. Therefore, as long as the population contains helpers at a high enough frequency that there are a finite number of patches between a pair of helpers in different species, stochastic effects ensure that a local distribution of helpers consisting of a set of at least two, but potentially many more, adjacent patches that contain two helpers, one of each species, may form. At the ends of this set, there may also be sequences of patches that contain one helper and one nonhelper, where all of the helpers in one of these sequences are from the same species. This local distribution is illustrated in Fig. 1.

Other local distributions of helpers may initially be present but when no two adjacent patches contain a helper of each species, natural selection eventually either eliminates helpers or gives rise to two adjacent patches that contain a helper of each species. Therefore, only helpers in a local distribution as described in the previous paragraph (and illustrated in Fig. 1) can be present in the population in the long term.

If a patch contains a helper of each species and is surrounded by two patches also containing a helper of each species, then selection in that patch does not impact the total number of helpers in the population as other helpers replaced deceased ones. Therefore, we can limit our attention to the edges of the distribution of helpers. The two edges are symmetric, so we consider only one of them (patches $i-1$, i and $i+1$ in Fig. 1).

The probability that a helper replaces a nonhelper and vice versa depends on the number of patches that contain a helper of one species and a nonhelper of the other (see Fig. S1 for details). We write the number of patches that contain only a single helper as s. For now, we assume that this number (s) can only change by one at a time through the replacement of an individual by the offspring of her neighbour. We relax this assumption in the next section and find that it does not affect our results. We can write the matrix of the relative rates of change in s.

$$\begin{array}{c|cccccc}
s & 0 & 1 & 2 & 3 & 4 & 5 \\
\hline
0 & -a_1 & a_1 & 0 & 0 & 0 & \dots \\
1 & a_2 & -a_2-a_3 & a_3 & 0 & 0 & \dots \\
2 & 0 & a_4 & -a_4-a_5 & a_5 & 0 & \dots \\
3 & 0 & 0 & a_4 & -a_4-a_5 & a_5 & \dots \\
4 & 0 & 0 & 0 & a_4 & -a_4-a_5 & \dots \\
5 & \dots & \dots & \dots & \dots & \dots & \dots
\end{array} \tag{6}$$

We can enter fecundity cost c for helpers and benefit b for individuals that share patches with helpers to calculate each of the values in matrix (6). The rates of increase and decrease in s are equal for all $s \geq 2$.

$$a_4 = \frac{1+b-c}{2+2b-c} + \frac{1}{2-c} > \frac{1+b}{2+2b-c} + \frac{1-c}{2-c} = a_5 \forall b, c > 0. \tag{7}$$

Hence, from the theory of Markov chains, there is a limiting distribution of the values of s. We calculate the long-term equilibrium frequency with which each value of s occurs in this distribution, p_s.

$$\begin{aligned}
p_0 &= \frac{a_2(a_4-a_5)}{a_1a_3 + a_1a_4 + a_2a_4 - (a_1+a_2)a_5} \\
p_1 &= \frac{a_1(a_4-a_5)}{a_1a_3 + a_1a_4 + a_2a_4 - (a_1+a_2)a_5} \\
p_{s\geq 2} &= \frac{a_1a_3}{a_1a_3 + a_1a_4 + a_2a_4 - (a_1+a_2)a_5}
\end{aligned} \tag{8}$$

Each a_s can be decomposed into a_{s+}, the rate at which s changes by the replacement of a nonhelper by a helper, and a_{s-}, the rate at which s changes by the replacement of a helper by a nonhelper. The average probability that a helper replaces a nonhelper is greater than the average probability that a nonhelper replaces a helper if

$$\begin{aligned}
&p_0(a_{1+} - a_{1-}) + p_1(a_{2+} - a_{2-} + a_{3+} - a_{3-}) \\
&\quad + p_{s\geq 2}(a_{4+} - a_{4-} + a_{5+} - a_{5-}) > 0.
\end{aligned} \tag{9}$$

The values of each a_{s+} and a_{s-} can be derived directly from the model

$$\begin{aligned}
&a_{1+} = 2\left(\frac{1+b-c}{2+b-c}\right),\ a_{1-} = 2\left(\frac{1}{2+b-c}\right), \\
&a_{2+} = \frac{1+b-c}{2+b-c},\ a_{2-} = \frac{1}{2+b-c},\ a_{3+} = \frac{1-c}{2-c}, \\
&a_{3-} = \frac{1+b}{2+2b-c},\ a_{4+} = \frac{1+b-c}{2+2b-c},\ a_{4-} = \frac{1}{2-c}, \\
&a_{5+} = \frac{1-c}{2-c},\ a_{5-} = \frac{1+b}{2+2b-c}
\end{aligned} \tag{10}$$

Substituting these into inequality (9) gives

$$\frac{2((b-4)b-(c-2)^2)c}{(4b+(c-2)^2)(2+b-c)} \tag{11}$$

Simplifying, we obtain inequality (1) of the main text. If inequality (1) is satisfied, helpers are expected to increase in number over time if the population is in the local distribution described at the beginning of this section and illustrated in Figs 1 and S1. That is, at least two patches containing a helper of each species surrounded on each side by a sequence of patches that contain a helper of one of the species but not of the other.

When inequality (1) is satisfied, the probability that a helper replaces a nonhelper is greater than *vice versa* in each species. Therefore, the probability that the patches that initially contain a helper of each species continue to do so forever is nonzero as the number of patches with a helper of each species can be described as a random walk bounded at zero where the probability of increase is greater than the probability of decrease. Hence, when inequality (1) is satisfied the expected number of helpers increases without limit over time. If inequality (1) is not satisfied, helpers are eventually eliminated.

Evolution of Helping: condition for the global frequency of helpers to increase under natural selection

In this section, we first analyse the effect of fresh mutational input at low frequency in the population (*a*). Then, we consider the impact of multiple instances of deceased individuals being replaced by neighbours in the same generation within a local distribution of helpers (*b*). Finally, we study the effect of local distributions of helpers meeting other helpers in the population (*c*).

(a) Further mutational input in the population

Nonhelpers randomly mutate to become helpers, and vice versa. We assume that rates of mutation in both directions are sufficiently low that, after one mutation, we can determine the effect of natural selection on helping prior to the occurrence of another mutation. We can ignore nonhelpers that mutate to become helpers: they are absorbed by larger distributions of helpers or eliminated by natural selection. Our simulations confirm that these assumptions do not require exceedingly low mutation rates (following section).

However, a local distribution of helpers can be disrupted by a mutation that arises in its midst (illustrated in Fig. S2). When this happens, there are two sequences of adjacent patches with a helper in each species joined by a single patch with a helper of one species and a nonhelper of the other. The nonhelpers and her descendants will always share a patch with a helper of the other species, unless her descendants reach the end of the sequence of patches with a helper in both species and join the global population of nonhelpers. Therefore, as long as the subpopulation of nonhelpers formed by the initial mutation avoids stochastic loss, they replace helpers from within a local distribution (illustrated in Fig. S2). Mutations are sufficiently rare that we assume local distributions grow beyond a sequence of three adjacent patches with a helper of each species before a mutation occurs. This ensures that mutations must occur at least two patches away from one end of the sequence. A sequence of at least two patches with a helper of each species must remain. Therefore, we can compare the expected rate at which new helpers are added at the far end of that sequence to the expected rate at which they are lost at the end where helpers are replaced by the subpopulation of mutant nonhelpers.

The rate at which helpers are lost is the rate at which nonhelpers replace helpers subtracted from the rate at which helpers replace nonhelpers when each receives the benefit of sharing a patch with a helper of the other species

$$\frac{1+b}{2+2b-c}-\frac{1+b-c}{2+2b-c}=\frac{c}{2+2b-c} \tag{12}$$

The LHS of inequality (11) gives the expected rate at which helpers at the far end of each sequence increase in number. This is equal to twice the rate at which helpers in one species increase in number. We subtract the value in eqn (12) from half the LHS of inequality (11) to find whether the rate at which helpers increase at the edge is greater than that at which they are lost in competition with the mutant subpopulation. This recovers inequality (2) from the main text.

(b) Multiple replacement by neighbours in the same generation within a local distribution of helpers

The only instance in which multiple replacement by neighbours matters is when both the last individual carrying one allele and the first carrying the other are replaced by genetically different individuals. The probability that this occurs in a single generation is therefore the probability that both are independently selected and replaced by neighbours. The effect of this double replacement is to create a subpopulation of nonhelpers at the end of a sequence of helpers in one species, the effect of which we have already studied. We therefore define the rate at which individuals are selected and replaced by neighbours to be small enough that a double replacement occurs rarely enough that the effect of natural selection can be measured between any double replacements. Therefore, natural selection still favours helping when inequality (2) is satisfied.

(c) Local distributions of helpers encounter others

The evolutionary process is only affected when there are fewer than two patches containing a nonhelper of each species separating the two local distributions. If there is only one patch containing a nonhelper of each species, then there must be helpers of the same species in the two neighbouring patches. If the nonhelper separating the two nearest helpers dies, it is certainly replaced by a helper. This gives rise to a continuous sequence of patches that contain a helper in one species. Therefore, the effect of two local distributions of helpers joining is the same as a nonhelping mutant arising in a local distribution of helpers (illustrated in Fig. S3). We have already shown in section (*a*) that when a subpopulation of nonhelpers arises within a local distribution of helpers, natural selection favours helping when inequality (2) is satisfied.

Simulations

(a) The effect of natural selection on helping in large populations

We run a numerical simulation of our model, relaxing the assumptions of infinite time and population size. We consider a ring of 10^6 patches. We initialize the population by randomly assigning each individual the helping allele with probability 0.02 and the nonhelping allele with probability 0.98. We run the simulation for a sequence of 2×10^{10} replacements where a clone of the previous inhabitant does not replace a deceased individual. For each of these replacements, we select a random individual in the population. The probability that a deceased individual is replaced by a mutant offspring, an offspring of the other genetic type, is 2×10^{-5}. If there is no mutation, the two conspecific neighbours compete to replace the deceased individual as detailed in our model. We perform five replicates for each set of parameter values displayed in Fig. 3. We consider the last 2×10^9 replacements for each replicate and count the number of times that helpers in a species have increased in number by more than 100. We assign a darker colour to the dot at parameter values where the number of helpers has increased more often, from white when helpers have never increased by 100 or more to black when this has happened each time.

We notice that at low cost, helpers often increase in frequency when our analytical results show that natural selection does not favour them. However, we can see (inequality (11) and eqn (12)) that cost is a factor in the rate at which helpers are gained and lost by natural selection. This means that when cost is low, natural selection is very weak, and so we would expect the number of helpers to occasionally increase over this timeframe (grey dots, but not black) even when natural selection does not favour helpers.

(b) Conditions for the expected local frequency of helpers to increase

We use a cycle of 250 patches, a sequence of 2.5×10^6 replacements, and assume that no mutations occur. Here, the population initially consists entirely of nonhelpers except for a single patch that contains a helper of each species. We perform 2000 replicates at each of the parameter values shown in Fig. 2. Given an initial frequency of 1/250 in each species, we would expect a neutral allele to fix 16 times in the simulations. If there are significantly more than 16 fixations (95% confidence level), we colour the parameter values in Fig. 2 black. If there are significantly fewer than 16 fixation, we colour the parameter values white. If the result is not significant, we colour the parameter values grey.

Fitness effects and relatedness when both conspecifics and heterospecifics are predictors

The fitness of a focal individual is determined by her own genotype, that of her two direct competitors, and the genotypes of the individuals share patches with each of these three. This yields 32 possible genotype combinations that determine fitness. We calculate the relative frequency of each of these combinations by considering a local distribution of helpers where there are at least five patches with a helper of each species. We use the probability distribution of s, the number of patches with a helper of one species and a nonhelper of the other, derived above, to calculate the relative frequency of each genotype combination.

We calculate the fitness coefficients using least-squares regression. To that end, we write the sum of the squared differences between the actual and predicted fitness given the genotypes present, weighted by the frequency of each of the 32 genotypic combinations

$$\sum_{o=1}^{32} q_o\big(w_o - C_{x_{0(o)}} + \sum_k B_k x_{k(o)} + \sum_L B_l x_{l(o)}\big)^2 \qquad (13)$$

where q_o is the frequency with which each combination occurs and $x_{0(o)}$ is the genic value of the focal individual, $x_{k(o)}$ are the genic values of conspecific predictors, $x_{l(o)}$ are those of heterospecific predictors, and w_o is actual fitness of a focal individual in that genotypic combination.

We solve for the least-squares regression coefficients C, B_k and B_l using expression (13). The relatedness terms, r_k and r_l, are the regressions of the genic value of a focal individual against that of its predictors. This is readily calculated using the q_o values. The solutions are too cumbersome to reproduce here (reproduced in Data S1), but the inclusive fitness effect of helping is

$$-C + \sum_K B_k r_k + \sum_L B_l r_l \qquad (14)$$

We find that expression (14) is positive if and only if inequality (1) is satisfied. We also find that

$$-C + \sum_K B_k r_k < 0. \qquad (15)$$

In order for natural selection to favour helping, a local distribution of helpers must be expected to increase in number. Hence, the fitness effects in heterospecifics, $\sum_L B_l r_l$, are essential for natural selection to favour helping when heterospecifics are used as predictors of fitness.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Data S1 Calculation of fitness effects and relatedness.

Figure S1 Number of patches that contain a single helper (s).

Figure S2 Further mutational input in the population.

Figure S3 Local distributions of helpers encounter others.

Data deposited at Dryad: doi:10.5061/dryad.962mb

Received 4 February 2013; revised 9 April 2013; accepted 6 May 2013