38th ALTENBERG WORKSHOP IN THEORETICAL BIOLOGY

The Convergent Evolution of Agriculture in Humans and Insects

Organized by

Peter Peregrine, Ted Schultz, and Richard Gawne

June 13 – 16, 2019

KLI, Klosterneuburg
Austria

Welcome

to the 38th Altenberg Workshop in Theoretical Biology. The Altenberg Workshops are interdisciplinary meetings organized by the KLI in Klosterneuburg, Austria. The workshop themes are selected for their potential impact on the advancement of biological theory. Leading experts in their fields are asked to invite a group of internationally recognized scientists for three days of open discussion in a relaxed atmosphere. By this procedure the KLI intends to generate new conceptual advances and research initiatives in the biosciences. We are delighted that you are able to participate in this workshop, and we wish you a productive and enjoyable stay.

Gerd B. Müller
President

The topic

Agriculture, defined here as the dietary reliance on domesticated organisms cultivated in engineered microenvironments, has evolved at least thirteen times among Attini (leaf-cutting fungus-farming ants), Macrotermitinae (termites), and Xyleborini (ambrosia beetles), and seven times among humans (Hominini). This seems a remarkable case of convergent evolution, and one that deserves to be carefully examined. How can we understand agriculture as a product of convergent evolution?

Two working groups were convened at the Santa Fe Institute to examine this question. The groups found that the convergent evolution of agriculture may derive from energetic benefits that include reduction in time spent foraging, reduced overall mobility, and a reduced reliance on wild protein sources that are often under intense competition from other species. There is also greater reliability or predictability in food supplies with agriculture (although catastrophic crop failures can, obviously, occur).

Agriculture is a highly successful evolutionary strategy in both humans and insects; indeed, it has been estimated that fully half of the biomass of the insect world and a large percentage of the earth's total biomass is constituted by the agricultural insects. Among humans, agriculture dominates all other food production systems, and has had a profound impact on the earth's ecosystems. Why is such a potent adaptation so relatively rare?

The working groups also examined this question, and found that developmental constraints appear not to limit the evolution of agriculture; rather, it is functional constraints that seem uniquely limiting. The groups identified a set of specific preconditions that must be present for agriculture to evolve, including (1) generalized foragers that create central places for food storage, distribution, and consumption; (2) some reliance on a plant or animal species that is genetically or behaviorally pre-adapted for domestication; (3) relatively intense group sociability and communication, particularly sociability and communication that crosses generations and allows for social learning or conditioning; (4) rapid replication of mutations or innovations; and (5) a relatively stable climate. The preconditions may be quite rare, thus making agriculture a rare adaptation.

The aims of this Altenberg workshop are both to share and evaluate findings from the Santa Fe Institute working group meetings and, perhaps more importantly, elaborate on them by developing a better understanding of the preconditions, sequential evolution, and social, biological, and environmental impacts of agriculture in a comparative framework. We hope our discussions and papers will provide new insights to help to further develop evolutionary theory.

Format

There will be 16 presentations, with 45 minutes allotted for each—roughly 30 minutes for each talk, followed by 15 minutes for Q&A and discussion. On Thursday we will meet for a welcome reception at the venue. On Friday we will begin with a short welcome address and introduction by the organizers, addressing the aims and framework of the workshop, and a brief introduction to the broader issues of agriculture by science writer Susan Milius, followed by six (6) presentations. Saturday is a full day of seven (7) presentations followed by a general discussion and a group dinner. On Sunday we have two (2) presentations and end with a general discussion, including publication plans. We hope discussion will continue during an afternoon cruise on the Danube and dinner at Schloss Dürnstein.

To support discussion during the sessions, we encourage all participants to send a rough draft of their presentation and/or some materials that are relevant to their topic to the organizers in advance of the workshop, to be circulated among the participants.

Manuscript preparation and publication

The Altenberg Workshops in Theoretical Biology are fully sponsored by the KLI. In turn, the Institute requests that all participants contribute a paper to a volume edited by the organizers. Altenberg Workshop results are usually published in the *Vienna Series in Theoretical Biology* (MIT Press). The contributors are not necessarily limited to the original participants; they may be complemented by additional experts and co-authors invited at the discretion of the participants.

We expect that participants will revise their drafts as a result of our discussions at the workshop and the ensuing review process. We aim for a September 2019 date for receipt of finished manuscripts for publication. The length of the contributions should be in the range of 8,000 – 10,000 words. The use of figures and photographs is encouraged. All contributions will be edited for style and content, and the figures, tables, and the like will be drafted in a common format. The editors will send specific instructions after the workshop.

Participants

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The Convergent Evolution of Agriculture in Humans and Insects

Thursday 13 June	Evening		
6.00 pm – 9.00 pm		Welcome reception (cold food provided) at the KLI	

Friday 14 June	Morning	Introduction to the Workshop	Chair: Peregrine
9.00 am – 10.00 am	P. Peregrine/ T. Schultz/ R. Gawne	Welcome address and introductions	
10.00 am – 10.30 am	S. Milius	The Other Kind of Insect Farming	
10.30 am – 11.00 am	Coffee		
11.00 am – 11:45 am	G. McGhee	Convergent Evolution of Agriculture in Bilaterian Animals: An Adaptive Landscape Perspective	
11.45 am – 12:30 pm	P. Peregrine	The Impact of Agriculture on Social Organization: A Comparative Analysis	
12.30 pm – 14:30 pm	Lunch	at the KLI	

Friday 14 June	Afternoon	Agricultural Crops	Chair: Fuller
2.30 pm – 3.15 pm	D. Fuller	Coevolution in the Arable Battlefield: Crop Morphology, Cultural Practice, and Parasitic Domesticoids	
3.15 pm – 4.00 pm	F. Denison	Domestication versus Taming of Crop Plants and Their Symbionts	
4.00 pm – 4.30 pm	Coffee		
4.30 pm – 5.15 pm	H. Kokko	How to Deal with Unpredictability in Life	
5.15 pm – 6.00 pm	D. Piperno (via D. Fuller):	Developmental Plasticity, Gene Expression, and Crop Plant Evolution	
6.00 pm		Departure for Dinner at a Viennese Heurigen	

Saturday 15 June	Morning	The Agricultural Insects	Chair: Schultz
9.00 am – 9.45 am	J. Korb	Fungus-Growing Termites: An Ecological Perspective	
9.45 am – 10.30 am	J. Hulcr	Ambrosia Symbiosis	
10.30 am – 11.00 am	Coffee		
11.00 am – 11.45 am	A. Ješovnik	Fungus-Farming Ants	
11.45 am – 12.30 pm	J. Boomsma	How Leucocoprineaceous Fungi Domesticated the Attine Ants	
12.30 pm – 2.30 pm	Lunch	at the KLI	

Saturday 15 June	Afternoon	The Evolution of Agriculture	Chair: Gawne
2.30 pm – 3.15 pm	N. Gerardo	The Evolution of Microbial Interactions within Ancient Ant Agriculture	
3.15 pm – 4.00 pm	D. Aanen	The Sociobiology of Domestication	
4.00 pm – 4.30 pm	Coffee		
4.30 pm – 5.15 pm	T. Schultz	Evolutionary Convergence of Ant and Human Agriculture	
5.15 pm – 6.15 pm		Discussion	
6.15 pm		Free evening for exploring Vienna	

Sunday 16 June	Morning	Outlook	Chair: Ješovnik
9.30 am – 10.15 am	P. Biedermann	Did Insects Invent Agriculture?	
10.15 am – 10.45 am	Coffee		
10.45 am – 11.30 am	R. Gawne	Distributional Constraints in the Development of Domesticated Forms	
11.30 am – 1.00 pm		Concluding Discussion & Publication Plans	
1.00 pm – 2.00 pm	Lunch	at the KLI	
2.15 pm		Departure for Danube boat trip and dinner at Schloß Dürnstein	

Abstracts

Susan MILIUS
Science News

The Other Kind of Insect Farming

Now is a great time to watch fast agricultural change in an example of indoor, high-density farming. An estimated 20 to 40 U.S. farms selling crickets and other insects are rushing to catch a recent uptick (from zero to detectible) in U.S and European consumer interest in eating insects. Small farms have grown crickets and other insects for fishing bait or reptile food for decades. Feeding humans, however, is pushing methods to evolve. Alas, companies lock away their data when a journalist knocks, but I can share a few tales from interviews see if the challenges of growing insects resonate across other forms of farming.

Biographical note:
Susan Milius is a journalist specializing in organismal and evolutionary biology at Science News's print magazine and web site. She has reported on studies of fungus-growing ants and other non-human farmers. In the last several years, she has started writing about food security, climate change and ideas for tweaking human agriculture.

George R. McGHEE
Rutgers University

Convergent Evolution of Agriculture in Bilaterian Animals: An Adaptive Landscape Perspective

Agriculture has evolved independently, convergently, in nine phylogenetic lineages of bilaterian animals: actinopterygian vertebrates, sarcopterygian vertebrates, polychaete annelids, patellogastropod molluscs, neogastropod molluscs, littorinoid molluscs, polyneopteran insects, hymenopteran insects, and coleopteran insects. Using a measure of agricultural complexity, it can be demonstrated that the most complex agricultural systems exist in terrestrial animals and lower-complexity agricultural systems exist in marine animals, regardless of whether the farmed crops are plants or fungi. From an adaptive landscape perspective, there appears to exist a limited number of ways to do agriculture that constitute the complexity levels of a single adaptive peak—regardless of whether the crop type is plants or fungi, and whether the habitat is marine or terrestrial. Independent agricultural-animal clades differ in the number of those limited ways they have discovered or been able to master.

Biographical note:

George McGhee is Distinguished Professor of Paleobiology at Rutgers University (New Brunswick, New Jersey, USA) and a Member of the KLI. He is the author of seven books, which detail his research interests: The Late Devonian Mass Extinction (1996), Theoretical Morphology (1999), When the Invasion of Land Failed: The Legacy of the Devonian Extinctions (2013), and Carboniferous Giants and Mass Extinction: The Late Paleozoic Ice Age World (2018), all published by Columbia University Press, The Geometry of Evolution: Adaptive Landscapes and Theoretical Morphospaces (2007), published by Cambridge University Press, Convergent Evolution: Limited Forms Most Beautiful (2011) and Convergent Evolution on Earth: Lessons for the Search for Extraterrestrial Life (2019), both published by the MIT Press in the Vienna Series in Theoretical Biology.

Peter N. PEREGRINE
Lawrence University

The Impact of Agriculture on Social Organization: A Comparative Analysis

A large dataset on the effects of agriculture on human, ant, and termite social organization was created for a workshop held at the Santa Fe Institute in 2016. In this paper I report on the analyses of these data, and demonstrate that agriculture appears to increase division of labor and to increase social control mechanisms within these societies. However, I also show that these data do not support the widely-held belief that agriculture leads to larger populations and greater levels of violence. I discuss these results in the context of Eastern North America and both the evolution of indigenous domesticates (bottle gourd, chenopodium, and sunflower (*Iva annua*)) and the adoption of domesticates from Mesoamerica (maize, beans, and squashes). I then consider some of the possible social benefits that may have led humans in Eastern North America to adopt agricultural lifeways.

Biographical note:

Peter Neal Peregrine is Professor of Anthropology and Museum Studies at Lawrence University in Appleton, Wisconsin. He is an archaeologist whose work focuses on the origins of social complexity. He has done extensive fieldwork in eastern North America and northern Syria, but his focus has shifted to comparative work examining long-term trends in human cultural evolution using extant archaeological data. He employs a complex adaptive systems approach in his research and envisions humans as highly proficient niche constructors.

Dorian Q. FULLER
University College London

Coevolution in the Arable Battlefield: Crop Morphology, Cultural Practice, and Parasitic Domesticoids

In the history of *Homo sapiens*, societies have undergone a transition to agriculture multiple times around the world, based on numerous independent plant domestications. The archaeological evidence makes clear that the crop domestication process represents repeated coevolution as seed crops became dependent on humans for dispersal, lost dormancy, and increased investment in more and larger seeds. The protracted nature of these transitions (1000s of plant generation and a dozens of human generations), highlights that is was not a conscious or human-directed process. What is more the process required evolution on the part of humans, although this mostly took place through cultural inheritance and technology. The coevolution between humans and domesticates was not, however, cut off from a wider environment but also attracted numerous parasitic domesticoids, pests and weeds, that also adapted to human dispersal and to drawing caloric energy from arable-cultural environment. This set in place an ongoing battlefield that has driven agronomic evolution for millennia.

Biographical note:

I am an archaeologist and a botanist, employing botanical methods to answer archaeological questions, especially about past subsistence, the origins and evolution of agriculture, and the evolution of plants under domestication. I have a wider interest in human-environment interactions, including how societies have dealt with climate change and how climate drivers, such as greenhouse gases, have been produced through prehistoric human activities. I also ponder how long-term cultural traditions, such as cooking traditions, have shaped the evolution of crops and economies, and how cultural traditions can be understood through combining archaeological evidence with historical linguistics. I have also contributed to the integration of archaeology and genetics, especially with regards to plant and animal domestication.

R. Ford DENISON
University of Minnesota

Domestication versus Taming of Crop Plants and Their Symbionts

Taming of animals refers to manipulation of the phenotype (including behavior) in an individual, whereas domestication refers to genetic changes in a population. For crop plants, desired phenotypes may be achieved either genetically, as in dwarfing genes for wheat or rice, or via taming-like phenotypic manipulation, as in grafting or pruning of fruit trees. This choice deserves more attention. Taming each individual plant may be faster and perhaps more flexible, but breeding a cultivar with the desired traits (a dwarf apple without grafting, say) could reduce long-term costs. Plants have imposed selection for domestication on some partners, via host sanctions against less-beneficial rhizobia, mycorrhizal fungi, and fig wasps. Taming of partners by plants has also been reported, enhancing the efficiency (nitrogen per carbon) of rhizobia and the host-fidelity of ants that defend acacias.

Biographical note:

After undergraduate study at Harvard and Evergreen, R. Ford Denison earned a Ph.D. in Crop Science from Cornell, working with Tom Sinclair, followed by postdocs with Bob Loomis and Park Nobel. He worked for USDA for seven years as a Plant Physiologist before being hired by the Department of Agronomy and Range Science at UC Davis. There, he directed the first ten years of a long-term experiment now in its 24th year, taught Crop Ecology, and did basic and applied research on the legume-rhizobia symbiosis. He took early retirement in 2005 to join his wife at the University of Minnesota, where he advises a three-site long-term experiment and continues laboratory and field research, writing, and lecturing, mostly on nitrogen fixation and on links between evolution and agriculture. He is the author of Darwinian Agriculture and about 100 articles in journals including American Naturalist, Plant Physiology, Field Crops Research, Nature, and Science.

Hanna KOKKO
University of Zurich

How to Deal with Unpredictability in Life

One potential rationale why cooperative breeding might be selected for is that by pooling resources, the variance in resource acquisition is diminished. Variance minimization has the gist of avoidance of ‘worst-case scenarios’, which in turn sounds like bet-hedging is at play, but not all situations of risk management qualify as real bet-hedging in a strict population genetic sense. I will clarify the mathematical underpinnings of bet-hedging theory in evolutionary ecology, and as a specific application, look at the conditions under which it pays to join forces to ensure a more continuous food supply.

Biographical note:

Hanna Kokko completed her PhD in 1997 at Helsinki University. She is now a Professor of Evolutionary Ecology at the University of Zurich, where she landed in 2014 after an Australian Laureate Fellowship. She has a longstanding interest in the mathematical logic that underpins biology — having published a textbook ‘Modelling for field biologists and other interesting people’ — and displays particular curiosity towards the evolution of reproductive strategies. She is an invited member of two academies of science (in Finland and in Australia) and the recipient of the 2010 Per Brinck Oikos award, a prize awarded annually for a world-leading ecologist.

Dolores R. PIPERNO
Smithsonian Institution Tropical Research Institute

Developmental Plasticity, Gene Expression, and Crop Plant Evolution

Plant domestication was at its core an evolutionary process involving both natural and human selection for traits favorable for harvesting and consumption. Ever-improving analytical methods for retrieving empirical data from archaeological sites, together with advances in genetic and experimental research on living crops and their wild ancestors are providing new understandings of, and processes for, domestication. They include phenotypic (developmental) plasticity and genetic assimilation, which despite domestication having first occurred during periods of profound global environmental change during the Pleistocene to Holocene transition, have been neglected concepts in plant domestication research.
This talk will discuss results of multi-year experimental research, including artificial selection studies, on plastic, other phenotypic, and gene expression changes in teosinte (*Zea mays* ssp. *parviglumis*), the wild ancestor of maize, and maize when grown under atmospheric CO_2 and temperature conditions that characterized the Late Pleistocene and early Holocene periods when teosinte was first exploited and then transformed into maize. The data invite reconsiderations of how domesticated phenotypes emerged in maize and question whether the living wild progenitors of maize and perhaps other major crops utilized in archaeobotanical and genetic research are faithful replicas of what the last foragers and first cultivators saw 13,000-9,000 years ago.

Biographical note:
Dolores R. Piperno (PhD 1983, Temple University) is Senior Scientist and Curator of South America Archaeology Emerita at the Smithsonian Tropical Research Institute, Panama and National Museum of Natural History, Washington DC. Her current projects involve the investigation of teosinte (wild maize) growth in the environmental conditions in which it was first collected and cultivated by humans, and the impact of prehistoric societies on Amazonian

forests. She is the author or editor of more than 90 articles and four books. Honors include election to the National Academy of Sciences and American Academy of Arts and Sciences; the Archaeological Institute of America Pomerance Career Award for Scientific Contributions to Archaeology; and the Orden de Vasco Nuñez de Balboa, the highest award given to a civilian by the Republic of Panama, for her contributions toward understanding the prehistoric cultures of Panama.

Judith KORB
University of Freiburg

Fungus-Growing Termites: An Ecological Perspective

Fungus-growing termites (Macrotermitinae) play important roles in paleotropical ecosystems. I will give an introduction into the ecology of fungus-growing termites with an emphasis on West African savannah ecosystems. Paying special attention to the importance of fungus cultivation, I will summarize our current understanding on factors that may influence a species ‘ecological success‘ (i.e, abundance and distribution). I will pinpoint major gaps in our current knowledge and try to draw comparisons to human agriculture.

Biographical note:

Judith Korb is an evolutionary biologist and ecologist interested in social evolution and working on the ecology of termites.

Jiri HULCR
University of Florida

Ambrosia Symbiosis

Ambrosia beetles were the first animals to evolve farming over 60M years ago and have diversified into >3,000 species in 14 independent clades. Likewise, the ambrosia crop originated in more than 6 different groups of fungi, ranging from plant pathogens to yeasts and wood degraders. One of the main research advantages of this system is its diverse evolutionary trajectories which enable true comparative evolutionary inquiry. After a decade of research into this system, my laboratory has developed two new perspectives: 1) There is not one, but many ambrosia symbioses. Each of the origins offers a unique symbiotic phenotype and degree of specificity. Their repeated commonalities enable rigorous tests of the unifying principles of animal-fungus farming. 2) The standard perspective of a deliberate beetle farmer and a domesticated fungal crop does not seem to reflect the biological reality. Our research suggests that it is the metabolic phenotype of the fungus which dictates the ecology of the symbiosis, from habitat preferences to the degree of mutual specificity.

Biographical note:

Jiri Hulcr is an associate professor of forest entomology at the University of Florida. He runs a lab that studies the relationships between wood boring beetles, fungi, trees and people. Stretching the span from fundamental evolutionary biology to applied forestry, Jiri is trying to understand how these organisms function and interact, and use that knowledge to protect our natural resources. Jiri got his PhD at the South Bohemia University in Czechia and another one at Michigan State University. Before Florida, he worked in various research positions at the University of Wisconsin, North Carolina State University, the Binantang Center in Papua New Guinea, and many other places around the world.

Ana JEŠOVNIK
Croatian Myrmecological Society

Fungus-Farming Ants

Fungus-farming ants are best known for their peculiar habit of growing fungus for food, a behavior that evolved much earlier than agriculture in humans: about 55-60 million years ago. There are 17 genera and 245 species of fungus-farming ants, distributed throughout the New World. They include rare, cryptic, and tiny species or “lower” fungus-farmers with colonies of 50-200 individuals that farm their fungus on decaying organic material, as well as ubiquitous and dominant leaf-cutter ants, whose enormous nests contain fungus gardens grown on freshly cut vegetation, and a range of species in between. Because of this fascinating symbiosis humans have been studying fungus-farming ants since the 19th century, but we have just recently began to understand the complex evolutionary history and environmental factors that lead to the rise and success of ant agriculture.

Biographical note:
Ana Ješovnik is a myrmecologist. She received her master’s degree (in biology and education) from the University of Zagreb, Croatia, and was subsequently employed as a biology teacher for 2 years. She then moved to the USA, where she pursued her PhD at University of Maryland and at Smithsonian’s National Museum of Natural History. For her PhD thesis she studied the fungus-farming ant genus Sericomyrmex, while through her side projects she explored other genera of attine ants, and their fungal cultivars. She is currently employed in the conservation department of the Ministry of Environment and Energy, in Zagreb, Croatia, and runs an NGO Croatian myrmecological society that focuses on ant research and popularizing ants in Croatia. In addition to her research on ants that practice agriculture, she has recently begun to investigate in which ways can ants help humans that practice agriculture.

Jacobus J. (Koos) BOOMSMA
University of Copenhagen

How Leucocoprinaceous Fungi Domesticated the Attine Ants

We are intuitively inclined to think of farmers as subjects and ‘crops’ as objects because agency is fundamentally asymmetric. Over the years, I have become increasingly uneasy with this way of thinking for the fungus-farming ants. Using recent microbial data, I will argue that conceptualizing this complex symbiotic lineage, which goes back ca. 60 MY and spans 16 recognized genera and ca. 250 described species, is more compelling when taking a fungal symbiont perspective. I hope to arrive at insights that will make it easier to appreciate the parallels and unique differences between fungus-growing social insects and other co-evolved farming symbioses.

Biographical note:

I studied biology at the Free University of Amsterdam and obtained my PhD there in 1982. After postdoctoral assignments in Utrecht, Oxford and Cornell, I moved to Aarhus University in 1990 and became a full Professor of Evolutionary Biology at the University of Copenhagen in 1999. I coordinated two EU Marie Curie Research Training Networks, and initiated and directed the Copenhagen Centre for Social Evolution since 2005. The Centre’s research focuses on the evolutionary biology and ecology of social insects and their parasitic and mutualistic symbionts, and increasingly uses molecular and genomic techniques for testing evolutionary hypotheses about cooperation and conflict. It also hosts an evolutionary medicine program using the extensive public health data of Denmark to test evolutionary hypotheses on why human health is compromised by pregnancy disorders and mental diseases. I have spent sabbatical time in Utrecht, Würzburg, Regensburg, Oxford and Berlin.

Nicole GERARDO
Emory University

The Evolution of Microbial Interactions within Ancient Ant Agriculture

The fungus-growing ant symbiosis is a model for the study of coevolution within the framework of ancient agriculture. Like most agriculture, the system consists not only of the farmers and their single crop but a complex array of microbial associates. These associates include pathogens that have evolved to specialize on the crops, as well as other microbes that mediate an array of processes, including pathogen protection, within the gardens. Here, I will overview the agricultural system and then focus on host-pathogen coevolution within the context of this ancient, diverse agricultural system.

Biographical note:
Nicole Gerardo is a Professor of Biology at Emory University in Atlanta, Georgia. Her lab's focus is on the evolutionary ecology of interactions between microbes and hosts. Such associations are shaped by ecological limitations on host and symbiont range, evolutionary trade-offs for both hosts and microbes, and host immunology. She combines genomic and experimental approaches to study these forces in diverse insect-microbe systems. To address these topics, she utilizes the versatility of systems in which both the hosts and their microbial partners and pathogens can be maintained in the laboratory.

Duur K. AANEN
Wageningen University & Research

The Sociobiology of Domestication

A defining characteristic of mutualistic host-symbiont associations is a difference in numbers: a single host is associated with a group of symbionts. According to this criterion, agriculture is a host-symbiont association as the farmer generally cultivates fields of crops and herds of livestock. Because of the difference in numbers between partners, domestication, the process whereby symbionts become closely associated with a host, essentially is a process of social evolution. How can symbionts become social, or behave socially, so that they collectively provide a benefit to the host, and how can the host influence symbiont sociality? I will consider the two main categories of explanation for social evolution, which are not mutually exclusive, kin selection and repression of competition. Examples of the first category are enforcement of monoculture cultivation by fungus-cultivating insects and selection for social chicken in human agriculture. An example of the second category is the sequestration of 'reproductive symbionts' from 'worker symbionts', which has been found in sucking louse gut symbionts. Intriguingly, in modern human agriculture a similar sequestration of 'germline' and 'soma' is found, with the germline being provided by specialized seed companies for crops or breeding companies for livestock. I conclude that host-interference is a major mechanism to facilitate sociality in a world that is otherwise dominated by individual-level selection and numerous tragedies of the commons.

Biographical note:

Duur Aanen is an associate professor in Evolutionary Genetics at Wageningen University, the Netherlands. After finishing his PhD on speciation of fungi at Wageningen University, he became a postdoc and later assistant professor at the University of Copenhagen and returned to Wageningen in 2006. Duur Aanen specializes on the origin and evolution of cooperation and uses fungi and the symbiosis between termites and Termitomyces fungi as his main model systems.

Ted R. SCHULTZ
Smithsonian Institution National Museum of Natural History

Evolutionary Convergence of Ant and Human Agriculture

Some scientists, including some biologists and anthropologists, consider the application of the term "agriculture" to describe the association between "attine" ants (subfamily Myrmicinae: tribe Attini: subtribe Attina) and their fungal symbionts to be anthropomorphic and therefore spurious. We will argue instead that, whether anthropomorphic or not, the term is accurate. It is not accurate because ant and human agriculture are homologous, which they obviously are not, but because both are examples of a particular category of symbiosis characterized by a number of striking similarities. These similarities are likely due to evolutionary convergence driven by similar selective forces. I will point out the similarities between ant and human agriculture and attempt to frame them within the larger category of agricultural and nutritional symbioses.

Biographical note:
My primary general interests include phylogenetics, ant macroevolution, and the evolution of symbiosis. My primary focused interest is the evolution and coevolution of fungus-farming ants and their fungal cultivars. I have devoted considerable effort to improving the phylogenies of both the fungus-farming ants and their associated fungi, most recently using phylogenomic methods. Observing and documenting patterns, or the lack of patterns, between the phylogenies of both symbionts at all levels (clades, species, and populations) is an essential first step for formulating hypotheses about and ultimately understanding the biological mechanisms that have driven and that maintain the diversity of attine ant-fungus associations.

Peter H. W. BIEDERMANN
University of Würzburg

Did Insects Invent Agriculture?

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”. 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, 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 and fungi are more than one billion years old. The earliest record for a possible insect-fungal association is ca. 400 million years old. 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. 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.

Biographical note:

Peter Biedermann received his B.Sc. in Biology from the University of Graz, Austria, and then moved to Switzerland to do his M.Sc. and Ph.D. at the University of Bern, Switzerland, on the behavioural ecology of fungus farming ambrosia beetles. In the following, he spent several years as a postdoc at the Max Planck Institute for Chemical Ecology in Jena, Germany, to investigate the associated microbes (fungi and bacteria) of ambrosia beetles and how the insects behaviourally and chemically manage them. In 2017, he received an Emmy Noether grant by the German Science foundation to found his own group at the University of Wuerzburg, Germany. Together with his group, he is now investigating (i) the beetles´ mechanisms to defend against fungal pathogens and to promote growth of their fungal crops, (ii) the ecological factors selecting for social behaviour and farming and (iii) similarities between agriculture in insects and humans.

Richard GAWNE
Tufts University

Distributional Constraints in the Development of Domesticated Forms

Domesticated plants and animals are often regarded as the end result of unintentional experiments that have elicited significant changes in morphological form. Many of the fundamental mechanisms that drive evolutionary change were discovered through the study of these organisms, and as such their importance is widely appreciated in evolutionary biology. Interestingly, the same can not be said for developmental biology. The development of domesticated plants and animals has been examined, but the fact that the study of these organisms might allow for the identification of large-scale patterns in the developmental process is not widely appreciated. Among other things, an analysis of data on the development of domesticated organisms highlights the fact that metabolic costs of tissues play an important role in determining the final form a plant or animal is able to reach. The cell cycle is costly, and resources spent on the growth of one structure are generally not available for use elsewhere. This ‘distributional constraint’ on resource allocation is likely to be a significant contributing factor in the production of domesticated morphologies, with some regions of morphospace becoming accessible only by limiting the developmental resources allocated to certain non-essential characters. A similar phenomenon can be identified in wild-type populations, suggesting that decisions about resource allocation made during development are an essential part of the ontogenetic process with important evolutionary implications.

Biographical note:

Rick Gawne completed his PhD on the development and evolution of tiger moth wing patterns at Duke University in 2017. During this time, he was a visiting student at the University of Copenhagen’s Center for Social Evolution, and the Smithsonian National Museum of Natural History, where he became interested in the evolution of agriculture, and the process of domestication. He was a postdoctoral fellow at the Konrad Lorenz Institute, and is now a postdoc in the

Center for Regenerative and Developmental Biology at Tufts University, where he works on morphogenesis and regenerative processes in Michael Levin's laboratory, using model systems such as planaria, and frogs.