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THE CULTIVAR SPECIALIZATION IN INSECTS AGRICULTURE

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ABSTRACT

In three insect orders, agriculture has developed independently: once in ants, once in termites, and seven times in ambrosia beetles. Despite the fact that these insect farmers are very distinct in some respects, they are strikingly similar in others, implying convergent evolution. Within their nests, all reproduce their cultivars as clonal monocultures, and in most instances, clonally over many farmer generations. Long-term clonal monoculture poses unique disease management challenges, but insect farmers have developed a variety of methods to combat crop diseases: They isolate their gardens from the rest of the world; they keep a close eye on them, controlling pathogens early in disease outbreaks; they occasionally access population-level storage tanks of genetically variable cultivars, while still propagating clonal monocultures across generations of farmers; and they manage, in addition to the primary cultivars, a variety of auxiliary microbes that provide disease suppression. Insect farmers seem to cultivate, and potentially “artificially select” for, integrated crop-microbe consortia rather than cultivating a single cultivar purely for nutrition. Crop domestication in the context of coevolving microbial consortia may, in fact, explain insect farmers' agricultural success.

KEYWORDS: Agriculture, Beetles, Cultivars, Escovopsis, Macrotermitine.

1. INTRODUCTION

Crop cultivation for nutrition has only developed a few times in the animal world. Fungus-eating ants, fungus-eating termites, ambrosia beetles, and, of course, humans are the most well-known and clear examples. Sustainable, high-yield agriculture is becoming critical for survival in a global economy with projected food shortages for humans, who began the transition from an ancestral hunter-gatherer existence to farming only about 10,000 years ago. Various research programmes are currently devoted to the optimization of agricultural productivity in the era of

increasingly environmental challenges. Humans have progressed in agriculture via a mix of intelligence, innovative planning, and a fair amount of chance and luck. Humans, on the other hand, have not yet looked at nonhuman agricultural systems, such as fungus-growing insects, for potential ideas for bettering agricultural methods[1].

This dearth of applied interest in insect agriculture is most likely due to a widespread belief that human agricultural systems are fundamentally different from insect systems. Humans, on the other hand, have learnt a great deal by studying the adaptive characteristics of other species, and similar issues like crop diseases afflict all farmers, independent of their phylogenetic locations or the phylogenetic positions of their crops (plant, fungus, or otherwise). Because crop diseases affect both human and insect agriculture, it may be worthwhile to look at the short- and long-term remedies that have converged in insect agriculture for potential application in human agriculture. This review's aim is to create such a synthesis[2].

1.1 Agricultural Evolution:

A comparison of ant, termite, and beetle fungi-culture reveals a number of convergent and divergent aspects of agricultural development.

1.1.1 Cultivar Transmission:

Fungal cultivars are transferred vertically by trophophoresy from parent to child generations in attine ant and xyleborine beetle agriculture. Female reproductive ants and beetles obtain inocula from their natal gardens, transport it in specialized pockets during early life dispersion flights, and utilize it as a starting culture for their new gardens. Trophophoretic vertical transmission also occurs in two macrotermite groups, with the exception that one of these two groups (the sole species *Macrotermes bellicosus*) transmits the fungus through the king, while the other group (the genus *Microtermes*) transmits the fungus by the queen. The remaining macrotermitines, in the rare instances where fungal transmission has been investigated, depend on horizontal absorption of fungal crops from the environment in each generation[3].

1.1.2 Crops Specialize:

The assumption of clade-clade communiques and topological congruence here between phylogenies of insect farmers as well as those of their cultivars is based on vertical transmission of cultivars. Indeed, significant groups of farmers (huge clades or paraphyletic classes, for example, the lower attine ants) rigidly specialize on major groupings of matching fungal cultivars in all insect farming systems. Higher (i.e., wide) phylogenetic levels show the anticipated farmer-cultivar congruence, perhaps due to ancient evolutionary codependencies that prevent farmers from switching to cultivars outside of their specialized main cultivar groupings.

However, phylogenetic patterns show that insect-farmer species sometimes move between fungal species or strains within these tightly restricted main cultivar groupings. This combination of lower-level, within-group switching and higher-level major-group specialization in insect farmers would be analogous to defined clades of specialized wheat-farmers, rice-farmers, potato-farmers, bean-farmers, etc. in humans, each of which is able to switch between varieties within their area of specialization (e.g., between wheat varieties and closely related species *suidae*). Switches to new main cultivar groupings among insect farmers have been very uncommon evolutionary occurrences[4].

1.1.3 *Cultivar Specialization:*

Though low-level switching between cultivar species and strains within major cultivar groups happens on occasion throughout evolutionary time, most insect farmer species interact with just a small subgroup of cultivars for long ecological periods (species or strains). For example, every attine ant species studied so far cultivates just a single phylogenetically restricted set of cultivars (e.g. a single fungus species), implying species specificity between ants and cultivars at relatively early stages of evolutionary diversification. Only one main cultivar of ambrosia beetles is linked with a certain beetle species within a geographic area, similar to ants.

Despite the fact that most beetles are linked with a species-specific main fungus across their entire geographic ranges, certain beetle species are associated with various primary cultivars in different geographic areas. There is a lot of diversity in cultivar specialization among macrotermitine species: Some macrotermitine species are restricted to a single, unique cultivar, while others grow a wide range of fungal cultivars, which they sometimes share with other macrotermitine species. Distinct cultivars may serve different main roles, supplying specialized, termite-adapted enzymes in some instances, while providing generalist food in other circumstances[5].

1.1.4 *Cultivar Sharing and Exchange:*

Even while each attine ant species specializes in a particular cultivar species, a given cultivar species may be cultivated by multiple sympatric ant species, and these sympatric ant species are not always closely related (e.g., they may represent different ant genera). Cultivar transfer between ant species may take place in a number of ways, both direct and indirect. Raids on adjacent colonies or, in polygynous organisms, cofounding of colonies by multiple queens who swap cultivars or recombine them in the cofounded garden are examples of direct routes. Cultivar breakouts from gardens, followed by a free-living (feral) life, and then reincorporation into a symbiosis when a separate attine colony imports the free-living strain into its nest, are examples of indirect routes.

The existing phylogenetic data for ambrosia beetles indicates to cultivar sharing across sympatric beetle species, although few studies have looked into this. As with the ants, distantly related ambrosia beetle species are occasionally linked with the same cultivar, implying fungal exchange, either direct or indirect. When various female beetles inhabit the same tree and the fungal companions cross-contaminate neighboring galleries, cultivar exchange across and among beetle species may occur. Most macrotermitine species acquire their fungus horizontally each generation, unlike attine ants and ambrosia beetles, which all transfer their cultivars vertically between generations. This means that novel termite-cultivar combinations emerge every generation, making cultivar interchange across species and lineages of the same species easier. Cultivar studies of sympatric macrotermitine communities show that cultivars are often exchanged across lineages via interspecific cultivar exchanges. In macrotermitines, intra-specific cultivar exchanges have not been studied yet[6].

1.1.5 *Sexual vs. Asexual Cultivar Propagation:*

All vertically transmitted insect cultivars, including attine ants, ambrosia beetles, and termites in the genus *Microtermes*, as well as the species *Macrotermes bellicosus*, seem to be reproduced asexually by their insect farmers over many farmer generations. Horizontally transmitted termite

cultivars, on the other hand (propagated by all other macrotermite genera), go through normal meiosis and sexual recombination.

DNA fingerprinting studies in attine ants show that all gardens of a single leafcutter colony contain a single cultivar clone (monoculture); that identical cultivar clones occur in different colonies of the same geographically widespread attine ant species; and that different sympatric ant species share genetically identical culti on occasion. Attine cultivar clones, in contrast to popular belief, are not old. Although attine crops are clonally propagated over many ant generations, recombination events involving either sexual (meiosis, mating) or parasexual (e.g., mitotic recombination, exchange of haploid nuclei) activities occur on a regular basis. The following are examples of evidence supporting recombination on a rare basis:

- I. Fruiting structures (mushrooms), which are found in almost all species of attine ants, defying the assumption that fruiting capacity would be lost over millions of years of strict clonality;
- II. Allele sequence divergence rates in attine cultivars that are comparable to those seen in closely related, sexually reproducing fungus; and
- III. Lower attine ant cultivars with tight genetic ties to free-living fungal populations, implying that these fungi are capable of migrating in and out of the symbiosis, that cultivar and wild lineages may frequently interbreed, or both. The genetic and natural-history data combined indicate mostly asexual cultivar propagation inside ant nests and over several generations, with occasional genetic recombination events.

A single cultivar monoculture is cultivated in a single termite colony, similar to attine ants. The *Termitomyces* cultivar is reproduced asexually inside termite nests by inoculating new garden substrate with asexual spores and, most likely, by transferring mycelium from older to younger gardens. Although there are no known free-living populations of *Termitomyces* species that are completely independent of termite farmers, they have retained the ancestral (presymbiotic) condition of regular sexual reproduction, and most *Termitomyces* cultivars are spread horizontally via sexual spores produced by fruiting bodies (mushrooms) growing on the external surface. The termite *Macrotermes natalensis*, for example, exhibits an outcrossing mating system in its *Termitomyces* cultivar. Only termite species with vertical uniparental propagation have asexual cultivar propagation lasting many generations. Phylogenetic patterns suggest that horizontal cultivar exchange occurs across nests of the same and different termite species on occasion, but it's unclear if this horizontal exchange is linked to cultivar sexual reproduction[7].

The main fungus in xyleborine beetles are strictly asexual, while the less specialized, auxiliary fungi are often sexual. The main fungi of all other non-xyleborine ambrosia beetles show a predominance of asexual reproduction in fungal cultivars, while the more incidental fungi are frequently sexual, indicating that this may have been the original state at the beginning of the xyleborine beetle-fungus symbiosis.

1.2 Co-evolutionary Modifications:

Farmer-cultivar specialization increases the possibility for coadaptation, in which one partner's evolutionary alteration induces the other partner's reciprocal co-evolutionary modification. It is relatively easy to identify evolutionary modifications in farmer species, such as specialized

morphological structures for trophophoretic transport of cultivars by females during dispersal flight (e.g., mycangia in beetles, infrabuccal pocket in ants), modifications of mandibles and guts of beetle and ant larvae for fungus-feeding, or the suite of behavioral, glandular, and olfactory adaptations. However, since cultivated fungi are intrinsically more difficult to examine, examples of evolutionary changes in cultivars have been more difficult to find.

The hyphal-tip swellings (gongylidia) generated by higher attine cultivars and the similar nodules produced by macrotermite cultivars are the finest instances of cultivar changes. Both gongylidia and nodules are nutrient-rich structures that farmers may easily harvest, consume, and feed to larvae or nymphs. Although the ambrosia shape of the beetle cultivars indicates evolutionary adaptation intended especially for efficient intake and digestion by the beetle larvae, nutrient-rich structures are not known for beetle gardens. Ambrosial growth is made up of densely packed conidiophores with a large number of spores that can only be produced in the presence of beetles.

Nonsymbiotic fungal species have not been found to produce ambrosia. *Ambrosiella* and *Raffaelea*, two of the most important fungus associated with ambrosia beetles, are both polyphyletic, and numerous lineages within each genus have converged on the same ambrosial form, implying evolutionary convergence owing to selection. Other possible co-evolutionary modifications that have yet to be investigated include insect cultivars' ability to reproduce predominantly asexually while under cultivation, as well as the cultivars' ability to survive storage in the dispersal pockets of beetles and ants, or passage through the alimentary canal of termites[8].

1.3 Cultivar Symbiont Selection:

Insect agriculture, from an evolutionary standpoint, is an example of cooperative interaction between farmer and cultivar lineages, with one utilizing the other for its own reproductive goals. When mutant over-exploiters (so-called cheater cultivars) enter a mutualism, such cooperative relationships are often fragile and may degrade over evolutionary time. Additional farmer-cultivar conflicts are expected, which may destabilize the mutualism, but at least two evolutionary processes protect the farmer-cultivar association's cooperative nature: Inherent in vertical cultivar transmission, partner feedback is an automatic feedback mechanism in which an uncooperative partner reduces the other partner's fitness to the extent that it reduces its own fitness; and, second, partner (symbiont) choice, in which farmers prefer associations with fruitful cultivars and discriminate against inadequate cultivars in specific situations. Partner choice is a particularly essential process when the evolutionary rates of two collaborating partners vary. The slower-evolving partner (e.g., the insect farmer) is expected to have a say in which variants of the faster-evolving partner (e.g., the fungal cultivar) are used, and thus the slower-evolving farmer imposes selection favoring beneficial symbiont variants and prevents the spread of non-beneficial cultivar mutants. Termite and beetle farmers have yet to investigate symbiont choice, but ant farmers can distinguish surprisingly fine genotypic differences between cultivars, suggesting that cultivar diversity in ant gardens may evolve through an analogue of "artificial selection," such as through mutation in the garden or the import of novel strains[9].

1.4 Disease's Impact on Insect Agriculture:

Ant, termite, and beetle gardens are often invaded by “weedy” fungus, which may cohabit with the crop at low or controllable levels. The garden is rapidly overtaken by these weeds if the gardening insects are removed or if their nests are abandoned. Wood-degrading fungi of the endophytic genus *Xylaria*, for example, are present in most fungus-growing ant and termite gardens, most likely because it is introduced with garden substrate. Though weeds such as *Xylaria* do not harm the cultivar directly, they compete for nutrients and therefore reduce crop production. *Escovopsis* species, ascomycete fungi found in fungus-growing ant colonies, are specialized para-sites that eat the cultivars directly and limit the nutrients available to the ants. In termite and beetle agriculture, weed fungi and bacteria are also recognized, although they have yet to be well investigated.

Garden output is reduced by *Escovopsis* infections, which lowers ant colony development and colony survival. *Escovopsis* is a taxonomic and geographically varied species. The parasite has been isolated from colonies of every attine species throughout their geographic ranges, and some *Escovopsis* lineages have evolved to parasitize certain cultivar lines. This high degree of host specificity suggests that *Escovopsis* has had a long history of host-parasite coevolution, in which cultivars, ants, and their mutualistic bacteria have likely co-adapted to defend against *Escovopsis* attack, and each *Escovopsis* species has become narrowly specialized to overcome the defenses of some hosts but not others[10].

2. DISCUSSION

Despite the fact that attine ants clonally reproduce their cultivars through generations over short evolutionary time periods, no ancient clone has been discovered. Instead, data suggests that lower attines acquire new cultivars from wild (sexually reproducing) fungal populations on sometimes, and that both lower and higher attines acquire new cultivars from other attines' nests on occasion. Higher attines cultivars that aren't known to have free-living populations nevertheless have the capacity to fruit and show patterns of DNA-sequence variation that indicate occasional genetic recombination via self-mating or genuine intercrossing across cultivar strains. While each attine ant colony's crop is a clonally propagated monoculture at any one moment, the fungal population outside the nest has the genetic diversity and resilience required for long-term disease control. As previously stated, sexual reproduction is the norm in termite cultivars that reacquire their cultivars horizontally each generation, and sexual reproduction may also occur in termite fungus that transfer their cultivars vertically between generations. It's unclear if the ambrosia beetles' principal cultivars can reproduce sexually on occasion. Access to a population-level pool of cultivar genetic diversity is a constant characteristic of insect agriculture that may offer alternate crops for coping with illness, at least for termites and ants, and probably for beetles as well.

All insect agriculturists check their gardens on a regular basis, and no area of the garden is left unattended for long enough to enable illnesses and fungivores to develop and proliferate. Because their societies include a non-reproducing worker caste, a significant percentage of which is devoted to garden maintenance, insect agriculturists, especially ants and termites, are able to engage in such extensive surveillance. The tiny size of the garden allows or intense surveillance by a single female or a small family of females in the case of beetles. Diseases are identified and eliminated in the early stages of infection, before they may spread and cause

substantial crop loss, thanks to intensive surveillance. Early identification is an efficient protection against new disease mutations that may develop higher virulence if left untreated, since these strains may be more easily managed with conventional therapies in the early stages of infection.

Garden treatment in attine ants involves the use of secretions from their meta-pleural and mandibular glands to clean substrate when it is carried into the nest, likely eliminating some or all weeds and pathogens from the surface before it is put to the fungal garden. Although antibiotic-producing glands in fungus-growing termites have not been investigated, certain nonfungus-growing termite secretions contain antibiotic characteristics. Antimicrobial glands in ambrosia beetles have yet to be discovered and investigated. Attine ants have additional antimicrobial defense in addition to glandular secretions. Actinomycete bacteria have colonized some or all of their integuments. These bacteria are known to hinder *Escovopsis* growth, and reducing actinomycetes in colonies has been shown to enhance *Escovopsis* infection in experiments. Antibiotics are produced by garden bacteria in the genus *Burkholderia*, which defend against the garden parasite *Escovopsis* as well as entomopathogenic illnesses of ants. Actinomycetes and other bacteria are found in termite gardens, and beetle gardens have a wide variety of bacterial secondary symbionts; nevertheless, the precise functions of these bacterial companions are unclear.

3. CONCLUSION

In contrast to insect farmers, secondary mutualistic microorganisms have the ability to develop at the same pace as coevolving garden pests, allowing mutualistic insect-microbe systems to react quickly to the introduction of new disease genotypes. Although the benefits of such fast microbial antibiotic resistance are apparent, their evolutionary maintenance is unknown. One option is that each farming civilization has access to a wide variety of microorganisms from which to choose specific, desirable kinds as required. This scenario begs the issue of how the insect farmers managed to keep such a varied variety of bacteria in their colonies in the face of both microbe competition and the frequent bottlenecks of the whole microbial "library" that probably happens at the start of every new insect colony.

Alternatively, the secondary bacteria may be naturally fast-mutating, allowing for the quick emergence of new beneficial genotypes to mount an adequate defensive response. This situation begs the issue of how insect farmers identify the most advantageous genotypes and select them for selective "amplification" against certain diseases. The lack of clear developmental processes for maintaining functional affiliations with coevolving, mutualistic microbes is not trivial, and future research should assess not only the diversity of microbial genotypes within individual farmer colonies, but also the mechanisms involved adaptive symbiont-choice selection of beneficial, novel microbial genotypes. Future study should look at whether the coevolution of many mutualistic-ally aligned partners, each mustering their own defense, results in a much more evolutionarily stable disease-management approach than if the insect farmers work alone in a co-evolutionary arms race against specific diseases.

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