3 If Group Selection Is Weak, What Can Agriculture Learn from Fungus-Farming Insects?

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The theme of this volume echoes the proposal by Mueller et al. (2005, 564) that "it may be fruitful to examine the short-term and long-term solutions that have evolved convergently in insect agriculture for possible application to human agriculture." Although they cited Denison, Kiers, and West (2003) in support of this idea, our 2003 review did not actually mention insect agriculture explicitly. However, like Darwin, we contrasted improvement of crop wild ancestors by natural selection, over millions of years, with "man's feeble efforts" (Darwin 1859, 61) to make further improvements. Could the long-term improvement of insect agriculture by natural selection offer useful ideas for human agriculture? Possibly, but we need to consider what natural selection can improve and what it cannot.

We argued that natural selection is unlikely to have missed simple improvements that would have consistently improved individual plant fitness. However, in contrast to individual plants, we argued that "there is no reason to expect the structure of natural ecosystems . . . to be a reliable blueprint for agricultural ecosystems" (Denison, Kiers, and West et al. 2003, 146). The fungal gardens of insects may be intermediate between individuals and ecosystems as potential targets of natural selection (Denison 2012). So, how likely is it that "solutions that have evolved convergently in insect agriculture" will be useful models for human agriculture?

To answer this key question, I first explain why natural selection has not consistently improved the overall organization of natural ecosystems—of things like species composition or spatial and temporal patterns. Then, I consider the extent to which these arguments apply to the organization of the fungal gardens of insects. Finally, I consider a specific aspect of insect agriculture: Namely, whether selection imposed by fungus-farming insects on their fungal cultivars or on other beneficial microbes are plausible contributors to their success.

If we measure the sustainability of agricultural practices by how long they can persist, then the survival of traditional rice-growing practices in Asia for over 4,000 years is certainly impressive (King 1911). But cattle have been raised for milk for at least 9,000 years (Evershed et al. 2008), and fungus-farming ants have been growing fungi for food for about 60 million years (Branstetter et al. 2017). Few natural ecosystems have persisted with little change for more than a few thousand years, given ice ages and human impacts on ecosystems worldwide.

Even if an ecosystem has persisted for only a few thousand years, we can say that its sustainability has been tested over time. But maybe a different version of that ecosystem (one with a different ratio of legumes to grasses, say, or more-uniform spatial distribution of trees) would not only have persisted, but would also have been more productive or more resilient under drought. For an entity to *improve* over time requires something beyond mere persistence. Competitive selection among alternatives is a well-understood mechanism for such improvements. For example, direct or indirect competition among individuals improves traits that benefit individuals, although this may not always benefit the species, community, or ecosystem (Denison 2012).

My doubts about modeling agriculture on natural ecosystems contrasts with claims that natural ecosystems are "the most appropriate standard available to sustainable agriculture" (Jackson and Piper 1989, 1592). I agree that, if we completely understood what features or processes make a particular natural ecosystem productive, sustainable, and so on, then it might make sense to copy those features or processes. This understanding-based approach is probably what Mueller et al. (2005) implied by "*possible* application to human agriculture." But if natural ecosystems are "beyond complete human comprehension" (Jackson and Piper 1989, 1591), then we risk copying ecosystem features or processes that undermine rather than support desired outcomes such as productivity and sustainability. Copying without understanding was the basis of South Pacific "cargo cults" and what Richard Feynman called "cargo-cult science" (Feynman 1985, 340), such as emphasizing fancy equipment over disproof of hypotheses. We therefore rejected "mindless mimicry" of natural ecosystems by human agriculture (Denison, Kiers, and West 2003, 146). Instead, we suggested that natural ecosystems could offer both "models to imitate" and "mistakes to avoid" (Denison, Kiers, and West 2003, 161). Is this also true of insect agriculture?

If we can be reasonably confident that something has been consistently improved by natural selection over millions of years, is it a good model for copying by humans, even if without complete understanding? Maybe. Natural selection may at least approach a local optimum, superior to any minor variants. Although there is no guarantee that it will find a global optimum, humans may not be able to do that either. For example, consider current attempts to dramatically improve crop photosynthesis. The C4 photosynthetic pathway has evolved repeatedly (Kellogg 1999), so it is reasonable to assume that it has some advantages over the older C3 pathway. Current attempts to transform C3 rice into a C4 crop may not succeed, but this might be worth trying even if we knew nothing about the mechanism of C4 photosynthesis and its potential benefits. But if the nearest natural ecosystem has three layers of leaves or a 70:30 ratio of grasses to legumes, should human agriculture copy those features, even without a thorough understanding of their consequences? Probably not. Similarly, before we knew about antagonism among fungal cultivars (Poulsen and Boomsma 2005), the success of insects' fungal monocultures over millions of years might have led us to overlook potential benefits of more diverse cropping systems.

Natural Selection Has Not Consistently Improved Ecosystem Organization

Our rejection of mindless mimicry of natural ecosystems was based on two hypotheses. First, natural selection is the only process that consistently improves biological entities

over millennia. To avoid semantic arguments, we can limit this to improvement by criteria relevant to agriculture. Second, natural selection has much less power to improve ecosystems than it does to improve genes and the traits of individuals (Dawkins 1976).

First, consider the relative power of natural selection to improve genes, genomes, individuals, groups, communities, and ecosystems. Some genomes enhance individual fitness (survival and reproduction) more than others. But high-fitness genomes are not inherited intact by offspring, at least in species with sexual recombination. So selection acts on genes, not genomes. Usually, the most successful alleles are those that enhance organismal fitness, but this is not always true. For example, natural selection can favor male-sterility alleles of cytoplasmic genes in plants (Dominguez 1995). This is because eliminating production of pollen, which does not carry cytoplasmic genes, frees resources for seeds, which do carry these genes. Cytoplasmic genes can therefore have a conflict of interest with nuclear genes, which are transmitted in both seeds and pollen. As expected, natural selection favors alleles of nuclear genes that restore male fertility (Dominguez 1995). Similarly, the fungal cultivars of ants are transmitted only by females, so the fungi could benefit from female-biasing the sex ratio of the ants (Mueller 2002).

Bacterial genomes may be passed more or less intact to offspring, albeit with some possibilities for horizontal gene transfer and recombination. But conflicts of interest among bacteria are common. To what extent do these conflicts undermine the potential benefits of symbiotic bacteria to plant hosts, or the potential benefits of bacteria to insects and their fungal cultivars? People may argue about whether a given microbial symbiont is "cheating" its host (Jones et al. 2015; Gano-Cohen et al. 2019), but what would be a "fair" exchange rate of nitrogen or phosphorus for plant carbohydrates? It may be simpler to think of a bacterial strain as a "free-rider" if it invests less than other strains in maintaining the health of a shared host plant or insect colony upon which they all depend (Kiers and Denison 2008).

Mathematical modeling showed that such cheating of fellow symbionts is often favored by natural selection, especially as the number of strains per host increases (West et al. 2002). For a legume-rhizobia symbiosis with a realistic number of rhizobial strains per plant, the model predicted that strains investing nothing in nitrogen fixation would outcompete those that invest anything. This would change, however, if legumes impose "sanctions" that reduce the relative fitness of rhizobia in root nodules that fix less nitrogen. Host-imposed sanctions against less beneficial bacteria were assumed not to "reform" the behavior of cheaters, but only to decrease their reproduction, making them less common in subsequent generations. Sanctions could result from hosts attacking less beneficial rhizobia or simply from allocating more resources to more beneficial root nodules. Sanctions against less beneficial rhizobia were subsequently reported in soybeans, where decreases in nodule oxygen permeability are apparently involved (Kiers et al. 2003), and in several other legume species (Simms et al. 2006; Oono, Anderson, and Denison 2011; Regus et al. 2017). Sanctions by *Medicago truncatula* against less beneficial mycorrhizal fungi have also been reported (Kiers et al. 2011), as have sanctions by figs against less beneficial fig wasps (Jander and Herre 2016). Sanctions complicate any definition of "cheater" based on actual symbiont fitness, because "cheating" (behavior that *would have* increased a symbiont's relative fitness, at the expense of the host, *in the absence of sanctions*) could result in lower *actual* fitness in a host that does impose sanctions.

Throughout the biological world, the evolutionary persistence of cooperation depends on mechanisms that limit the fitness payoff to cheaters. Individuals have evolved mechanisms such as nuclear genes that restore male fertility (Dominguez 1995) to reduce the negative effects of conflicts of interest among genes. Some (most?) species that host symbionts have evolved mechanisms (e.g., sanctions) to reduce the negative effects of conflicts of interest among symbionts (Kiers et al. 2011; Oono, Anderson, and Denison 2011; Jander and Herre 2016). These mechanisms enhance individual host fitness in the species that evolved them. Furthermore, the mechanisms are inherited accurately through DNA.

At the ecosystem level, in contrast, there are no documented mechanisms to limit individual behaviors that undermine ecosystem stability or productivity. In contrast to individuals, ecosystems do not inherit species composition or spatial patterns from other ecosystems with anything like the accuracy of DNA-based inheritance. Furthermore, communities and ecosystems do not compete as unified entities the way individuals do. This is because, unlike genes in individuals, species in ecosystems can disperse independently.

In communities and ecosystems, we find many conflicts of interest, which natural selection among individuals has little or no power to resolve. For example, the wild ancestors of our crops inherited traits that enhanced individual plant fitness in past environments, but many of those traits are counterproductive from a community perspective (Denison 2012). Although a plant community with only short plants would waste fewer resources on stems, leaving more for seeds, natural selection favors taller plants that outcompete shorter neighbors for light. Similarly, solar tracking by upper leaves increases shading of lower leaves enough that it can decrease total photosynthesis (Denison, Fedders, and Harter 2010), but natural selection has kept solar tracking, perhaps because many shadows fall on competing neighbors. Natural selection can lead to wasteful overinvestment in roots that "steal" soil water from neighbors, increasing their own productivity but decreasing that of their neighbors more (Zhang, Sun, and Jiang 1999). Individual Irish elk bulls with larger antlers than their challengers won more mates, even as the large antlers were contributing to species extinction (Moen, Pastor, and Cohen 1999). Because natural selection is driven mainly by competition among individuals, it does not always promote the collective interests of each species, much less those of the entire community.

Quantitative comparisons of natural versus human-managed ecosystems, including wild rice or reindeer managed with minimal external inputs, support the conclusion that humans can sometimes design agricultural ecosystems that outperform natural ones, particularly in their ability to export human-edible food (Denison 2012). For example, some reindeer herders enhance productivity by maintaining a female-biased sex ratio (Muuttoranta and Mäki-Tanila 2012), in contrast to the natural 50:50 ratio. They presumably thought of this independently, rather than copying fungi that manipulate insect sex ratios. Similarly, deploying crop diversity over time, via complex crop rotations, may control pests and pathogens better than mimicking natural ecosystems that have similar mixtures of plants in successive years (Xu 2011).

Has Group Selection or Kin Selection Improved Insect Agriculture?

To what extent do the arguments against mindless mimicry extend from ecosystems to insect farms? In contrast to ecosystems, colonies of ants and termites do compete. Fur-

thermore, the behavioral traits of workers in successful colonies are inherited via the queen's DNA. To what extent have the genetically controlled agricultural practices of fungus-farming insects been optimized by group (or kin) selection, driven by competition among colonies?

Recent modeling (Gardner and Grafen 2009, 666) confirms that "between-group selection can lead to group adaptation, but only . . . where within-group selection can be considered to have negligible impact upon phenotypic evolution." With respect to social insects—the term "eusocial" is now used very differently than when it was coined (Batra 1995)—Gardner and Grafen argue that worker policing of reproduction by other workers may meet this criterion, whereas worker sterility per se is neither necessary nor sufficient. Although within-colony conflict may still occur over issues such as queen formation (Hughes and Boomsma 2008) or the sex ratio of offspring (Mehdiabadi, Reeve, and Mueller 2003), it seems unlikely that within-colony conflicts over agricultural practices would undermine selection among different colonies (competing directly or indirectly for territory or resources) for more effective practices.

But can selection among different colonies also maintain colony-benefiting activities of fungal cultivars and other beneficial microbes, when those activities have a metabolic or other cost to the microbes? That seems much less likely. Even if microbes reproduce clonally, a clone will inevitably include less beneficial mutants. The power of within-group selection to undermine cooperation increases rapidly with group size. Mathematical modeling suggests that group size of less than 25 unrelated individuals is needed for natural selection among groups to maintain within-group cooperation (Levin and Kilmer 1974).

Consider bacteria that make a chemical that kills the weed fungus *Escovopsis* (Currie et al. 1999). Each cell that makes the chemical must pay some metabolic cost not paid by mutant strains that do not make that chemical. Unless bacterial cells whose secretions kill *Escovopsis* somehow enhance their own reproduction, relative to mutants that make fewer or different antifungals, within-colony selection will favor the mutants. Given the very large number of bacterial individuals in a colony and the large number of bacterial generations over the life of a colony, it seems very unlikely that natural selection among different colonies is sufficient to outweigh within-colony selection favoring cheating bacteria.

Consistent with this hypothesis, *Pseudonocardia*, which lives on ants and can suppress *Escovopsis* (Currie et al. 1999), can also "kill or strongly suppress ant-cultivated fungi" (Sen et al. 2009, 17807). Suggested alternative roles for these microbes could include "protection of ants or sanitation of the nest" (Sen et al. 2009, 17809). However, free-rider mutants that fail to provide these functions would still have a reproductive advantage, if selection occurs only at the level of the nest. Similarly, within-ant selection for free-riders could override among-ant selection for bacteria whose secretions protect ants from pathogens. An alternative, individual-based hypothesis is that production of antifungal compounds confers a fitness benefit to bacteria (an individual cell or a cluster of clonemates) that outweighs its metabolic cost. A plausible individual-cell benefit to *Pseudonocardia* from producing antifungal compounds involves interactions with (competition with or predation on) black yeasts with which they share the bodies of fungus-growing ants. These yeasts compete with and suppress the growth of *Pseudonocardia* (Little and Currie 2008), so there could be an individual benefit to the bacteria from making antifungals that suppress nearby yeast cells. Suppression of *Escovopsis* by the same antifungals would then

be a beneficial side effect that the ants could exploit, albeit with some possible risk to their fungal cultivar.

Based on the above, it seems unlikely that selection among colonies can override within-colony selection for bacterial free-riders that invest less in suppressing pest fungi. Given reasonable mutation rates and short bacterial generation times, bottlenecks during colony formation would provide only short-term relief. Similar arguments could apply to the fungal cultivars: although among-colony selection would favor more beneficial fungal genotypes, within-colony selection might favor fungal traits that enhance fungal fitness at the expense of the insects. Two examples of possible fungal "cheating" traits are (1) manipulation of insect sex ratio, mentioned as a hypothetical possibility above, and (2) sexual reproduction and dispersal of fungi from the colony (Mueller 2002).

If the fungi produced hormones that increased the frequency of female insects, that could reduce fitness of the insects, but it would benefit the fungi. This is because only females transmit fungi to new colonies (Mueller 2002). However, it is not clear that fungal "individuals"—a complex concept in fungi, not explored here—would benefit, relative to fungal free-riders that skip the metabolic cost of making the hormone. Human pathogens offer an analogous case, where the progress of infection depends on the production of metabolically expensive molecules by the pathogen. In such cases, virulent populations can be invaded by less virulent free-riders (Köhler, Buckling, and van Delden 2009). Similarly, individual-versus-community conflicts among fungi provide an alternative explanation for their apparent failure actually to manipulate insect sex ratio (Mueller, 2002). Sexual reproduction by fungi, in contrast, might offer an individual benefit. It is therefore not surprising that there are numerous reports of fungal fruiting structures that "are actively destroyed by ants" (Mueller 2002, S90) although there may be cases in which sexual reproduction by the fungi benefits ants. Self-dispersal could also offer individual fitness benefits to fungi, but it seems to be rare (Mueller 2002).

How Effective Is Selection among Microbes Imposed by Fungus-Growing Insects?

I have argued above that among-colony selection is too weak to prevent the evolution of harmful free-riding in the fungal cultivars of insects and the bacteria that potentially protect those cultivars. But among-colony selection may be fairly effective in favoring the evolution of insect behaviors that benefit the whole colony. High within-colony relatedness, especially ancestrally (Boomsma et al. 2011), and limited reproductive opportunities for workers should minimize, although not eliminate (Mehdiabadi, Reeve, and Mueller 2003; Hughes and Boomsma 2008), conflicts of interest that might undermine efficient agricultural practices. One such practice could be for insects to impose selection on their fungal crops, on bacteria that kill *Escovopsis*, or perhaps even on "integrated crop-microbe consortia" (Mueller et al. 2005, 563). Where among-colony selection fails, with respect to beneficial microbes, can insect-imposed selection fill the gap?

An insect can presumably select some volume of material—a "patch" of fungal garden—to be transplanted, discarded, or perhaps treated with antifungal secretions (Fernández-Marín et al. 2006, 2009). But any evolutionary improvement in crop fungi or beneficial bacteria

by such processes depends on (1) the ability of insects to identify "good" and "bad" patches and (2) within-patch genetic diversity being low relative to diversity among different patches. These two requirements will be discussed in order.

Insects imposing selection on fungal cultivars seems roughly analogous to what human plant breeders do, but the vigor of individual plants may influence some plant breeders more than it should. Insects may be less likely to make this mistake, since individual bacterial cells are so small. True, some of the target traits for which plant breeders select can be evaluated easily in individual plants. Disease resistance and flavor are two examples. But I have argued that most increases in yield potential—the yield of groups of plants, given good control of pests and disease—have required accepting tradeoffs between individual plant fitness and whole-crop yield (Denison 2015). In a historical example, Peter Jennings (1964) targeted shorter stature and more erect leaves in designing the first Green Revolution rice (figure 3.1), reversing some effects of past natural selection and sacrificing competitiveness (Jennings and de Jesus 1968). Both traits were among those proposed by Colin Donald for a more cooperative "ideotype" of wheat (Donald 1968). In practice, selection for cooperative traits has often come from selecting among plots containing many plants of a single genotype, without much consideration of tradeoffs. By selecting among field plots for yield, plant breeders increased leaf angle and reduced the excessive size of tassels (the male flowers of maize) without having either as a specific objective (Duvick and Cassman 1999), although this took 60 years. Further exploitation

Figure 3.1
Traits that enhance individual fitness in mixtures, such as greater height in plants or decreased investment in "public goods" by beneficial microbes, tend to undermine community productivity. For example, IR8 rice yielded more grain than older varieties because it invested less in trying to grow above its neighbors. Photo by R. Ford Denison.

of tradeoffs between individual competitiveness and yield remains a promising route for genetic improvement of crop plants (Denison 2015; Anten and Vermeulen 2016; Weiner 2019). It is unclear whether tradeoff-blind selection among plots of genetically uniform plants (current practice in late stages of crop improvement) or a tradeoff-based approach (like that of Jennings or Donald) will work best. In rice, Yuan et al. (2011, 168) found that selection based on yield increased yield more than "trait-based selection," but their unexplained target traits were inconsistent with a tradeoff-based approach. In particular, their target height for "trait-based" breeding was greater than a tradeoff-based approach would suggest (Donald 1968; Denison 2012).

Returning to insects, they might be good at identifying which patches produce the most edible fungi. As for bacteria, even if they could identify patches with bigger individual bacterial cells, it seems unlikely that they would favor those patches under the faulty assumption that a community of such cells will control *Escovopsis* better.

So we turn to the second criterion: low within-patch diversity. This requirement might be met for crop fungi. However, bacterial diversity is probably much greater, due to population size, even if we consider only a single strain and its mutants. Therefore, the ability of insects to improve "microbial consortia" by selecting among garden patches would seem to be severely constrained by the "effective deme sizes of less than 25 and usually closer to 10" criterion of Levin and Kilmer (1974, 544).

Despite this theory, some published experimental results have appeared to show beneficial microbial consortia evolving under human-imposed selection (Swenson, Wilson, and Elias 2000; Panke-Buisse et al. 2014). If these results are valid, or if we obtain clear evidence for beneficial microbial consortia from insect-imposed group selection, evolutionary theory might need to be revised. Swenson, Wilson, and Elias (2000, 9112) noted that, under current theory, their "artificial ecosystem selection" experiments (selecting soils for better or worse plant growth) "should not have worked." Unfortunately, their experiment did not really show whether their version of group selection actually worked. The main problem was pseudo-replication. In each generation, a single good- or poor-growth composite soil sample (pooled from several plants each with good or poor growth) was used to inoculate replicate test plants. Thus, there was replication to show whether the two soil inocula had consistent effects on plant growth, but no replication of selection regime. Even ignoring this problem, their results cast doubt on a consistent effect of selection. Both selection regimes showed seemingly random but parallel changes in plant growth—changing growing conditions?—for ten generations. In generation 10, plants from both selection regimes had much less growth than in any previous generation. Then growth improved in both, but more so in the plants inoculated with soil from good-growth plants. Given divergence, from whatever cause, there is a 50% probability that the good-growth treatment would be superior, by chance.

A similar experiment, selecting for soil-microbe effects on flowering date in *Arabidopsis* (Panke-Buisse et al., 2014), had the same pseudo-replication problem. If we treat each of these publications as a replicate supporting the same general conclusion, ignoring the risk of publication bias, we still have only N=2. So, someone needs to repeat these soil experiments with true replication. Standard practice in experimental-evolution experiments is to maintain multiple independent lineages for each selection regime (Garland and Rose 2009), as we recently did in selecting for multicellularity (Ratcliff et al. 2012). For selec-

tion among microbiomes, Mueller and Sachs (2015) recommend a minimum of six independent lines for each selection regime, noting that all six would have to show the same directional response for statistical significance in a sign test.

Like the soil-selection experiments, the convergent evolution of similar agricultural practices in ants and termites has a sample size of only two. The multiple evolutionary origins of agriculture in ambrosia beetles offer more statistical power, but perhaps less convergence (chapter 7, this volume).

In summary, the hypothesis that insect-imposed selection among garden patches can effectively favor more beneficial strains seems somewhat plausible for fungal cultivars, assuming low within-patch diversity, but not for beneficial bacteria. For example, I would expect bacteria to evolve to make whatever antifungal compounds maximize their own ratio of benefits to costs (including inclusive-fitness effects on nearby clonemates), whatever the effect on *Escovopsis* and the fungal cultivar. However, if someone shows that insects really are imposing effective selection for microbial consortia that benefit the whole colony, beyond what can be explained by microbial inclusive fitness, that would be an exciting result, requiring changes to our current understanding of natural selection. This result would also suggest that it might be possible for our crops to impose beneficial selection on entire microbial communities around their roots, rather than only on the intimate partners (rhizobia and mycorrhizal fungi) that are subject to host sanctions (Kiers and Denison 2008). The main point of this chapter is that I do not expect this to happen.

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