Fijian farming ants resolve the guns-or-butter dilemma for their crop plants

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Abilities to cultivate or manage members of other species evolved repeatedly, and in a few taxa the managed symbionts were domesticated, representing one of the great innovations in evolution (1, 2), one which transformed human history (3, 4). For early farmers, to what extent were agricultural practices tailored to local environmental conditions, and how were conflicts of interest resolved to maximize crop yield? Early stages of plant cultivation likely occurred in home gardens, when sedentary people manipulated wild plants under nearly natural conditions, by selectively growing, defending, and fertilizing favored ones (3, 4). Home gardens promote agrobiodiversity (5) and likely were crucibles of domestication, as people exerted control over food production (3, 4). In so doing, they selected for advantageous traits, and through a process that Darwin (6) termed artificial selection, their plants phenotypically and genomically diverged from ancestral forms (7), concomitant with decreasing gene flow between them and wild relatives (8). Some cultigens became increasingly dependent on farmers for propagation, and humans increasingly depended on them to sustain their diets (3, 4). The stunning success of agriculture has left contemporary societies reliant on large-scale farms that utilize sophisticated technology and complex mathematical models to enable farmers to provide optimal conditions for the diverse, sometimes conflicting, factors that influence crop yield (9). But diverse taxa already confronted this challenge, since agriculture evolved repeatedly (2, 10–12). A recent study of farming-ant behavior (13) reveals a Darwinian solution to the problem of managing the conflicting demands of crop plants for light, nutrients, and protection.

On the Road to Domestication

The management of undomesticated heterospecifics occurs in diverse species, including stingless bees (10), social amoebae (11), and deep-sea yeti crabs (12). Cultivation led to domestication in far fewer nonhuman taxa, restricted to termites (14), ants (2, 13, 15), and beetles (16). Domestication hinges on crop improvements, including managing conflicts of interest (17), refining agricultural practices (2, 4), and genomic changes in the partners (7, 18). For farmers it requires balancing needs for specific light levels and resolving the guns-or-butter question for their crops (9, 17).

In the Fiji archipelago, an endemic ant, *Philidris nagasau*, obligately farms six epiphytic plants (*Squamellaria*) that are also obligate symbionts (13, 19). This mutualism is nearly 2 million y old and affords a remarkable opportunity to study the evolution of domestication, including novel behavioral farming practices and crop modifications. Some *Squamellaria* are dispersed by birds and occur throughout the archipelago. Those that are obligately ant farmed, however, have extremely small ranges, being restricted to two nearby islands (19). *Philidris* ants selectively collect seeds, plant them on host trees, defend seedlings and adults from herbivores, and manure them with nitrogenous wastes. In exchange, plants house ants within a network of highly modified hypocotyl-derived tubers that form domatia. Plants also provide sugars and amino acids from floral nectaries, in quantities to sustain societies of up to 250,000 workers (13, 19). Finally, plants provide a sustainable solution to the universal social problem of waste management by developing highly modified internal wall structures that function as latrines to efficiently capture and recycle nutrients and water from ant fecal matter (19).

Epiphytic plants that drape the large branches and trunks of canopy trees compete for light and face extra challenges in obtaining water and essential nutrients because they are not rooted in soil. Chomicki et al. (13) documented gradients in their light environments and discovered a wonderful natural experiment with which to explore critical questions for the evolution of agriculture. Plants grown in full sun offered 7.5 times more floral resources than those in full shade, demonstrating crop yield is maximized when ants plant seeds to maximize sun exposure. In the canopy, usually herbivory is higher on sun leaves versus shade leaves (20), so larger sun plants should be more frequently eaten by insect herbivores. But this is not the case for

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Squamellaria, nor do the plants rely on physical or chemical defenses. Rather, quantitative behavioral observations and field experiments indicate ants increase their patrolling behavior near sun plants versus shade plants, so relaxed vigilance probably accounts for higher levels of herbivory in the shade, rather than unusual patterns of herbivore abundance. Just as more valuable cash crops justify increased expenditures on defense relative to low-value crops, so too ants invest more in defending valuable sun plants and slack off on lower-value shade plants.

Trouble Down on the Farm

When seeds are planted in full sun, they grow larger and produce more ant food; this win-win situation obviates the guns-or-butter question. For other traits, or for other bio-agricultural systems, self-interests of partners may not be congruent, because effective management may divert crop somatic or reproductive efforts from their optima to meet the needs of the farmers, depending on which parts are consumed and means of propagation. Fungus-farming ants show how such nutritional conflicts may have societal consequences. A basal ant, for example, provides its undomesticated cultivar with a carbohydrate-rich, protein-poor, diet that maximizes growth rates of edible hyphae (17), but at higher intake rates of organic matter, the additional protein results in the production of inedible mushrooms. As the more powerful partner (2), ants manage but do not fully control the conflict since the fungus is not domesticated and they cannot prevent investment in reproductive tissues; an inability to fully resolve the conflict may have impeded the evolution of large-scale societies (17).

A nutritional conflict also characterizes *Philidris* farming, yet mature colonies are large (13), hinting at a resolution. Sun plants have more ants and receive more ant manure, so Chomicki et al. (13) measured this nutritional benefit by quantifying nitrogen content for an array of tissues. Contrary to expectations, sun leaves had the lowest nitrogen content per unit mass of all tissues, and the sun–shade difference was greatest for the specialized latrine tissue. Plant growth rate, colony size, and nitrogen inputs are correlated across light levels, so differences in nitrogen content do not arise from a simple dilution effect (13). Isotopic analyses show that nitrogen inputs depend on the ants' diet, which differs according to light environment. Shade plants seem unable to produce sufficient food for their ants, forcing the farmers to hunt more often to supplement their diet with arthropod prey or nectar from other sources (13). These alternatives increase relative inputs of exogenous nitrogen to shade plants (19).

Darwinian Solutions to Age-Old Problems

The ants confront a light-mediated trade-off in the quality of the agricultural services they provide, as defense is highest for sun plants, and nutritional services are highest for shade ones. This guns-or-butter trade-off raises the question of whether ants manage exposure to light environments over time and larger spatial scales. Light matters. Farmed plants were located significantly higher in the canopy and more exposed than those dispersed by birds. Among farmed species, seedlings occurred more frequently on trunks that received direct sunlight than on those that did not, suggesting that ants evaluate light environments when making behavioral decisions on planting; the cognitive processes underlying their evaluations remain to be explored. Farmed plants of a given colony generally live within a single light exposure, preferably full sun, as colonies in shade were smaller. It is unknown whether shade plants provide other benefits to the ants, such as ameliorating the thermal challenges of canopy life (21).

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Another long-standing problem faced by farmers around the world is water conservation. Further study may reveal additional subtleties related to water management, because the epiphyte environment is hot and dry. One adaptation to these conditions is Crassulacean acid metabolism (CAM) photosynthesis, which saves significant amounts of water; its evolution is correlated with other water-saving traits (22) and evolved in three of six farmed *Squamellaria* species (19). Curiously, even though a favored species, *Squamellaria wilsonii*, grows best when planted in full sun, it has thin leaves and is not a CAM plant. It is unknown whether ants assist plants with water management, but a diet that is largely derived from plant secretions will generate fecal material that is largely water. Is this a service to manage water scarcity, an agricultural alternative to CAM?

To ascertain how ant behavioral practices shaped evolutionary change in crop traits, Chomicki et al. (13) scored hydnophytine plant species for traits related to the production of food rewards, structural modifications to house ants and recycle their wastes, and tolerance of high-light environments. Mapping these traits on the plant phylogeny shows that farming behavior significantly shaped physiological tolerance for high-light environments, which evolved independently four times, coincident with the rapid evolution of traits for producing food rewards, developing domatia, and absorbing and processing fecal matter.

Fijian ants resolved the problem of trying to balance crop nutrition, defense, and growth conditions to maximize yield. Like human farmers, they confront fundamental trade-offs in the quality of proffered agricultural services, and like us, they aim to maximize short-term payouts by selecting high-light environments that are optimal for plant growth and yield, no matter the cost to the plants with lower payment for services in providing fertilizer. Under the intense tropical sun, increased plant size increases production of ant food, supporting larger numbers of worker ants. Colony size is correlated with amount of fecal nitrogenous inputs going back to meet plant nutritional needs. These feedback loops underlie the sustainability of the Fijian ant agricultural society, highlighting the linkage between food production and population regulation, which is a solution to another common agricultural problem, which human society also confronts.

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