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The Convergent Evolution of Agriculture: A Systematic Comparative Analysis

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A central question of this volume is the extent to which human and insect agriculture is an example of convergent evolution. To help explore that question, I conducted a comparative study of human and insect agricultural systems to see if there are empirical similarities and differences that might indicate a convergent evolutionary process. Data for this study were collected through a questionnaire consisting of 60 dichotomous or ordinal variables completed by four experts on specific insect species or human cultural groups (different cultural groups were considered different “species” for the purposes of this study). Seven indices were created from these data and used to test six hypotheses concerning similarities and differences between human and insect agricultural systems and the impact of agriculture on human and insect societies. I found that while humans and insects differed in terms of agricultural practices, there were remarkable similarities in the impact of agriculture on human and insect societies. I suggest this has important implications for understanding the evolution of agriculture as a convergent process.

Human Agriculture

In this section I provide a brief introduction to agriculture as it is practiced by humans and the impacts that have been hypothesized to have stemmed from it. I define *agriculture* following the other authors in the volume, as economic reliance on domesticated plants and animals. *Domesticated* refers to genetic modification of one species by another in a way that appears to benefit the domesticating species but reduces the fitness of the domesticated species in the wild.

Agriculture evolved independently at least seven times among humans (Bellwood 2005), but the processes through which domestication and agriculture evolved appear to differ, sometimes dramatically, in each area (see figure 2.1). For example, in the Fertile Crescent (the general area of the Zagros Mountains and Tigris/Euphrates Valley in modern Lebanon, Turkey, Syria, and Iraq), agriculture appears to have evolved as foragers harvesting grasses artificially selected for desired characteristics, including a larger seed that did not fall off the stalk while harvesting and with a husk that was easy to remove. This led to grasses that could not readily reproduce in the wild, but could be readily harvested and

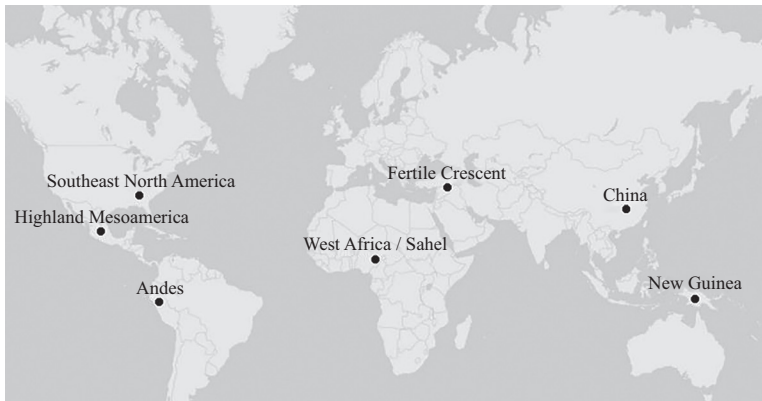


Figure 2.1
Seven locations where human agriculture originated.

sown by humans (Zeder 2011). In contrast, the bottle gourd was domesticated (or further domesticated—there is controversy over the bottle gourd’s origins) in Mesoamerica not as a food source but as a utensil for carrying liquids, and the process of domestication did not strictly consist of the selection for desired traits in the bottle gourd but also of geographical expansion as humans transplanted bottle gourds to locations where they did not typically grow (Asch and Hart 2004).

The evolution of agriculture among humans is considered one of the key events in human history, one that globally transformed human societies (see, e.g., Morgan 1877; Childe 1936; Barker 2006). While the causes of this “Neolithic revolution” have been debated for decades (see Bellwood 2005, 19–25, for a quick overview of these debates), the consequences have been less so. Most scholars agree that the transition to agriculture is associated with (and perhaps causally so) increases in population, sedentism, social complexity, and the elaboration of material culture (see, e.g., Diamond 2002; Jobling, Hurler, and Tyler-Smith 2004, 305–306; Dow and Reed 2015). In addition, many scholars believe that agriculture led to a decline in health and to increased conflict between groups (e.g., Larsen 2018).

In North America, for example, the adoption of maize-based agriculture led to a dramatic increase in dental caries (cavities) and diseases related to poor nutrition such as porotic hyperostosis (“spongy” cranial bones) and enamel hypoplasia (linear growth irregularities on the teeth) (Cohen and Crane-Kramer 2007). In locations such as the central Mississippi River valley large agricultural communities emerged with formal political leaders who orchestrated large social and religious events such as feasting and calendrical ceremonies. Long-distance trade in both exotic raw materials and manufactured goods intensified, leading to the creation of trade entrepôts across midcontinental North America. Conflict between local agricultural groups increased, and political-economic systems began to regularly collapse and rebuild, probably due to both external and internal conflict often associated with crop failure (Milner 2004, 165–168).

Thus the evolution of agriculture among humans has long been understood to have led to profound changes in demography, health and nutrition, and social organization. To what extent is this true for the agricultural insects?

A Comparative Perspective on the Evolution of Agriculture

In this section I outline the materials and methods used here to better understand the impact of agriculture on both human and insect societies. I assume that the reader can obtain an understanding of the variety of insect agriculture from other chapters in this volume, so I will not cover that here. I will, however, attempt to clearly distinguish the systematic comparative method used here from the comparative examples provided by many of this volume's authors.

While most research on the evolution and impact of agriculture has been in the form of case studies focused on individual sites or regions (e.g., Cowan and Watson 2006; Price and Bar-Yosef 2011; Barker and Goucher 2015) or, in the case of insects, of species (see, e.g., chapter 9, this volume), this study takes a different approach. Here I perform a systematic comparative study of 29 human and insect agricultural cases. The underlying logic of systematic comparison is to look across cases to identify broad similarities and differences using statistical analyses. If statistically robust associations can be identified from a wide range of cases, then there is no a priori reason to assume that they are not generalizable to all agricultural organisms. An additional strength of this type of comparison is that it allows one to test whether or not an assumed predictive condition is empirically associated with assumed effects across a wide range of cases. Finally, such comparison allows patterns of traits and relationships between variables to be described probabilistically, which in turn provides the potential to test the statistical significance (or to evaluate, from a Bayesian perspective, the likelihood) of identified relationships (Ember and Ember 2009).

A relatively large and well-defined sample is required to perform systematic comparative analyses of this type. The sample must provide examples from the entire range of expected variation, and the cases must be, as much as possible, independent of one another in order to avoid autocorrelation. Here I employ a random sample of 15 human cases from the eHRAF Collection of Archaeology (ehrafarchaeology.yale.edu) and a sample of 14 insect cases (three ant, seven termite, and four beetle) suggested by other authors in this volume. These cases are listed in table 2.1.

The human cases, which I have employed in previous research (Peregrine, Ember, and Ember 2004, 2007), represent a sample of evolutionary sequences from three centers of independent agricultural evolution: Mesopotamia, Highland Mesoamerica, and the Central Andes. Being sequences, these cases allow for both synchronic (assuming all cases exist at the same time) and diachronic (looking over time within each sequence) analysis. The insect cases were selected by the individual experts who coded them (Ted Schultz for ants, Duur Aanen for termites, and Jiri Hulcr for beetles—an effort for which I thank them heartily). These cases were, like the human cases, intended to be proxies for evolutionary sequences (e.g., from lower attines to leaf-cutter ants), but after long discussion it was decided that the lack of certainty about insect evolution makes the identification of evolutionary “sequences” for termites and beetles impossible, so no diachronic analyses were performed.

In addition to a carefully selected sample, systematic comparison also requires clearly defined and reliably coded variables. Both the insect and human cases were coded on a total of 60 dichotomous or ordinal variables as presented in table 2.2. Evaluation of reliability showed that the variables are all low inference and reliability is very good (over

Table 2.1
Cases used in the analyses

Highland Mesoamerican Archaic
Highland Mesoamerican Early Preclassic
Highland Mesoamerican Late Preclassic
Central Mexico Classic
Central Mexico Postclassic
Epipaleolithic
Aceramic Neolithic
Ceramic Neolithic
Ubaid
Late Chalcolithic Mesopotamia
Highland Andean Archaic
Highland Andean Formative
Chavin
Andean Regional Development
Huari
Ants lower attine
Ants higher attine
Ants leaf-cutter
Termites clade I (Acantho)
Termites clade II (Odonto)
Termites clade III (Macro)
Termites clade IIIa (Macro b)
Termites clade V (Synacantho)
Termites clade V (Ancistro)
Termites clade VI (Micro)
Beetles (Ambrosiophilus)
Beetles (Xylosandrus)
Beetles (Trypodendron)
Beetles (Xyleborus)

90% inter-coder agreement). For analysis the variables were standardized and combined into the seven indices shown in table 2.3. Alpha values for each index, also given in table 2.3, indicate that all indices are reliable (alpha values approaching 1.0 indicate high scale reliability; see DeVellis 2012).

Analyses were performed using SPSS (IBM Corporation 2019) and the nonparametric statistics options, as at least one of the variables in all of the analyses was ordinal. Mann-Whitney U tests were used for comparison of insects versus humans, and Kruskal-Wallis H tests were used to compare cases with different degrees of dependence on agriculture. Tau-b correlations were also computed for these comparisons to examine possible linear associations. Bayesian analyses were also performed using the SPSS Bayesian statistics options, but there were no major differences between the nonparametric findings and Bayesian estimates, so only the nonparametric tests are discussed here because they are much simpler to interpret.

Table 2.2
Codebook

I. "Agricultural" practice variables

VI.1 Selecting substrate (universal)

1 = low specificity

2 = moderate specificity

3 = high specificity

9 = missing

VI.2 Internal sustainability (harvested domesticates provide source for next crop cycle)

1 = 0 to 33%

2 = 34 to 67%

3 = 68 to 100%

9 = missing

VI.3 Planting crops

1 = low investment

2 = moderate investment

3 = high investment

9 = missing

VI.4 Preparing substrate

1 = low investment

2 = moderate investment

3 = high investment

9 = missing

VI.5 Dimensions of substrate

1 = 2d

2 = 3d

9 = missing

VI.6 Temporal variation in cultivation

1 = discrete (seasonal/crop rotation/fallowing)

2 = continuous

9 = missing

VI.7 Diversity of domesticates (at a single location/within a single group)

1 = single domesticate

2 = two or three domesticates

3 = four or more domesticates

9 = missing

VI.8 Monitoring crops for disease or thieves/predators

1 = 0 to 33% of the time

2 = 34 to 67% of the time

3 = 68 to 100% of the time

9 = missing

VI.9 "Weeding": Physical removal of invasive pests/predators

1 = 0 to 33% of pests removed

2 = 34 to 67% of pests removed

3 = 68 to 100% of pests removed

9 = missing

(continued)

Table 2.2
(continued)

VI.10 Engineering for optimal growth condition (climate control, watering, etc.)

- 1 = low investment
- 2 = moderate investment
- 3 = high investment
- 9 = missing

VI.13 Fertilizing: Organic

- 1 = 0 to 33% of crops treated
- 2 = 34 to 67% of crops treated
- 3 = 68 to 100% of crops treated
- 9 = missing

VI.15 Reproductive isolation from free-living populations (reproductive barriers)

- 1 = low isolation
- 2 = moderate isolation
- 3 = high isolation
- 9 = missing

VI.16 Controlling breeding partners (controlling recombination and sexual selection)

- 1 = low control
- 2 = moderate control
- 3 = extensive control
- 9 = missing

VI.17 Artificial selection for domesticate improvement

- 1 = no selection performed
 - 2 = selection done, but less than annually
 - 3 = selection common (annually or more frequent)
 - 9 = missing
-

II. Agriculture process variables

VII.1 Degree of dependence on domesticated resources (estimated through caloric intake or productive effort)

- 1 = 0 to 33% of crops
- 2 = 34 to 67% of crops
- 3 = 68 to 100% of crops
- 9 = missing

VII.2 Sociality

- 1 = asocial/solitary
- 2 = ultrasocial/communal
- 3 = eusocial
- 9 = missing

VII.3 Task specialization

- 1 = no agricultural task specialists
- 2 = one or two specialists
- 3 = three or more specialists
- 9 = missing

VII.4 Use of extrasomatic technology

- 1 = absent
 - 2 = present
 - 9 = missing
-

Table 2.2
(continued)

VII.6 Information transmission

- 1 = genetic
- 2 = developmental
- 3 = traditional
- 9 = missing

VII.7 Storage of domesticates

- 1 = absent
 - 2 = seasonal but less than a year
 - 3 = more than a year
 - 9 = missing
-

III. Uses of domesticates variables

VIII.1 Subsistence foods

- 1 = absent
- 2 = present
- 9 = missing

VIII.2 Secondary foods

- 1 = absent
- 2 = present
- 9 = missing

VIII.3 "Drug" foods

- 1 = absent
- 2 = present
- 9 = missing

VIII.4 Raw materials

- 1 = absent
- 2 = present
- 9 = missing

VIII.5 Utensils

- 1 = absent
- 2 = present
- 9 = missing

VIII.6 Labor

- 1 = absent
 - 2 = present
 - 9 = missing
-

IV. Biological impacts of agriculture variables

VIV.1 Population density

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VIV.2 Community size

- 1 = declines
 - 2 = stable
-

(continued)

Table 2.2
(continued)

3 = increases
9 = missing
VIV.3 Number of communities
1 = declines
2 = stable
3 = increases
9 = missing
VIV.4 Catchment area
1 = declines
2 = stable
3 = increases
9 = missing
VIV.6 Longevity
1 = declines
2 = stable
3 = increases
9 = missing
VIV.8 Sex ratios
1 = declines
2 = stable
3 = increases
9 = missing
VIV.11 Age of reproduction
1 = declines
2 = stable
3 = increases
9 = missing
VIV.13 Pathogen load
1 = declines
2 = stable
3 = increases
9 = missing
VIV.14 Nutrition
1 = declines
2 = stable
3 = increases
9 = missing
VIV.16 “Wear and tear”
1 = declines
2 = stable
3 = increases
9 = missing
VIV.19 Ecological diversity
1 = declines
2 = stable
3 = increases
9 = missing

Table 2.2
(continued)

VIV.20 Ecological assemblage

- 1 = declines
 - 2 = stable
 - 3 = increases
 - 9 = missing
-

V. "Sociocultural" impacts of agriculture variables

VV.1 Sedentarism

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.2 Intra-community communication/coordination

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.3 Inter-community communication/coordination

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.4 Intra-community territoriality/ownership

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.5 Inter-community territoriality/ownership

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.6 Intra-community violence

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.7 Inter-community violence

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.8 Intra-community exchange/transmission/diffusion

- 1 = declines
 - 2 = stable
 - 3 = increases
 - 9 = missing
-

(continued)

Table 2.2
(continued)

VV.9 Inter-community exchange/transmission/diffusion

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.10 Kinship structure

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.11 Size of kin group

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.12 Access to and control of resources

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.13 Access to and control of reproduction (social and physical)

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.14 Access to leadership

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.15 Differential survivorship

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.18 Diversity of tasks

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.19 Specialization of tasks

- 1 = declines
 - 2 = stable
 - 3 = increases
 - 9 = missing
-

Table 2.2
(continued)

VV.21 Genetic social control mechanisms

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.23 Authoritarian social control mechanisms

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.28 Pheromonal communication

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.30 Acoustic communication

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

VV.31 Visual communication

- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

Table 2.3
Indices used in the analysis

Index name	Mean of the listed standardized variables	Cronbach's alpha
Agricultural Practices	VII.1, VII.2, VII.3, VII.4, VI.5, VI.6, VI.7, VI.8, VI.9, VI.10, VI.13, VI.15, VI.16	0.908
Agricultural Processes	VII.1, VII.3, VII.4, VII.7	0.831
Agricultural Product Uses	VIII.1, VIII.2, VIII.3, VIII.4, VIII.5, VIII.6	0.899
Demographics	VIV.1, VIV.2, VIV.6, VIV.8, VIV.11	0.907
Community Relations	VV.2, VV.3, VV.4, VV.5, VV.6, VV.7, VV.8, VV.9	0.837
Task Specialization	VV.18, VV.19	0.948
Social Control	VV.20, VV.22, VV.23, VV.24, VV.26	0.749

Results

In this section I present the results of the systematic comparisons. Some of them are not surprising, but others indicate important similarities among all of the cases that, I will argue in the conclusions, indicate convergent evolution. The analyses discussed in this section are all presented in table 2.4, which also gives the six specific hypotheses tested here. These hypotheses were developed during two working group meetings on agriculture in humans and insects held at the Santa Fe Institute in 2014 and 2016 (see Introduction, this volume).

The analysis confirms the first hypothesis, that insects are generally obligate agriculturalists while humans are not. This finding is not surprising, but does raise a general conceptual issue with the analyses of hypotheses 4 to 6. Since the insects are obligate agriculturalists, it is reasonable to ask how one can consider variation in dependence on agriculture as an independent variable, as there is no variation among the insects coded for this project. The answer is that humans and insects are considered equivalent cases here. Future scholars might add nonagricultural insect cases to the dataset to see if the results change, but doing so is not necessary to evaluate hypotheses 4 to 6. For those hypotheses cases are treated as equivalent, just as are environmental context, language group, political organization, or any other variable that might be considered important in the evaluation of a different hypothesis. Here, all that is examined is the impact of domestication on the cases, whether or not they are insects or humans.

The analysis indicates that insects and humans differ in the range of domesticates employed, as expected under hypothesis 2. Specifically, humans use a wider range of domesticates. In Highland Mexico, for example, the three primary crops used were from completely different orders: *Poales* (corn), *Fabales* (beans), and *Curcubitales* (squash) (Bellwood 2005). In contrast, all fungus-farming ants cultivate a single order of fungus, *Agaricales* (see chapter 8, this volume). This illustrates the related fact that not only do insects tend to be obligate agriculturalists, but they also tend to focus on a specific domesticated species. The differences in the range of domesticates used is mirrored by great differences in the management of domesticated crops.

Humans also employ a far greater diversity of crop management methods than do insects, as expected under hypothesis 3. Insects employ very specific management techniques for creating and maintaining substrates, planting crops, controlling weeds and pests, and the like. Insects also tend to have “enclosed” agricultural systems that are isolated from outside environmental fluctuations, pests, weeds, and so on (see, e.g., the discussion in chapter 6, this volume). The most “open” and diverse insect management system occurs among the ambrosia beetles, which cultivate symbiont fungi in tunnels that they bore into dead or stressed trees (Hulcr and Stelinski 2017; chapter 7, this volume). In contrast, because of the diversity of plants humans cultivate and because humans practice agriculture in a wide range of environments, humans require flexible means of management that are adapted to specific plants in specific environments. Nowhere is this clearer than in Peru where specific varieties of potatoes were developed for individual temperature, sunlight, and altitude conditions—perhaps as many as 4,000 different varieties (Brush et al. 1995).

Turning to the impact of agriculture, the analysis indicates that greater dependence on domesticates produces demographic changes, but these are not directly associated with an

Table 2.4
Results of hypothesis tests

H₁ Insects are generally obligate agriculturalists while humans are not.

Independent variable = species
 Dependent variable = VII.1 Degree of dependence on domesticates
 Mann-Whitney U = 10 (p < .000)
 Mean rank: humans = 8.67; insects = 19.50

H₂ Insects and humans differ in the range of domesticates employed.

Independent variable = species
 Dependent variables = Ag. Uses Index
 Mann-Whitney U = 10 (p < .000)
 Mean rank: humans = 17.33; insects = 6.50

H₃ Insects and humans differ in the management of domesticated crops.

Independent variable = species
 Dependent variables = Ag. Process Index; Ag. Practice Index
 Ag. Proc. Index: Mann-Whitney U = 22 (p < .003)
 Mean Rank: Humans = 9.47; Insects = 18.30
 Ag. Prac. Index: Mann-Whitney U = 19 (p < .003)
 Mean rank: humans = 8.86; insects = 17.60

H₄ Greater dependence on domesticates produces demographic changes.

Independent variable = VII.1 Degree of dependence on domesticates
 Dependent variables = Demographics Index
 Tau-b = .342 (p < .043)
 Kruskal-Wallis H = 4.72 (p < .047, 1-tailed)

Mean rank:	0 to 33%	= 7.20
	34 to 67%	= 12.75
	68 to 100%	= 15.58

H₅ Greater dependence on domesticates produces greater task specialization.

Independent variable = VII.1 Degree of dependence on domesticates
 Dependent variables = Task Specialization Index
 Tau-b = .54 (p < .005)
 Kruskal-Wallis H = 9.82 (p < .007)

Mean rank:	0 to 33%	= 6.10
	34 to 67%	= 13.25
	68 to 100%	= 15.71

H₆ Greater dependence on domesticates produces greater social control.

Independent variable = VII.1 Degree of dependence on domesticates
 Dependent variables = Social Control Index
 Tau-b = .62 (p < .006)
 Kruskal-Wallis H = 4.72 (p < .016)

Mean Rank:	0 to 33%	= 3.40
	34 to 67%	= 10.06
	68 to 100%	= 11.25

increase in population or community size, primarily because there is more variation in the population density and community size of groups with a low dependence on agriculture. Thus the underlying notion in hypothesis 4, that population increases with greater dependence on domesticates, is not supported. Looking more broadly at demographics, however, there is an overall increase in population size, fertility, and longevity in more agricultural groups. For example, Ješovnik and Schultz (chapter 8, this volume) describe a colony of *Atta* leaf-cutter ants as being the “equivalent of a large vertebrate herbivore in terms of biomass, life span, and consumption.” A massive transformation of demographics is also seen in humans, whose agricultural communities tend to be larger and to have higher rates of juvenile mortality than nonagricultural ones (Cohen and Crane-Kramer 2007).

As hypothesis 5 suggests, greater dependence on domesticates produces greater task specialization. This relationship makes sense, as the cultivation of domesticates requires individuals to bring select skills and expertise to the process. Among humans these skills often relate to technology, from the creation of tools (e.g., metalwork), to the extraction of raw materials to produce those tools (e.g., mining), and to the movement and marketing of both raw materials and finished products. Agriculture among humans also tends to require specialization in such skills and knowledge that provide continued access to agricultural lands—for example, establishing legal ownership and transfer, enforcing rules of ownership and use, and protecting lands from outsiders. Among insects specialization often takes the form of behavioral variation, with individuals spending their lives gathering raw materials (e.g., leaves), “weeding” crops, or harvesting. Indeed, specialization among insect farming lineages is often produced through specific phenotypic variations (see, e.g., chapters 6, 7, 8, and 14, this volume).

Finally, and as hypothesized, greater dependence on domesticates produces greater degrees of social control. This makes sense for humans, given the need for specialization and protection of agricultural lands. Laws must be followed to ensure access to land and resources and to maintain open markets for the exchange of raw materials, finished goods, and agricultural products. Enforcement of some kind must also be present or those laws are meaningless. The relationship between social control and agriculture is less clear among insects, as they are often eusocial, and thus control of behavior is intrinsic to the group (Wilson 1971). Among insects, this social control takes the form of eusociality in general and phenotypic specialization specifically. Aanen and Anten (chapter 4, this volume) discuss this in terms of kin selection and the social evolution of cooperative behavior, specifically in gut microbiota where nonreproductive symbionts can only increase fitness by maximizing host fitness.

The systematic comparative analysis thus demonstrates that while humans and insects differ in terms of agricultural practices, the evolution of agriculture produces similar changes in social organization. These findings lead to the conclusions I present in the next section.

The Convergent Evolution of Agriculture in Humans and Insects

Many of the chapters in this volume highlight variation in both human and insect agriculture, identifying both unique and shared features among them. These chapters frequently take a comparative approach, either within species or between them, but none takes the systematic comparative approach employed here. The approach here provides a quantita-

tive and statistical perspective on the similarities and differences between human and insect agriculture. The major differences, and those pointed out in many of this volume's chapters, are in the variety of domesticates that are relied upon and the degree to which that reliance is obligate. It is clear that humans have far greater diversity in the domesticates employed than any of the insects and are far less dependent upon those domesticates for survival. Those are interesting findings, but, to me, not as interesting as the ones concerning social similarities and differences.

It is surprising that, despite the diversity in domesticates, the diversity in agricultural practices, and the diversity in species considered in this volume, agriculture appears to have similar social impacts in most of the cases discussed. In the analyses here those similarities are quantified to show empirically that dependence on agriculture is directly associated with greater degrees of task specialization and social control. Agricultural societies are more "politically" and "economically" centralized in both insects and humans. Although not considered here, other chapters (e.g., chapters 3, 4, and 5, this volume) make the case that agricultural societies are more cooperative or integrated than nonagricultural ones.

Clearly agriculture is a successful adaptation. The agricultural insects dominate their environments (e.g., chapters 6, 8, and 14, this volume), and I suggest that it is heightened sociality and social control that provide the ability to do this (chapters 4 and 14, this volume). A dependence on agriculture makes cooperation and specialization necessary (chapters 3 and 8, this volume), but this also means that social control mechanisms to maintain cooperation and division of labor are necessary. What agricultural systems create, then, is a complex, centralized society that can use its coordinated strength to outcompete other organisms in its environment. This is precisely why human agriculture has long been seen as a precursor of states and empires, and it is why agricultural insects can come to dominate their environments.

I argue that these similarities in social impacts across agricultural species points to convergent evolution—not convergence that is rooted in a particular means of getting food, but rather one that is rooted in a food production system that promotes highly coordinated and cooperative behavior. There are other ways of accomplishing this, and many of the social insects have evolved some form of tight coordination and cooperation. But agriculture takes this a step further, and this is where agriculture itself becomes important. Not only do agricultural societies demand coordination and cooperation, but they also provide a more reliable food source than foraging and thus allow for demographic changes that foster overall fitness. Simply put, agricultural societies can outcompete nonagricultural ones in the same environment. They can support more individuals than foraging, they offer ready mechanisms for defense, and they create a context where coordination provides a better survival option to would-be defectors than self-interested behavior.

If agriculture provides all these evolutionary benefits, then one may reasonably ask why agriculture is not more common. Here McGhee (chapter 1, this volume) provides excellent guidance. He points out that agricultural behavior occurs not only in humans and insects, but also among fishes and mollusks, so that it is more widespread among species than one might perhaps think. But McGhee also demonstrates that there are significant functional constraints surrounding the evolution of agriculture so that the conditions allowing agriculture to evolve may be fairly rare. Given the apparent range of organisms that have been found to be agricultural and the strict functional constraints limiting the ability for organisms

to evolve agricultural systems, it is perhaps not surprising that, though a widespread and successful adaptation, agriculture is relatively rare.

Returning to the central question of this volume, whether or not agriculture is an example of convergent evolution, I suggest the systematic comparative analysis presented here provides an obvious answer: yes.

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