38th ALTENBERG WORKSHOP IN THEORETICAL BIOLOGY

The Convergent Evolution of Agriculture in Humans and Insects

Extended Abstracts

Did insects invent agriculture?

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<u>Overview</u>

Agriculture has been defined as "The science or practice of farming, including cultivation of the soil for the growing of crops and the rearing of animals to provide food, wool, and other products" (1). Is agriculture only practiced by humans, or can agriculture be more than that? A case for similarities between agriculture in ants and humans has been made (2), and here we further expand on the concept of agriculture in humans and agriculture as practiced by insects.

Insects originated ca. 479 million years ago (3) and fungi are more than one billion years old (4). The earliest record for a possible insect-fungal association is ca. 400 million years old (5). This ancient association stands in stark contrast to the appearance of *Homo sapiens,* ca. 200,000 years ago. The long co-evolution between insects and fungi has resulted in mutualisms evolving in 14 insect families in six orders, and 16 fungal orders (6). The main roles for these mutualisms are nutrition, protection (i.e., defense), and dispersal. We submit that in order to survive, *Homo sapiens* had to "invent" agriculture, but in reality, insects had already invented agriculture.

<u>Approach</u>

We recently finished the first comprehensive literature review on the ecology and evolution of insect-fungal associations (6). This data will be used here to define levels of agriculture in insects and their evolutionary ecology in comparison to farming of plants, animals, and mushrooms by humans. Moreover, if we focus on the definition for agriculture that states "and other products" (see above) we can consider that the production of essential medications by humans, such as antibiotics, is a modern form of fungal or bacterial farming for defensive purposes, at which insects are old players. Finally, humans are, like all animals, associated with symbionts, which also includes fungi. Gouba and Drancourt (7) reported 335 fungal species in 158 genera in humans, with the majority occurring in the digestive tract. The mechanisms of trans-generational passage, long-term establishment, and any possible beneficial associations are beginning to receive intense research attention, and it will be interesting if the human body resembles mechanisms employed by fungiculturing insects. Overall, these striking similarities between farming insects and humans as well as human fungal symbioses suggest that common ecological and evolutionary processes are at play.

<u>Findings</u>

Biedermann and Vega (6) showed that advanced fungiculture, defined by dispersal, nutritional supply, mechanical and antimicrobial protection of ectosymbiotic fungi is present in three insect orders (Coleoptera, Blattodea and Hymenoptera) with at least 15 independent evolutionary origins in each the insects and the fungi. Primitive agriculture, defined by dispersal and either nutritional supply or antimicrobial protection of the fungi, has four additional evolutionary origins in the same insect orders that grow six different lineages of fungi. All other insect-fungal associations found are simple mutualisms in which fungi are only supplied with nutrients or dispersed by insects, such as in galling midges, some aphids, some scale insect, and a moth. By comparison, classical human agriculture, i.e., the cultivation of crops, is advanced using the definition given above and evolved at least nine times independently (2). Some forms of cultivation, however, should be defined as primitive if they do not include protection or nutrient supplementation by humans. Tree plantations fall in this category. Most forestry would fall in the simple mutualism or even parasitism by humans, depending whether trees are planted and maintained (e.g., fertilization, protection) in any way.

For insects, ecology is clearly a major driver of their association with fungi. First, insects that farm fungi for food are particularly abundant in nutritionally extreme habitats, like wood (high polymer content), fruits (high sugar content) and cadavers (high nitrogen content). Second, insects that farm fungi for protection typically have vulnerable life-stages that the fungi can help to protect mechanically or by producing antimicrobial compounds. Third, mutually obligate dependencies between fungi and insects evolved only under stable environmental conditions in which those associations prevail for at least one of the insects' developmental periods. Stable climatic conditions following the Pleistocene glaciation have been suggested to have facilitated the multiple origins of human agriculture all over the world about 10,000 years ago (2,8). Moreover, today humans are extracting and identifying antibiotics from all kinds of fungal and bacterial microorganisms (9,10).

Vertical transmission of fungal spores between generations is another important factor for stabilizing fungiculture because it aligns the fitness between the farmers and their crops (6). All insects with primitive or advanced fungiculture (but see termites; 11) evolved specific spore-carrying organs, so called mycetangia, to vertically transmit their fungal crops (12,13). The evolution of mycetangia in insects for the transportation of specific fungi could be analogous to humans serving as moving receptacles for the transportation of bacteria and fungi. There is evidence for vertical transmission of some fungi in humans (14). Even though bacteria have received ample attention as part of the human microbiome, the study of fungi in the human body (mycobiome) is in its infancy (15,16). It is clear that some fungi can cause diseases in insects and humans, but it has not yet been established whether there are mutualisms between fungi and humans although fungi in the human gut have been reported not only to influence immunity but also to maintain intestinal homeostasis (17). Similarly, fungi can be ubiquitous on insect cuticles, just as fungi are present on human skin (18).

Implications

From an evolutionary point of view, it makes sense to differentiate and classify forms of agriculture by the benefits they provide to farmers and their crops. This allows to develop hypotheses on the ecologies that predisposed some animals (including humans) to develop obligate dependencies with their cultivars. Stability appears to be of crucial importance for obligate associations to establish in insects and humans. Furthermore, there is a vast trove of knowledge on insect-fungal associations, in contrast to the human mycobiome. As studies on the human mycobiome advance, it won't be surprising if the findings reveal that fungi are not simply accidental passengers, but influential members of the human microbiota with important implications in understanding human health issues.

References

1. English Oxford Living Dictionaries. 2019. https://en.oxforddictionaries.com/definition/agriculture
2. Schultz, T.R. et al. 2005. Reciprocal illumination. A comparison of agriculture in humans and in fungus-growing ants. In: *Insect-Fungal Associations* (F. E. Vega and M. Blackwell, Eds.), pp. 149–190, Oxford University Press.
3. Misof, B. et al. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346, 763–767.
4. Lutzoni, F. et al. 2018. Contemporaneous radiations of fungi and plants linked to symbiosis. *Nature Communications* 9, 5451.

5. Sherwood-Pike, M.A., and J. Gray. 1985. Silurian fungal remains: probable records of the class Ascomycetes. *Lethaia* 18, 1–20.
6. Biedermann, P.H.W., and F.E. Vega. Ecology and evolution of insect-fungus mutualisms. *Annual Review of Entomology* in press.
7. Gouba, N., and M. Drancourt. 2015. Digestive tract mycobiota: a source of infection. *Médecine et maladies infectieuses* 45, 9–16.
8. Smith, B.D. et al. 1995. The Emergence of Agriculture. Scientific American Library, W.H. Freeman & Co., 232 pp.
9. Clardy, J. et al. 2009. The natural history of antibiotics. *Current Biology* 19 (11), R437–R441.
10. Chevrette, M.G. et al. 2019. The antimicrobial potential of *Streptomyces* from insect microbiomes. *Nature Communications* 10, 516.
11. Korb, J., and D. Aanen. 2003. The evolution of uniparental transmission of fungal symbionts in fungus-growing termites (Macrotermitinae). *Behavioral Ecology and Sociobiology* 53, 65–71.
12. Francke-Grosmann, H. 1956. Hautdrüsen als Träger der Pilzsymbiose bei Ambrosiakäfern. *Zeitschrift für Ökologie und Morphologie der Tiere* 45, 275–308.
13. Francke-Grosmann, H. 1967. Ectosymbiosis in wood-inhabiting beetles. In: *Symbiosis* (S. M. Henry, Ed.), pp. 141–205, Academic Press.
14. Ward, T.L. et al. 2018. Development of the human mycobiome over the first month of life and across body sites. *mSystems* 3, e00140-17.
15. Cui, L. et al. 2013. The human mycobiome in health and disease. *Genome Medicine* 5, 63.
16. Nash, A.K. et al. 2017. The gut mycobiome of the Human Microbiome Project healthy cohort. *Microbiome* 5, 153.
17. Forbes, J.D. et al. 2019. A fungal world: could the gut mycobiome be involved in neurological disease? *Frontiers in Microbiology* 9, 3249.
18. Jo, J.-H. et al. 2017. Topographical and physiological differences of the skin mycobiome in health and disease. *Virulence* 8, 324–333.