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Review

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Inclusive fitness in agriculture

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Trade-offs between individual fitness and the collective performance of crop and below-ground symbiont communities are common in agriculture. Plant competitiveness for light and soil resources is key to individual fitness, but higher investments in stems and roots by a plant community to compete for those resources ultimately reduce crop yields. Similarly, rhizobia and mycorrhizal fungi may increase their individual fitness by diverting resources to their own reproduction, even if they could have benefited collectively by providing their shared crop host with more nitrogen and phosphorus, respectively. Past selection for inclusive fitness (benefits to others, weighted by their relatedness) is unlikely to have favoured community performance over individual fitness. The limited evidence for kin recognition in plants and microbes changes this conclusion only slightly. We therefore argue that there is still ample opportunity for human-imposed selection to improve cooperation among crop plants and their symbionts so that they use limited resources more efficiently. This evolutionarily informed approach will require a better understanding of how interactions among crops, and interactions with their symbionts, affected their inclusive fitness in the past and what that implies for current interactions.

1. Introduction

Optimizing crop yields depends, among other factors, on the efficiency with which communities of plants and their microbial symbionts use resources such as sunlight, water and nutrients. Natural selection has had millions of years to enhance those aspects of resource-use efficiency that increase individual fitness. Further breeding improvements in individually beneficial traits of crops are therefore likely to be difficult [1,2]. There may still be significant untapped potential for improving community resource-use efficiency, but we argue that this will usually require reversing past selection for individual fitness. For example, Green-Revolution yield improvements in wheat and rice were gained by breeding for shorter plants, an approach that invests less in stems and more in grain. This breeding strategy successfully increased yields but at a cost to individual competitiveness: higher-yielding Green-Revolution rice cultivars are easily outcompeted by earlier cultivars, because they are less competitive for light [3].

Similarly, natural selection has favoured highly competitive microbial symbionts of crop and wild plant species, such that the symbionts enhance their own fitness, not necessarily the fitness of their host. How much should rhizobia or mycorrhizal fungi invest in supplying their plant hosts with nitrogen or phosphorus, respectively? Each individual plant is infected by multiple strains of symbionts, such as rhizobia and/or mycorrhizal fungi. This raises the potential for a tragedy of the commons, in which each microbial symbiont could enhance its fitness through diversion of resources to its own reproduction, at the expense of nitrogen fixation or phosphorus delivery [4,5]. The ability of some host plants to preferentially allocate resources to different root nodules or different mycorrhizal strains (sometimes called 'host sanctions') can reduce fitness benefits to such microbial 'cheaters' in both systems [6–10]. Nonetheless, these symbionts may still invest less in mutualistic activities than would be optimal in agriculture, where the aim is to increase community-level efficiency. These examples of individual-versus-community trade-offs are a common theme in agriculture.

The above discussion has implicitly assumed that past evolution of crops, their wild ancestors and their symbionts was driven only by individual fitness, namely the extent to which an individual's descendants are included in the next generation. Past selection can also favour inclusive fitness, a measure of the transmission of an individual's allele copies to future generations, either directly or via the reproductive success of other individuals with which they share alleles, also called indirect fitness [11]. Reproduction by relatives tends to increase the inclusive fitness of an organism. Past selection for inclusive fitness might have favoured more cooperative genotypes which would help to enhance the efficiency of crop and symbiont communities.

There are clear negative effects of individual selection on community-level efficiency. How much has selection for inclusive fitness ameliorated these negative effects? This is the central question of this essay. Past selection, based on inclusive fitness, may have somewhat constrained the evolution of selfish traits that increase an individual plant's or symbiont's own fitness at the expense of its neighbours. This is interesting for agriculture, because the goal is to increase community-level efficiency, even if it comes at a cost to individual fitness. For example, an allele for increased plant height might increase a plant's individual fitness, by increasing its competitiveness for light. But if the neighbours shaded by that plant are its close relatives, they are more likely (relative to a random plant) to also have the increased-height allele. Mutual shading by these plants and their greater investment in stems rather than seeds could reduce their collective seed production, perhaps limiting any increase in the frequency of the increased-height allele. So, increased plant height might increase inclusive fitness less than it increases individual fitness.

Similarly, if there were high relatedness among rhizobia infecting the same individual plant, this could select against rhizobia that divert resources from nitrogen fixation to their own reproduction. This is because nitrogen-deficient plants have lower photosynthesis rates [12], reducing potential carbon supply to the rhizobia. Thus, high within-plant relatedness would select for greater investment in the nitrogen fixation that benefits all the rhizobia sharing a given host plant [5].

We argue, however, that past selection for inclusive fitness has probably not been sufficient to achieve the full potential of cooperation among plants, nor between plants and their symbionts. Further improvement through plant breeding and crop symbiont management should therefore be possible. There are two different ways in which selection for inclusive fitness could favour the evolution of greater cooperation among plants and symbionts. First, frequent interaction with relatives over many generations could increase the frequency of alleles for unconditional cooperation with neighbours, if individual costs are low enough. Second, more sporadic interaction with relatives could favour the evolution of the ability to recognize kin (termed kin discrimination), for example, in plant interactions among roots, to assess the overall relatedness of neighbours. If crop plants or symbionts have such abilities, that could allow kin discrimination or phenotypic plasticity in traits that affect the fitness of neighbours. The extent to which crops and symbionts actually recognize kin or assess the overall relatedness of neighbours is an important empirical question, discussed below.

If either crops or symbionts do have positive responses to the relatedness of their neighbours, that could have immediate

applications in agriculture. This is because humans can influence the relatedness among neighbouring crop plants and among symbionts that share host plants. For example, even if we plant two or more genotypes of the same crop species on a farm, we usually group plants of the same genotype together rather than planting mixtures. Similarly, we may increase the within-host relatedness of rhizobia by inoculating seeds with a single clone.

In contrast to kin discrimination, what if relatedness only affects cooperation through evolutionary processes over generations? In that case, we may need to focus more on symbiont evolution than crop evolution. We may have more control over relatedness among plants than among symbionts, because of competition with unrelated, indigenous rhizobia and mycorrhizae in the soil. Nevertheless, the effects of relatedness on contemporary evolution will often be greater for symbionts than for crop plants. This is because, in industrial agriculture, crops are usually grown from purchased seed, rather than seed produced on the same field in a previous year. Therefore, any effects that relatedness among plants might have on crop evolution in production fields will often be swamped by deliberate selection imposed by plant breeders elsewhere. This conclusion would not necessarily apply to farmers practising 'evolutionary plant breeding' [13], i.e. replanting seed produced on their farms to encourage local adaptation.

We will address crops, rhizobia and mycorrhizal fungi separately. Each section begins with examples of conflicts between individual fitness and community-level efficiency. We then discuss how past selection for inclusive fitness might, in some cases, have favoured community efficiency. Finally, we consider future opportunities for further improvement, through human-imposed group selection or other means.

2. Crops

Breeders have the ability to select for greater cooperation among crop plants, increasing their collective yield at the expense of their individual fitness. We contrast 'cooperation' with wasteful competition, such as when individual plants invest in increased height without actually increasing their collective capture of solar radiation. Breeding for more cooperative plants with higher collective yield can involve either some form of human-imposed group selection, such as selection based on the yield of single-genotype field plots, or selection for specific traits that are key to cooperation. Individual-plant fitness depends on acquisition of resources (e.g. light, water or nitrogen) by a plant and the efficiency with which resources are used to make seeds. Any trait that simultaneously enhances resource acquisition and resource-use efficiency has already been subject to positive selection over millions of years, perhaps leaving little room for improvement by plant breeders. Exceptions to this generalization include adaptation to current conditions in agriculture that differ greatly from those in the past natural environments, such as greater soil fertility, tillage, increased atmospheric CO₂ [14] or novel pests.

Often, however, there are trade-offs between resource acquisition and resource-use efficiency [15,16] or trade-offs between individual competitiveness versus yield. The former impose certain constraints on crop improvement, whereas the latter can represent opportunities missed by past natural

selection. Breeders can use these individual-versus-community trade-offs to their advantage.

(a) Potential conflicts between individual-plant fitness and community productivity

Consider a trait that doubles a plant's competitiveness for some fitness-limiting resource, i.e. which lets it acquire twice as much of that resource as its neighbours do. Even if that trait also reduced its resource-use efficiency by 25%—less photosynthesis per photon absorbed, say—it would probably increase individual fitness. As discussed below, the increased resource acquisition has come at the expense of neighbouring plants, decreasing overall seed production by the plant community, i.e. crop yield. Thus, although seed production is key to both crop yield and individual fitness, some traits that enhanced individual fitness (by increasing seed production by an individual plant) in past environments can decrease crop yield (seed production per hectare) today. This offers potential opportunities for plant breeders to develop crops with greater resource-use efficiency in ways that were missed by past natural selection because of trade-offs with individual competitiveness.

A classic paper by Donald [17] is best known for coining the term, 'ideotype', a plant with 'model characteristics' for enhancing yield. He made several specific suggestions for model traits he thought would increase wheat yield under well-managed conditions. But, his most important contribution, we argue, was the explicit central hypothesis that there are strong trade-offs 'between the competitive ability of cultivars against other genotypes on the one hand, and their capacity for yield in pure culture' [17, p. 385].

The specific traits Donald proposed were not arbitrary, but linked to this trade-off hypothesis. These traits included short stature, for greater allocation of resources to grain rather than stem. If a whole field of shorter plants was grown together, then this could increase collective yield. An individual short plant shaded by taller plants, however, will capture fewer photons, photosynthesize less and produce fewer seeds than its neighbours. So, tall neighbours would have to be excluded to realize the whole-crop efficiency of shorter crop individuals.

Some tests of ideotype breeding have used traits that appear to conflict with Donald's hypothesis and his specific suggestions for ideotype traits. For example, Yuan *et al.* [18] compared rice genotypes selected for ideotype traits thought to influence yield with genotypes selected for yield alone. They found that direct selection for yield was more effective. But their stated height goal was 120 cm, which is taller than current cultivars and therefore inconsistent with Donald's call for shorter height and a less competitive ideotype. Because their ideotype lines ended up taller than either the reference cultivars or the lines selected for yield, the lower yield of the ideotype lines is actually exactly what Donald's hypothesis predicts.

Other ideotype traits proposed by Donald [17] included more erect leaves. With the sun overhead, horizontal leaves intercept more photons, so individual selection can favour horizontal leaves. Photosynthesis shows diminishing returns with irradiance, however, and horizontal leaves cast larger shadows on leaves below. In agriculture, a field of plants with vertical leaves (high radiation-use efficiency), spaced closely to increase total photon capture, would have greater

collective photosynthesis and yield than a field of plants with horizontal leaves. Similarly, solar tracking can reduce whole-crop photosynthesis [19], because leaves that track the sun cast larger shadows. To the extent that those shadows fall on neighbours, rather than a plant's own leaves, shading can increase the relative fitness of the plant casting the shadows. Tassels, the male flowers of maize plants, consume resources directly and they also reduce photosynthesis by shading leaves [20]. Again, the shaded leaves are usually those of neighbouring plants.

Next, consider water-use efficiency. At the leaf level, water-use efficiency is the ratio of photosynthetic CO₂ uptake to transpirational evaporation of water from leaves. This efficiency is three times as great on cool mornings relative to hot afternoons [21]. Partial stomatal closure each afternoon would reduce daily photosynthesis and crop growth rate, but it could reduce water use even more. So, if a limited supply of water in the soil is the main constraint on the duration of crop growth, afternoon stomatal closure could enhance final yield. Individual selection, however, would never favour such restraint in using soil water, if the water conserved would be used by competing neighbours who would then compete with the focal plant for light and soil nutrients.

Allocation to roots is another example where there is strong potential for trade-offs between individual fitness and the collective performance of plant communities. Zhang *et al.* [22] showed that individual selection favours greater investment in roots than is optimal for overall productivity in water-limited environments. Total water uptake by the plant community is not increased when a plant sends roots into soil already explored by its neighbours, but the focal plant appropriates a larger fraction of the available water.

Although we have emphasized trade-offs between competitiveness and community productivity, maximizing individual fitness may not always maximize individual competitiveness. For example, Weiner *et al.* [23] has argued that cooperative suppression of weeds may be a public good neglected by individual selection. He notes that crop-plant growth that enhances individual escape from shading may not be optimal for collective shading of weeds.

(b) Inclusive fitness and cooperation among neighbouring plants

How does an inclusive-fitness perspective change these conclusions? To the extent that the wild ancestors of our crops had limited seed dispersal, neighbouring plants may often have been close relatives, sharing more alleles than the species as a whole. A plant that shares light or water with closely related neighbours may thereby increase the reproduction of plants that have the same 'cooperative' alleles, such as alleles for shorter stature, more vertical leaves or more conservative use of water. Interactions among relatives could also, perhaps, have reduced selection for greater investment in tassels or root extension under neighbours.

Did the wild ancestors of crops experience strong selection for cooperation with neighbours, based on inclusive fitness? Assume that a focal plant that refrains from invading the soil under a particular neighbour will reduce its own individual fitness, but increase the fitness of the neighbour. How much would the neighbour have to benefit, for

inclusive-fitness benefits to outweigh the direct benefit forgone by the focal plant?

Neighbouring cross-pollinated plants will rarely be more closely related than half-sibs, which have a genealogical relatedness of one-fourth. Hamilton's rule [24] implies that an allele for root restraint would tend to spread if the benefits of restraint to a neighbouring half-sib's reproduction is four times the reproductive cost of restraint to the focal plant. Over the evolutionary history of our crops and their wild ancestors, it seems unlikely that the benefit-to-cost ratio for root restraint would consistently exceed fourfold. After all, some of the water left in the soil by a root-restraint plant would evaporate, benefiting none of the plants.

If the potential collective benefits to crops from cooperation-enhanced water-use efficiency translated into a 50% yield increase under some drought conditions, that would dwarf the 6% increase claimed for transgenic drought tolerance [25], while still falling well short of the fourfold benefit needed to evolve via inclusive fitness.

What if *all* the plants in some local population were half-sibs? Then, a randomly aided plant would have, on average, the same restraint-allele frequency as the population as a whole. Therefore, increasing its reproduction would have no effect on the population frequency of the allele. The only value of Hamilton's r that makes this true—however low the cost and however great the benefit of restraint—is zero. This is why Grafen [26] has defined Hamilton's r for two individuals as the extent to which genetic similarity between them exceeds that in the population as a whole. By this definition, Hamilton's r will usually be less than one-fourth for cross-pollinated plants, at least for neighbours interacting at random. More generally, although limited dispersal increases relatedness among neighbours, the resulting selection for increased altruism can be balanced by increased competition among relatives for limited resources [27].

What if plants could recognize kin and cooperate preferentially with them? For example, they could be more aggressive in extending roots beneath non-kin than beneath kin. In diverse natural communities, plants that limit root extension under kin could still acquire similar amounts of soil resources, and use the resources not wasted on extra roots to make more seeds. There is some evidence that this may be possible. Dudley & File [28] reported that *Cakile edentula* (sea rocket) plants growing with siblings allocated less biomass to fine roots than when they were grown with non-relatives, consistent with kin recognition and root restraint. It has been suggested, however, that their results could be a side-effect of changes in root allocation with plant size [29]—plants grown with non-kin tended to be larger. Of eight wild species tested in another study, only *Trifolium repens* (which grows clonally) increased allocation to reproduction when crowded by siblings but not non-siblings [30]. Milla *et al.* [31] found that *Lupinus angustifolius* plants growing with unrelated neighbours made significantly more flowers and seeds than those growing with siblings, despite faster early growth, and suggested that apparent kin discrimination could be a side-effect of self/non-self-recognition.

A plant is even more closely related to itself than to siblings and there have been several reports of self/non-self-recognition. Lateral roots of pea plants grew more towards non-self than self-roots [32], which would presumably reduce a plant's wasteful over-exploration of the soil it dominates. Rice roots, however, were reported to overlap more with self than

non-self-roots [33]. Soya bean plants invested more in roots when they shared a pot, with soil per plant held constant [34]. This result seems consistent with restrained competition against one's own roots, but plants tend to grow larger roots in larger pots, independent of interactions among roots [35].

It is not clear what mechanisms allow kin recognition, to the extent that it occurs. There is some evidence that root exudates may allow kin recognition in plants [36]. A consistent 'greenbeard' link between root exudate profiles and traits that mediate cooperation seems unlikely, however, because there would be selection for mimicking the signals of altruists, but not their altruistic behaviour. It has been proposed that plants can 'sense' the relatedness of other plants connected to the same mycorrhizal fungal network, as discussed in the section on mycorrhizae, but this has only been tested in one species [37]. Even if plants do have kin-recognition mechanisms, then selection for cooperation with putative kin could be weak, especially if mistaken identity is common.

The overall conclusion for this section is that past selection for inclusive fitness probably had some tendency to favour constitutively more cooperative (e.g. shorter, erect-leaf, root-restraint) plant genotypes, relative to individual selection. This effect would have been undermined, however, because a plant's costs of restraint in resource use would often have been similar to (as opposed to much less than) the benefit to neighbours. If past neighbours were rarely more related than half-sibs, selection for constitutive restraint would only have operated when benefits exceeded costs by a factor of four. The possibility of inducible restraint linked to kin recognition, for which there is some evidence in plants, would weaken this conclusion only slightly. Today's high relatedness among neighbouring crop plants is beyond the range commonly experienced by their ancestors, so even kin recognition is unlikely to trigger restraint unless benefits greatly exceed costs.

(c) Prospects for improving cooperation among crop plants

As discussed above, uniformly high genetic relatedness (all half-sibs or even clonal populations) does not necessarily select for cooperation [27]. This means growing crops in single-genotype fields (and planting seed produced in that field) would not necessarily select for greater cooperation. But what if past selection over a range of relatedness conditions somehow led to crops that detect and respond to today's higher levels of relatedness?

Assume, for the sake of argument, that (i) a given crop species has evolved reliable assessment of relatedness closer than half-sibs, and (ii) the crop follows Hamilton's rule. A plant interacting with a genetically identical neighbour might then restrain its own height and root expansion whenever the neighbour's benefit exceeded its own cost. What would be the implications for agriculture?

When grown in single-genotype fields, such a crop might already exhibit high levels of cooperation, even without human-imposed selection for among-plant cooperation. That would limit the potential for further improvement by plant breeders. This assumes that postulated traits for cooperation among kin were not lost during domestication or with subsequent plant breeding. However, the opposite may, sometimes, be the case. Zhu & Zhang [38] found that root allocation by a modern wheat cultivar decreased as its own

frequency increased in mixtures, consistent with cooperation (root restraint) among kin, which would enhance efficiency. An older cultivar did not show this response. In general, we expect complex traits like kin recognition to be lost more easily than they are gained, so it will be interesting to see whether newer cultivars consistently show greater such responses.

Although kin recognition in crops and their wild ancestors merits further research, past selection for inclusive fitness does not appear to have exhausted the potential for cooperation among plants to enhance resource-use efficiency and yield of crops. Plant breeders deciding which genotypes to retain, based on the collective yields of single-genotype plots, are already imposing selection for group-beneficial traits. An alternative approach is to consider individual-versus-community trade-offs in proposing specific breeding objectives [1,17].

A focus on specific traits linked to individual-versus-community trade-offs may give faster improvement in those traits, relative to selection among groups of genetically uniform plants for yield. Selection for short stature and erect leaves led to the high-yielding Green-Revolution rice variety, IR8 [39]. By contrast, although selection for maize yield resulted in increased leaf angle and reduced tassel size, those changes took almost 60 years [40]. Australian wheat breeders substantially increased allocation to grain at the expense of stem (another of Donald's ideotypes), but it took 126 years [41]. Although selection for yield may be slow to improve specific cooperative traits, a potential advantage is that it may improve cooperative traits that we have yet to identify or understand [23]. To the extent that either approach has succeeded, it implies that any past kin or group selection in nature has been relatively ineffective in favouring cooperative traits—at least for those forms of cooperation useful under current agricultural conditions.

It is not clear whether future improvements in cooperation among crop plants will come from trade-off-cognizant ideotype breeding or hypothesis-free, human-imposed selection for whole-crop performance. Either way, we suggest that the potential of these approaches has yet to be exhausted, either by kin selection prior to domestication or by subsequent plant breeding efforts, and offers a more promising route to crop improvement than those that ignore individual-versus-community trade-offs.

3. Rhizobia

Rhizobia are soil bacteria best known as symbionts in legume root nodules, where they typically convert nitrogen gas from the soil atmosphere into forms useful to their plant hosts. Depending on the crop and the conditions, they can supply a large fraction of the nitrogen needs of legume crops and forages. Other phases of the rhizobial life cycle are much less studied [42], but may be key to rhizobial fitness. Rhizobia reach populations of 10^5 – 10^{10} cells per nodule, depending on host species and conditions, an enormous potential fitness gain for a single nodule-founding bacterium. What fraction of those rhizobia then escape back into the soil is a key unanswered question, but even a 1000-fold fitness gain from a few months of symbiosis is probably more than what the bacterium would usually achieve in the soil.

Inside nodules, rhizobia may also acquire resources that enhance survival and reproduction after they return to the soil. For example, a rhizobial cell may acquire enough

phosphorus in a nodule to support up to five generations in low-phosphorus soil [43] and enough energy-rich polyhydroxybutyrate (PHB) to reproduce up to threefold without an external carbon source [44]. The recent discovery of rhizobial bet-hedging under starvation hints at risk/benefit trade-offs in the soil [45,46]. Our discussion of rhizobia will largely be focused on the trade-offs rhizobia face inside nodules, however, because these are better understood and directly relevant to agricultural resource-use efficiency.

(a) Potential conflicts between fitness of rhizobia and their legume hosts

Given the fitness benefits of forming a nodule with a legume host, it is easy to understand why genes for infecting legumes persist in rhizobial populations. The benefits are potentially so great that rhizobia have even evolved ways to form more nodules than the plant may need. Some rhizobia produce rhizobitoxine, which interferes with plant signalling via the hormone ethylene. Rhizobitoxine can increase the number of nodules per plant [47], perhaps beyond what is optimal for plant fitness. A recent comparison between rhizobial strains differing in rhizobitoxine production found that the rhizobitoxine-producing strain supported less plant growth, but obtained more PHB in symbiosis, relative to the strain that did not produce rhizobitoxine [48].

Once rhizobia are inside a nodule, some legume species cause rhizobia to lose the ability to reproduce as they differentiate into the nitrogen-fixing, bacteroid form [49]. This extreme rhizobial differentiation apparently reduces the respiration cost of nitrogen fixation [50], so it is not surprising that legumes have evolved this trait repeatedly [51].

Losing the ability to reproduce reduces the individual fitness of a rhizobial cell, however, even relative to the limited opportunities for reproduction in the soil. So why do rhizobia retain alleles for infecting legumes in whose nodules they may become non-reproductive? A key point is that not all the rhizobia in these nodules are non-reproductive. The million or so per nodule that have not yet differentiated into bacteroids retain the ability to reproduce, so infecting legumes can still greatly increase the number of descendants of a nodule-founding rhizobial cell [52].

Once they have reproduced inside a nodule, why do rhizobia fix nitrogen and give most of it to their legume host? In hosts where bacteroids are reproductive, resources that a bacteroid uses to fix nitrogen for its host could presumably have been diverted to support its own reproduction instead. Nitrogen-fixation is an energy-intensive process which competes with accumulation of PHB by rhizobial cells. Mutants unable to make PHB fix more nitrogen [53], whereas mutants unable to fix nitrogen make more PHB. The latter is true, at least, when the nodule also contains rhizobia that do fix nitrogen [54]. In hosts where bacteroids are non-reproductive, PHB hoarding has no obvious fitness benefit to an individual bacteroid, but neither can a non-reproductive bacteroid gain a direct fitness benefit from providing its host with nitrogen.

(b) Implications of inclusive fitness for rhizobia

The evolutionary persistence of nitrogen fixation by either reproductive or non-reproductive bacteroids must be due to inclusive fitness benefits to rhizobia. At what scale does

inclusive fitness operate? By supplying their host with nitrogen, rhizobia enhance photosynthesis and growth [12]. This could increase carbon supply to all the rhizobia infecting that host plant, some of which will be genetically identical clonemates.

Empirical and modelling studies suggest, however, that relatedness among rhizobia sharing a plant is rarely great enough to select for investment in the ‘public good’ of nitrogen fixation. Each individual plant may be infected by 10 or more strains of rhizobia [55]. Even with only two strains per plant, with neither strain common in the bulk soil, Hamilton’s r is only approximately 0.5. With that relatedness, the evolutionarily stable rhizobial investment in nitrogen fixation can be as low as zero, depending on the availability of nitrogen in the soil [5]. If the soil is already dominated by those two strains, in equal numbers, then release of rhizobia from that plant may have no effect on overall allele frequency. In that case, the effective relatedness for Hamilton’s-rule calculations is zero—there would be no inclusive fitness benefit to a rhizobial strain from enhancing plant growth and overall carbon supply to rhizobia [26,56].

As opposed to the level of the whole plant, rhizobial relatedness is much greater at the level of individual nodules. Most nodules are thought to contain one, or perhaps two, strains. If plants respond to differences in nitrogen fixation among nodules, in ways that affect the fitness of rhizobia inside, then there is a strong inclusive-fitness benefit to fixing nitrogen, regardless of the total number of strains per plant [5]. Consistent with this hypothesis, fitness-reducing ‘host sanctions’ against non-fixing nodules have been reported in soya bean [6], in wild lupines [7] and in both peas and alfalfa [10]. The latter two species are interesting, because bacteroids are non-reproductive in those hosts. The individual fitness of those nitrogen-fixing bacteroids is zero, but fixing nitrogen holds off sanctions that would affect their reproductive clonemates in the same nodule.

Although the symbiosis between legumes and rhizobia is among the best studied mutualisms, some important basic and applied questions remain unanswered. For example, how important are interactions among rhizobia, in bulk soil, in the rhizosphere, during the infection process, in nitrogen-fixing nodules and during nodule senescence? Quorum-sensing ‘signals’ in the rhizosphere could facilitate within-strain cooperation, perhaps at the expense of other strains. For example, some rhizobial strains produce toxic bacteriocins, which kill other strains [57]. If it takes a high population density to produce a killing dose, then linking bacteriocin production to strain-specific quorum sensing [58] could increase inclusive fitness. As an alternative role for quorum sensing, high densities could trigger dispersal from roots that already have many more rhizobia than could possibly nodulate. But could quorum sensing be co-opted for manipulation? For example, could overproduction by one strain of a quorum-sensing signal used by a second strain lead to dispersal of the second strain, reducing competition for nodulation?

Similar issues could arise within nodules. In one study, up to 32% of soya bean nodules contained two different strains of rhizobia [59]. Can rhizobia detect the presence of a second strain in the same nodule? If so, does that trigger production of bacteriocins? Does rhizobial investment in nitrogen fixation depend on within-nodule relatedness? For example, are there rhizobial strains that switch from fixing

nitrogen in single-strain nodules (to forestall sanctions) to ‘free-riding’ in mixed nodules?

(c) Prospects for improving rhizobial mutualism

Humans can have some effect on rhizobial population densities and perhaps relatedness, but the implications for agricultural management are not clear. Rhizobial population density in soil presumably increases somewhat with the frequency of their legume hosts in rotation or with host abundance in intercrops, of which grass/legume pastures are the most widespread example. The frequency of mixed nodules tends to increase with rhizobial population density in the soil [60]. If mixed nodules either trigger more ‘free-riding’ immediately or relax selection for nitrogen fixation, then the increased rhizobial density from growing legumes more often, in rotations, could indirectly undermine rhizobial mutualism. This effect could be small, however, relative to the many other factors farmers consider in designing crop rotations. Similarly, tillage might slightly reduce within-plant rhizobial relatedness, but factors such as weed pressure and risk of erosion would usually dominate decisions about tillage [61].

Applying rhizobia as seed inocula tends to increase within-plant relatedness of rhizobial strains. Rhizobia applied as seed inocula rarely become dominant in soils where that rhizobial species is already present, however, and they often occupy only a small fraction of nodules [62]. A major increase in within-plant rhizobial relatedness—enough to select for greater mutualism—would be difficult. Legume cultivars that preferentially favour inoculum strains would increase within-plant rhizobial relatedness, but the direct effects of favouring specific inoculum strains on nodule occupancy and subsequent soil populations would outweigh evolutionary effects linked to relatedness. Furthermore, indigenous strains can adopt the recognition signals of inoculum strains, via mutation and selection or horizontal gene transfer [63]. Developing crops that increase within-plant rhizobial relatedness, to promote the gradual evolution of greater rhizobial mutualism via kin selection, is unlikely to be an efficient use of plant-breeding resources.

The above discussion assumes that relatedness among rhizobia selects for cooperation among rhizobia and that greater cooperation among rhizobia implies more nitrogen fixation. The latter assumption may not always be true. High among-nodule relatedness could reduce differences in nitrogen-fixing efficiency among nodules, limiting a plant’s ability to increase the nitrogen return on its carbon investment by preferentially allocating resources to the most efficient nodules. Given strong sanctions against less efficient nodules, however, high within-nodule relatedness should select for more rhizobial investment in nitrogen fixation. This statement is based on the untested assumption that greater within-nodule relatedness would not lead to more effective manipulation of the host by the rhizobia.

Based on our current understanding, the most promising approach to increasing nitrogen-fixation efficiency is to breed legume crops that reliably impose rhizobial-fitness-reducing sanctions against all but their most efficient nodules. These sanction-imposing crops could gradually enrich the soil with the most beneficial indigenous strains [1]. There is considerable room for improvement in this plant trait. Sanctions imposed by current cultivars may only reduce rhizobial fitness by 50% or so, and rhizobia may fix as little as 50% of their potential without consistently triggering sanctions

[64]. A field comparison among soya bean cultivars demonstrated considerable genetic variability in host responses to non-fixing rhizobia, consistent with relaxed selection among plants for strict sanctions on high-nitrogen soils [65].

Interactions between selection for higher inclusive fitness and sanctions depend on the mechanism of sanctions. If sanctions are imposed at the level of individual nodules, rather than on individual rhizobial cells, then legume-host mechanisms that maximize within-nodule relatedness could be a key element of the stricter-sanctions breeding strategy. This would be particularly true for legumes in whose nodules the nitrogen-fixing bacteroids have lost the ability to reproduce [4]. To selectively favour the more mutualistic strain in nodules containing two strains of non-reproductive bacteroids and their reproductive clonemates, the plant would have to impose sanctions on the reproductive rhizobia whose bacteroid clonemates fixed too little nitrogen. It is not clear that this response would be beneficial for individual legume plants, nor is it clear whether this is physiologically possible. The limited data available suggest that sanctions in these species are apparently imposed on the nodule as a whole, although there have been conflicting reports on whether reduced allocation of resources to non-fixing nodules reduces the reproduction of rhizobia inside [10,66].

Given conflicts of interest among rhizobia infecting the same plant—they are each other's most likely competitors for the next host—it is unlikely that natural selection has maximized rhizobial investment in nitrogen fixation. Improving cooperation in this somewhat-cooperative symbiosis seems possible, but this will require a better understanding of how interactions among rhizobia affect their inclusive fitness.

4. Mycorrhizae

Arbuscular mycorrhizal (AM) fungi are among the most widespread and ecologically important soil microbes in the world: they are responsible for massive global nutrient transfer, carbon sequestration and soil stabilization [67]. These fungi manage to colonize between 60% and 80% of all plant species (including most crop plants) by penetrating the root epidermis of hosts, and forming underground networks that can connect multiple plant individuals. AM fungi are obligate biotrophs that depend on plants for their carbon requirements. In exchange for host carbon, the fungi provide plants with nutrients (e.g. phosphorus, nitrogen, trace minerals) and other benefits such as pathogen protection, making them valued components of agroecosystems. While agronomists and plant breeders have long recognized that mycorrhizal fungi can influence crop yields, there has been little to no progress in improving use of the symbiosis to increase agricultural output [68]. Crops are often coated with fungal propagules based on the assumption that they are limited by either the abundance or functioning of mycorrhizal strains [69], however they rarely respond to these inoculation treatments. What drives this lack of response is poorly understood. An inclusive fitness vantage point could help.

(a) Conflicts between fitness of mycorrhizae and their plant hosts

Similar to rhizobia, mycorrhizal fungi face potential conflicts between individual fitness and community-level efficiency.

Mycorrhizal fungi collect and transfer nutrients to their host, which can constitute the majority of plant phosphorus uptake [70]. This investment in nutrient transfer can be costly for the fungus but beneficial to the host, creating a potential conflict of interest [56]. For instance, fungal investments in extraradical hyphae and arbuscules have been shown to be positively correlated with benefits provided to host plants [71], whereas vesicles and hoarding of long-chained polyphosphates tend to indicate storage strategies benefiting the fungus [9]. Gaining access to new hosts (and their carbon) requires that the fungi increase investment in large runner hyphae and less in collecting phosphorus [72], which essentially drains the host plant while promoting the fungus [73].

Fungal strains differ in many traits indicative of their mutualistic strategies, including amount of carbon extracted from their hosts [74,75], amount of lipids allocated to storage [76], rate of transfer of phosphorus to their host plants [77] and even their ability to regulate the expression of host phosphate transporters [78]. These are traits that could be selected for or against in breeding programmes to optimize resource-use efficiency by crop hosts [68], including manipulating nutrient transfer to maximize benefits to the host plant, even if it comes at a cost to the fungal symbiont.

(b) Implications of inclusive fitness for fungal symbionts

Like rhizobia, mycorrhizal fungi must (on average) increase their inclusive fitness by providing nutrients to the host, or this trait would disappear [61,68,79]. However, unlike rhizobia, past selection has favoured cooperation at more than one level. Mycorrhizal fungi cooperate at the level of related individuals, but also nucleotypes (i.e. multiple nuclei that coexist together without any separation) cooperate within a single individual. This 'intra-individual' cooperation among nucleotypes arises because of the hypothesized multi-genomic nature of some fungal strains. For decades, scientists have worked under the assumption that AM fungi are asexually reproducing organisms (see [80]). However, recent work suggests they can contain genetically different nuclei within the same individual [81]. While the level of genetic difference among nuclei is still a topic of heated debate [81,82], it is well established that a single AM fungal spore can contain hundreds of nuclei [83–85]. From this individual spore, an array of genetically different progeny—displaying different phenotypes—can potentially arise [86]. While the exact mechanism is not well understood, the fungal phenotype is thought to be a reflection of the frequency of different nucleotypes within the individual fungus [87,88]. This has important implications because it means that selection can act at the level of nuclei within an individual fungus, potentially affecting community-level efficiency.

Like spores, hyphal networks contain genetically distinct nuclei. Adaptation within a hyphal network to local conditions is hypothesized to occur via changes in these nucleotype frequencies [89], most likely because of some form of group selection in which parts of the fungi that have a better nucleotype composition grow and reproduce more. This could potentially allow the fungus to be genotypically different in different parts of the same network and to produce offspring displaying a broad range of genetic and phenotypic changes in response to changing selection

pressures, for example host shifts [89]. These differences among offspring from a single individual involve alterations in the relative frequency of already existing nuclei, not new mutations. Angelard *et al.* [89] demonstrated that in some cases (but not all), these changes in nuclei frequencies can be adaptive for the fungus resulting in greater fitness than in the original phenotype. Changes in nucleotype frequencies can also be beneficial to the host: genetic exchange between mycorrhizal strains was shown to increase growth of rice hosts [90], and is therefore of great interest to agronomists.

While the multi-genomic nature of the fungus may increase its adaptability, this genetic system also introduces the potential for conflict within an individual fungus, reducing selection for inclusive fitness. Specifically, if a single nucleotype can alter its ability to transmit to the next generation, even at a cost to the individual fungus level, or to the host, then it will be selected to do so [91]. It is not yet known how these nuclei interact within a network: do nuclei move freely through the hyphae or do nuclei move as related 'patches'? Ultimately, techniques that allow researchers to manipulate the frequency of different nucleotypes in an individual will be the most useful in advancing our understanding of how inclusive fitness operates among nuclei, and therefore important in maximizing community-level efficiency.

Similar to the way a nucleotype can potentially increase its inclusive fitness by cooperating with related nucleotypes in an individual hyphal network, cooperation among different, but related, fungal individuals (i.e. an established fungal network derived from a single spore) has the potential to confer inclusive fitness benefits. The concept of 'relatedness' among fungal strains is more complex owing to this multinucleate nature. Grafen [26] defined the relatedness (for some cooperation allele) based on the frequency of that allele in the focal individual, in the beneficiaries of cooperation and in the overall population. For diploids, allele frequency could be 0, 0.5 or 1.0. For multinucleate individuals, such as mycorrhizal fungi, this same definition would hold, but would cover a wider range of values.

Fungal individuals are also able to cooperate by fusing together (anastomosis) with relatives into one shared hyphal network [92], even when hyphae originate from different host plants. It is hypothesized that fusion confers fungal benefits by facilitating the exchange of nuclei and introducing new genetic material [81], although mechanisms, for example the partitioning of mitochondrial DNA [93], are only beginning to be understood. Fusion, even in the absence of genetic exchange, may increase the size and performance of the hyphal network by increasing its interconnectedness. This allows for improved uptake of heterogeneously distributed resources [94], benefitting hyphae that would otherwise have less access to resources.

One question is whether (and if yes, why) high-resource hyphae allow sharing via fusion. For example, germinating spores (with little to no resources) can tap into the network without appearing to contribute to the collective good [95]. A possible explanation is that local resource supplies are often transient, so connecting to a partner (even if it is resource-poor) may reduce future risks. Fusion may also make the network more robust to damages [96]. Discrimination mechanisms prevent vegetative fusions among distantly related fungi. Incompatibility (and even cell death at point of contact) has been noted between fungi of different species [97].

Even if fusion increases fitness, and even if limiting fusion to kin reduces risks of within-organism conflict, it is unlikely that mycorrhizal fungi experience inclusive fitness benefits at the group level (e.g. sharing in collective benefits at the level of the whole plant host). Like rhizobial symbionts [5], mycorrhizal fungi face a similar tragedy of commons, because host plants are typically colonized by several genetically different strains [98,99]. Relatedness among fungal strains sharing a plant is generally not enough to select for investment in the 'public good' of transferring high amounts of phosphorus. Why then do mycorrhizal strains transfer phosphorus at all if they could adopt a strategy in which host carbon resources are diverted to fungal reproduction (e.g. spores) or storage (e.g. carbon stored in fungal vesicles)?

Recent works suggest that host plants are able to differentially distribute resources among competing strains on their root systems, allocating more carbon resources to those providing more phosphorus [8,9]. Similar to sanctions against rhizobia that fail to fix nitrogen [6], this mechanism helps select for cooperative fungal strategies by increasing the fitness of strains that transfer more nutrients to the host over those that transfer less. In addition, similar to legumes [65], it has been suggested that host plants are not equivalent in their ability to discriminate among fungi of varying quality [100].

In cases where relatedness among fungi on a single root system is high, this may have an added benefit for the host. A recent study tested a gradient of mycorrhizal genetic relatedness on the growth of host plants and found an approximately 30% increase in host biomass when plants were grown with closely related mycorrhizal strains compared with distantly related pairs of strains [101]. It is interesting that high within-host genetic diversity appears harmful to hosts [101]. It could be argued that higher symbiont diversity could potentially help drive 'prices' down for host plants as fungal strains compete for limited carbon resources. Alternatively, high within-host genetic diversity could lead to more antagonistic interactions among strains, at a cost to host benefit. Analogous antagonistic interactions among fungal strains prevent leaf-cutter ants from growing multiple strains of fungus [102], even though increased diversity might reduce risks from pathogens that attack the ants' fungal gardens. In nature, conflicts of interest among communities of mycorrhizal fungi colonizing the same host are probably intense enough to select for such antagonistic interactions. Whether antagonistic interactions among mycorrhizal strains competing for a single host are similar to those in ant fungi (or to rhizobial bacteriocins) is unknown. It has been shown, however, that direct competition can alter allocation strategies of coexisting fungal strains, for instance the ratio that a strain invests in colonizing outside the host root (extraradical hyphae) to colonizing inside a host root (intraradical hyphae) [103]. This suggests that competing strains are at least detected, so antagonistic responses seem plausible.

(c) Common mycelium networks and improving benefits to crops

From an applied point of view, agronomists are most interested in understanding how mycorrhizae affect host benefits and crop yields. One of the most promising avenues for research is on the role of common mycelium networks (CMNs) that form among plants [94]. CMNs are the extensive underground webs that allow fungi to forage for nutrients

and connect roots of different plant species. These networks, which can have diameters of 10 m [104], are critical for giving plants access to nutrients beyond their own root zone.

From a plant evolution perspective, a CMN can be thought of as a social good because it depends on carbon donations from all connected plants in the network. Such a network, if restricted to plant kin, could theoretically enhance the fitness of sibling groups, relative to groups of strangers. For example, plant siblings connected into a single fungal network could gain more consistent access to nutrients and water compared with if they were competing for these same resources. File *et al.* [37] found that investment in a common mycorrhizal network (as measured by network size and root colonization) was greater if plant individuals in the network were kin. They argued that in nature plants tend to live in dense communities where relatedness is high, and this would select for investing in kin-accessible public goods, such as size of CMN.

Consistently high relatedness might, however, reduce selection for kin recognition. Kin recognition via a mycorrhizal network [37] is even harder to understand than kin recognition among directly interacting roots. More evidence is needed to test whether plants are consistently able to sense the level of relatedness of plants connected into the same mycorrhizal network. This type of recognition is theoretically important, because non-relatives (including plants of different species) can be connected in a single network, which potentially selects against social investment. For example, Walder *et al.* [105] found that when flax and sorghum plants were connected into the same CMN, there was strong asymmetry in terms of exchange: flax invested little carbon, but received the vast majority of the nitrogen and phosphorus from the CMN, whereas sorghum received little, but invested high amounts of carbon. By contrast, work on artificial root systems (*in vitro* root organ cultures) found that root systems supplying more carbon were consistently rewarded with more phosphorus from the CMN, suggesting a higher symmetry in benefit [9].

While the dynamics of carbon investment by individual plants in CMNs is not clear, there is still theoretical potential for breeders to use CMNs as a means to increase homogenization of nutrients in a field. Responses to nutrients show diminishing returns, so even though transfers from high- to low-nutrient areas might somewhat reduce growth in high-nutrient areas, that would be outweighed by increased growth in low-nutrient areas. The key would be to select for high social investment within a CMN. If crop plants somehow discriminate against non-kin connected to the same CMN, then maintaining low crop-plant diversity (i.e. all related kin) within the local network could be beneficial. High crop-plant diversity could still be valuable at larger spatial scales. Alternatively, breeders could select against within-species discrimination, while perhaps maintaining discrimination against weeds.

In addition to increasing access to nutrients, CMNs may function as conduits for information. It has been demonstrated that networks can transmit compounds among neighbouring plants [106]. In some cases, this transmission has been shown to increase disease resistance of neighbouring plants of the same species. Gene expression for pathogen protection in healthy tomato plants was upregulated when connected to tomatoes infected with leaf early blight [107]. Similarly, in bean plants, the presence of a CMN determined how neighbouring bean plants responded to an aphid-infected host: connections of neighbouring

plants to the network increased herbivore defences before attack [108]. This suggests that CMNs help mediate plant responses to threats [109], which could have major applied benefits if developed.

One question is whether the signals conducted through the mycorrhizal network represent an adaptive response to help protect related plant kin from pathogen or herbivore attack, or if neighbouring plants connected into the network are simply 'eavesdropping' on cues being leaked. Individual selection would increase sensitivity to cues leaked by neighbours, independent of relatedness, but only kin selection could enhance transmission of signals [110,111]. If plants connected in a single network are closely related, then signalling may be an adaptation to help kin, while sharing less information with non-relatives than might occur with gaseous signals. But, how frequently this is the case in nature is unknown.

5. Conclusion

Humans can impose much stronger selection for traits with community-level benefits than normally occurs in nature. Past natural selection for inclusive fitness would have enhanced cooperative traits when costs to individual fitness were small enough, but there are many cases where selection for individual competitiveness against genetically diverse neighbours would have trumped community productivity. There is some evidence for kin discrimination in plants and by their microbial symbionts, but this has not led to perfect cooperation among plants or symbionts, even in lower-diversity agricultural contexts.

This means there is still significant untapped potential for improving community resource-use efficiency, via enhancing cooperation among crop individuals and between crops and their symbionts. In crops, we have already seen this in the form of human-imposed selection for cooperative traits (height, leaf angle, root allocation) in rice, wheat and maize to increase collective yields at the cost of individual fitness.

Translating this progress to root symbionts might be more difficult. Conceptually, this would involve decreasing the conflict between crops and their symbionts, and conflict among the symbionts themselves. This could be achieved by aligning the fitness of the symbiont more directly with that of the host. In the near term, breeding crops that impose stronger selection for microbial mutualism is the most promising approach [1,65]. Eventually, it may be possible to increase the so-called organismality of the partnership [112]. In this approach, the symbiont would be integrated into the host, much like a mitochondria is integrated into a eukaryotic cell, ultimately decreasing the vulnerability of the partnership to defection. This seems theoretically possible for rhizobia, which are already enclosed inside plant cells when they fix nitrogen. The nutrients supplied by mycorrhizal fungi, however, are taken up by fungal cells out in the soil. An 'organelle' that extends outside its host would raise interesting inclusive-fitness questions. A range of such agriculture-inspired questions could be research fodder for generations of evolutionary biologists to come.

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