Human and Insect Agriculture Codebook, Version 2 (20NOV14)

Species / Culture __Fungus-Farming Ants____

Coder __Ted Schultz____

Comments:

I have created three columns for coding: (i) lower fungus-farming ants (e.g., Cyphomyrmex longiscapus), (ii) non-leaf-cutting higher attine ants (e.g., Trachymyrmex septentrionalis), and (iii) leaf-cutter ants (e.g., Atta cephalotes). I have done this to more accurately reflect transitions that take place in fungus-farming ant evolution subsequent to the origin of farming. For variables that compare non-agriculturalists to agriculturalists, I have, for column (i), compared lower fungus-farming ants to their closest non-fungus-farming relatives, the dacetine ants (including Lenomyrmex, Acanthognathus, and Daceton, among others). In scoring column ii, however, I have compared non-leaf-cutting higher-attine ants with lower attine ants, and in scoring column iii, I have compared leaf-cutter ants to non-leaf-cutting higher-attine ants. While this may sound confusing in the abstract, I think that it is easy to understand when examining the scoring and that it best reflects the purpose of the scoring. (In the human analogy, comparing lower fungus-farming ants with leaf-cutter ants is like comparing subsistence agriculture with industrial-scale agriculture, with the non-leaf-cutting higher fungus-farmers somewhere in between.

I have interpreted "community" to mean "colony" and this works out for most variables, but for some variables it may introduce problems. An ant colony is, functionally, an organism, so when it comes to, e.g., population-biological questions about birth and death rates or density dependence, it is probably better to think at the level of a colony within a population of colonies rather than an individual within a single colony. Given this problem, my scores should be considered tentative and may require correction.

Variables **Comments and references**

I. "Agricultural" practice variables

VI.1 Selecting substrate (universal)
- 1 = low specificity
- 2 = moderate specificity
- 3 = high specificity
- 9 = missing

COMMENTS: Species-specific data are hard to come by, but in general "lower" attines harvest a mixture of insect frass, seeds, flower stamens, and other detritus of plant origin that is presumably not yet invaded by other microbes (fungi or bacteria). Transitional "higher" attines such as Trachymyrmex and Sericomyrmex species may also forage for most of these substrates, but some (most? all?) species may also cut tender shoots of fresh vegetation (flower petals, flower stamens). In the early stages of colony foundation, leaf-cutting ants (Atta and especially Acromyrmex spp.) may also take frass and other non-cut substrates, but mature colonies tend to focus entirely on cut vegetation (leaves in some species, grasses in others). So scoring depends strongly on what is meant by "specificity," but since there is an apparent evolutionary gradation from lower to higher specificity, I am scoring this 1/2/3.

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

COMMENTS: I would guess that daughter nests obtain domesticates from the maternal nest 99% of the time. Over evolutionary time scales, however, replacement fungi are acquired either from the wild or from nests of other fungus-farming ants. But all cultivars are drawn from a limited group of species in the tribe Leucocoprineae (except for a large clade of species in the genus Apterostigma, which cultivates pterulaceous fungi).

VI.3 Planting crops
- 1 = low investment
- 2 = moderate investment
- 3 = high investment
- 9 = missing

COMMENTS: The ants are obligate agriculturalists.

VI.4 Preparing substrate
- 1 = low investment
- 2 = moderate investment
- 3 = high investment
- 9 = missing

VI.5 Dimensions of substrate

Variables **Comments and references**

1 = 2d
2 = 3d
9 = missing

VI.6 Temporal variation in cultivation
1 = discrete (seasonal/crop rotation/fallowing)
2 = continuous
9 = missing

COMMENTS: Exceptions occur in temperate-zone species that are constrained to "hibernate" in winter months, but these are the exceptions to the rule.

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

COMMENTS: There is one domesticate strain in a given colony at a given time (and usually for the entire life of the colony).

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

COMMENTS: Intensive monitoring.

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

COMMENTS: Intensive weeding.

VI.10 Engineering for optimal growth condition (climate control, watering, etc.)
1 = low investment
2 = moderate investment
3 = high investment

9 = missing

COMMENTS: Wet-forest-dwelling fungus-farming ants may require the least amount of work to make their gardens happy, but even they have to worry about, e.g., too much moisture.

VI.11 Pests: Chemical control
1 = 0 to 33% of crops treated
2 = 34 to 67% of crops treated
3 = 68 to 100% of crops treated
9 = missing

COMMENTS: Guesses. The true extent of chemical control (originating in the metapleural gland, possibly the mandibular gland) is unknown. References include Fernandes-Marin, Bot et al., others.

VI.12 Pests: Microbial control
1 = 0 to 33% of crops treated
2 = 34 to 67% of crops treated
3 = 68 to 100% of crops treated
9 = missing

COMMENTS: Guesses. References to come.

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

COMMENTS: This is unclear relative to attine ants. All substrates are organic. In some (all?) species fecal droplets are applied, but their purpose is unclear and may be to provide digestive enzymes originating from the fungus. (Ref. Martin, Bot et al.)

VI.14 Fertilizing: Synthetic chemical
1 = 0 to 33% of crops treated
2 = 34 to 67% of crops treated
3 = 68 to 100% of crops treated
9 = missing

COMMENTS: That's a human thing.

VI.15 Reproductive isolation from free-living populations (reproductive barriers)
1 = low isolation
2 = moderate isolation
3 = high isolation
9 = missing

COMMENTS: This is a very important variable and is poorly understood in most attine ant species. It is important to remember that there are at least two types of free-living populations: (i) genuinely wild-type (ancestral) populations from which the original domesticates were drawn and (ii) populations of "escaped" domesticates. If domestication favors alleles, gene combinations, or other genetic modifications that differ from those present in wild populations (which is almost the definition of "domestication"), then interbreeding with ancestral wild-type (type i) populations will dilute those modifications, whereas interbreeding with type ii wild populations will not, unless the type ii population is sufficiently old and/or selection pressures in the wild greatly differ from selection pressures under domestication. In the case of interbreeding with type i populations, the degree of dilution will vary depending on: (i) the relative effective sizes of the wild and domesticated populations, (ii) the difference between domesticated and wild selection regimes, (iii) the strength of selection in each regime, (iv) the degree of interbreeding (rare vs. common). The current paradigm is that lower attines reacquire their fungi from the wild frequently over evolutionary time periods, but even in lower attine species we have discovered evidence for long-term associations with particular fungal species, suggesting that, when fungi are reacquired, they are reacquired with prejudice, so the ants may be exerting strong selection pressures on single fungal species, in effect "domesticating" the entire wild population, at least on local geographic scales.

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

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

COMMENTS: This is poorly studied, but it is clear that over ecological time periods (multiple ant and fungal generations) the ants are exerting total control over fungal mating, essentially preventing it. In higher attines there are no known wild populations of fungi, yet fungal sex occurs.

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

COMMENTS: The ant equivalent of artificial selection must have occurred in the higher attine ants because the fungi are clearly genetically modified relative to their ancestors (e.g., they are polyploid), although this could also be described as coevolution or symbiotic evolution rather than artificial selection exerted by the ants on their associated fungi. Because artificial selection is usually thought to require intent, I am scoring this 9/9/9.

Variables **Comments and references**

VI.18 Genetic engineering for domesticate improvement (e.g. GMO)
1 = absent
2 = present
9 = missing

COMMENTS: The higher attine domesticates are polyploid, but this does not qualify as deliberate, human-style "genetic engineering." Score: 1/1/1

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

COMMENTS: As far as we know, the larvae depend entirely on the fungus and the adults depend largely on the fungi for nutrition; adults also imbibe and share fruit juice and nectar.

VII.2 Sociality
1 = asocial/solitary
2 = ultrasocial/communal
3 = eusocial
9 = missing

COMMENTS: The leaf-cutting ants, particularly in the genus Atta, qualify as "highly eusocial."

VII.3 Task specialization
1 = no agricultural task specialists
2 = one or two specialists
3 = three or more specialists
9 = missing

COMMENTS: This is poorly studied in lower attine ants. The states as defined are difficult to interpret for lower attine ants. Many ant species practice temporal polyethism, in which adults specialize in different tasks at different stages of their lives. During the lifetime of an individual lower attine worker ant, a significant period may be spent specializing on agricultural tasks. I interpret this to conform to state 2, "one or two specialists." However, ants are capable of performing other tasks if individuals performing those tasks are removed, so in that sense they are not obligate specialists. (But neither are humans, hence my interpretation.) Score: 2/2/3.

VII.4 Use of extrasomatic technology
1 = absent

2 = present
9 = missing

COMMENTS: I code this as state 2 because attine ants construct more or less elaborate nests with tunnels and chambers, ventilation systems, and, in the case of leaf-cutters in the genus Atta, elaborate highways for well-coordinated ant traffic that serves as a model for human traffic algorithms.

VII.5 Use of somatic technology/specialization
1 = absent
2 = present
9 = missing

COMMENTS: Morphological adapatations for fungus-farming are not readily apparent in lower-attine ants, which look very much like non-fungus-farming ants. But they are modified in some ways, espcially with regard to their chemosensory abilities to recognize their resident fungi.

VII.6 Information transmission
1 = genetic
2 = developmental
3 = traditional
9 = missing

COMMENTS: No known culture in ants, although, in addition to genetic transmission, ants can transmit information about, e.g., location of food sources, presence of danger, etc.

VII.7 Storage of domesticates
1 = absent
2 = seasonal but less than a year
3 = more than a year
9 = missing

COMMENTS: Except in a few temperate-zone species, fungus gardens are present year-round and are never fully consumed. Unlike human crops, the garden is at once an active crop and a stored product. I have therefore scored this as state 3 for fungus-farming ants, but alternative scoring is possible depending on the interpretation of "storage," i.e., if it is interpreted as explicitly independent of cultivation (in which case this should be rescored as state 1, absent).

III Uses of domesticates variables

VIII.1 Subsistence foods
1 = absent
2 = present
9 = missing

COMMENTS: The ants require their fungi for survival.

VIII.2 Secondary foods
1 = absent
2 = present
9 = missing

COMMENTS: I scored this as 1/1/1 because the ants grow only one thing and obligately depend on it.

VIII.3 “Drug” foods
1 = absent
2 = present
9 = missing

COMMENTS: The cultivar could serve to provide non-nutritive substances, but this remains unknown. I have scored this as state 1, absent, but it could alternatively be scored as state 9.

VIII.4 Raw materials
1 = absent
2 = present
9 = missing

COMMENTS: In a subset of the Pterulaceae-cultivating Apterostigma species, the ants weave the aerial hyphae together to form a presumably protective, tent-like veil around their gardens. So it would not be accurate to say that the ant fungi never serve a non-food function. Nonetheless, I've scored this as 1/1/1.

VIII.5 Utensils
1 = absent
2 = present
9 = missing

COMMENTS: 1/1/1

VIII.6 Labor
1 = absent
2 = present
9 = missing

COMMENTS: 1/1/1

VIII.7 Protection
1 = absent
2 = present
9 = missing

COMMENTS: There is evidence that fungal coats, present on larvae in (nearly?) all species and "planted" on adults in the winter in at least one temperate-zone species, play a non-nutritive, protective role. See also my comments about the protective veil in VII.4. So I'm scoring this 2/2/2.

VIII.8 Detoxification
- 1 = absent
- 2 = present
- 9 = missing

COMMENTS: The fungus certainly detoxifies plant compounds that would otherwise harm the ants, but since the ants would not independently consume plant material, I have scored this as state 1, absent.

IV. Biological impacts of agriculture variables

VIV.1 Population density
- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

COMMENTS: I am unaware of data comparing population densities in non-fungus-farming vs. fungus-farming ants and in lower vs. higher attine ants. This is complicated by the unit of measure, alternatively number of individuals per unit area vs. number of colonies per unit area. (VIV.3 below would seem to cover the latter, number of colonies per unit area, so I will interpret this variable in terms of number of individuals per unit area.) In spite of these difficulties, rather than code this as unknown, I will guess that population densities, in terms of number of individuals in any given lower fungus-farming ant species (vs. lower fungus-farming ant species in aggregate, an important distinction) is stable relative to their closest non-fungus-farming relatives, whereas I will guess that the population densities of non-leaf-cutting higher attine species are relatively higher (Seal and Tschinkel 2006). Without question the number of individuals of leaf-cutting species per unit area is vastly larger than in other ant species, fungus-farming or not.

Seal, J. N., and W. R. Tschinkel. 2006. Colony productivity of the fungus-gardening ant *Trachymyrmex septentrionalis* (Hymenoptera: Formicidae) in a Florida pine forest. *Annals of the Entomological Society of America* 99:673-682.

VIV.2 Community size
- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

COMMENTS: I am interpreting this as colony size and scoring it 2/2/3.

VIV.3 Number of communities
- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

Variables **Comments and references**

COMMENTS: I am interpreting this as number of colonies per species per unit area. Data are lacking (see above comment for VIV.1); however, leaf-cutter colonies are larger (i.e., contain many more individuals) and, in general, there are less of them per unit area than lower attine colonies, which are smaller (i.e, contain far fewer individuals) and are far more abundant per unit area. In order to capture this I am guessing 2/2/1 rather than scoring this as unknown.

VIV.4 Catchment area
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: Thinking in terms of an ant colony (rather than of an ant species), I interpret this as foraging territory and scoring 2/3/3.

VIV.5 Genetic changes
1 = absent
2 = present
9 = missing

COMMENTS: Relative to non-fungus-farming ants, genetic modifications are present. Likewise, genetic changes separate lower attine, higher attine, and leaf-cutter species.
Nygaard et al. in press; Jesovnik et al. in press.

VIV.6 Longevity
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: I have interpreted this to mean colony lifespan, which is equal to the queen lifespan. This varies across species but I am guessing that, in general, lower attines have colony lifespans similar to those of their non-fungus-farming relatives, whereas higher attines (non-leaf-cutting and leaf-cutting) have relatively longer lifespans. Score: 2/3/3

VIV.7 Age distribution
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: There are some "sociometric" studies out there that may indicate how long adults live and that may quantify the ratio of larvae to pupae to adults in a mature nest, but such studies are few and they focus on non-fungus-farming ants. I cite one below but I think the value of this variable is unknown. Score: ?/?/?
Tschinkel, W. R. 1987. Seasonal life history and nest architecture of a winter-active ant, *Prenolepis imparis*. *Insectes Sociaux* 34:143-164.

VIV.8 Sex ratios
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: This is a subject of interest in ants in general and it applies to the numbers of males vs. females produced by a given colony. I am unaware of known differences in sex ratios between fungus-farming vs. non-fungus-farming ants, or in lower vs. higher fungus-farming ants. There are, however, significant differences in mating frequencies between leaf-cutting ants vs. all other fungus-farming and closely related non-fungus-farming ants. Leaf-cutting ants are multiply mated, leading to diluted levels of relatedness among leaf-cutter worker populations. This is not captured by any of the variables here. Anyway, I'm scoring this 2/2/2 under the assumption that sex ratios don't change, but it could easily be rescored ?/?/?

VIV.9 Birth rate
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: This could be the rate at which individual ants are produced in a colony or it could be the rate at which new colonies (i.e., successful daughter queens) are produced. Larger colonies produce more sexual offspring and more workers per unit time than do smaller colonies, but survival rates may be different. I have scored this ?/?/?

VIV.10 Death rate
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: The "birth rate" comments apply equally here. Again, scored as ?/?/?

VIV.11 Age of reproduction
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: This varies across species, but in general lower attine ants have ages of reproduction similar to their non-fungus-farming close relatives, i.e., colonies usually reach reproductive maturity within one year after nest-founding, so I have scored this as state 2, stable. In non-leaf-cutting higher attines age of reproduction could be longer, but data are difficult to find, so I have also scored this as state 2, stable. In leaf-cutters, it is reached only after 4-5 years, but this is likely a function of colony size -- it takes longer for a large colony to reach reproductive maturity. Final score: 2/2/3

Seal, J. N., and W. R. Tschinkel. 2006. Colony productivity of the fungus-gardening ant *Trachymyrmex septentrionalis* (Hymenoptera: Formicidae) in a Florida pine forest. *Annals of the Entomological Society of America* 99:673-682.
Seal, J. N., and W. R. Tschinkel. 2007. Energetics of newly-mated queens and colony founding in the fungus-gardening ants Cyphomyrmex rimosus and Trachymyrmex septentrionalis (Hymenoptera : Formicidae). *Physiological Entomology* 32:8-15.

VIV.12 Density dependence
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: Based on input from Peter, and given that this variable is kind of meaningless when applied to individuals within a colony, this probably should be interpreted with regard to whether colonies are clustered more or less densely and whether reproductives tend to mate more or less locally. Unfortunately, I'm not sure enough is known about this in fungus-farming ants except that I am fairly certain that in terms of area (e.g., square meters), leaf-cutter colonies occur more sparsely (i.e., are more widely separated) than are colonies of lower attines or of non-leaf-cutting higher attines. This is largely due to ecology because leaf-cutter colonies are bigger and require more territory and more resources. I'm taking a guess and coding this 2/2/1, but it may actually be 2/3/1 based in part on the reference below.
Seal, J. N., and W. R. Tschinkel. 2006. Colony productivity of the fungus-gardening ant *Trachymyrmex septentrionalis* (Hymenoptera: Formicidae) in a Florida pine forest. *Annals of the Entomological Society of America* 99:673-682.

VIV.13 Pathogen load
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: I am assuming this does not include pathogens of the cultivars. Even so, there are few comparative data. I am guessing, however, that pathogen load on fungus-farming ants is similar to pathogen load on non-fungus-farming ants and scoring this 2/2/2.
Schmid-Hempel, P. 1998, *Parasites in Social Insects*: Monographs in Behavior and Ecology. Princeton, New Jersey, Princeton University Press.

VIV.14 Nutrition
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: Fungus-farming ants are nutritionally dependent on their cultivars. For example, unlike all other known ants, they lack the ability to synthesize arginine, which is presumably supplied by their fungi. That said, it is not clear that attine fungal cultivars are nutritionally superior to the food sources (mainly arthropod prey) of their non-fungus-farming close relatives, so I am scoring this as state 2/2/2, stable.

VIV.15 Zoonotics
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: I am interpreting the ant analogue to be diseases that ants can acquire from their gardens. In fact, the garden pathogen Escovopsis is in the Hypocreales, which also includes some insect pathogens, e.g., Beauveria, but there is no reason to believe that diseases of the garden have evolved to infect the ants, so I'm scoring this 2/2/2
Schmid-Hempel, P. 1998, *Parasites in Social Insects*: Monographs in Behavior and Ecology. Princeton, New Jersey, Princeton University Press.

VIV.16 “Wear and tear”
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: Based on input from Peter, this has to do with increased somatic stress and damage caused by an agricultural lifestyle. I am not sure there is any difference between lower attine ants and their non-fungus-growing close relatives, or between lower fungus farmers and non-leaf-cutting fungus-farming ants, but there may be an effect in leaf-cutter ants. Although the mandibles of all ants wear down with age, the mandibles of the cutting caste of leaf-cutting ants become noticeably more worn, especially in the grass-cutting species, so I am tentatively scoring this 2/2/3.

VIV.17 Plastic responses
1 = absent
2 = present
9 = missing

COMMENTS: Peter indicates that this refers to changes in phenotypic traits due to agriculture. Lower fungus farmers and non-leaf-cutting higher fungus farmers are phenotypically very similar to non-fungus-farming ants, but leaf-cutting ants have physical castes, so I am scoring this 1/1/2.

VIV.18 Microbiota
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: It appears that fungus-farming ants harbor integumental microbes that are not present in their non-fungus-farming relatives, although this has been poorly investigated in the latter. Scored 3/2/2 but open to debate.

VIV.19 Ecological diversity
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: According to Peter, this refers to the effect of farming on local ecological diversity. This is a hard one to answer because what we observe now is the outcome of millions of years of evolution during which local ecological assemblages have become modified in response to fungus-farming ants (and vice versa). So even if the advent of, e.g., leaf-cutting agriculture had a major effect on the ecosystem, now that ecosystem has bounced back. Certainly there are all kinds of clear adaptation to leaf-cutters in local plants (e.g., damage-induced expression of fungicidal chemicals) and there are entire ecosystems of arthropods living in leaf-cutter nests and especially in their waste dumps. So I am going to code this as 2/3/3 because for the most part higher attines and especially leaf-cutters have increased the number of ecological niches available to organisms.

VIV.20 Ecological assemblage
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: Since, for the reasons mentioned in the previous comment, the number of species is increased due to higher attines, I think that the ecological assemblage is also increased, but perhaps I am misunderstanding this variable or confusing it with the previous one.

V. "Sociocultural" impacts of agriculture variables

VV.1 Sedentarism
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: With few exceptions (e.g., army ants) all ants are central-place foragers, bound in space by the locations of their nests. Certainly fungus farming ants differ little from their non-fungus-farming close relatives in this regard. Scored 2/2/2

VV.2 Intra-community communication/ coordination
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: Lower fungus-farming ants probably differ little from their non-fungus-farming close relatives in this regard, but there is some reason to believe that non-leaf-cutting higher attines may have more division of labor, including incipient caste polymorphism, presumably requiring increasingly nuanced coordination of activities. The leaf-cutters are clearly much more complex in this regard. Scored 2/3/3

VV.3 Inter-community communication/ coordination
- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

COMMENTS: Whether fungus-farming or not, colonies of the same ant species are essentially competitors. The only need for communication may be to set territorial boundaries. Scored 2/2/2

VV.4 Intra-community territoriality/ ownership
- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

COMMENTS: Although there are inherent genetic conflicts of interest between workers in social insect colonies, it is not clear that they are different in fungus-farming vs. non-fungus-farming species. Likewise, it's not clear that they differ between lower fungus farmers and non-leaf-cutting fungus farmers, all of which are singly mated. Leaf-cutters are multiply mated, however, introducing lower worker relatedness (multiple patrilines) and possible additional conflicts of interest. However, leaf-cutters have crossed a point of no return, i.e., they have transitioned into a highly eusocial state, which, arguably, reduces or makes irrelevant at least some genetic conflicts of interest. Scored 2/2/2

VV.5 Inter-community territoriality/ ownership
- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

COMMENTS: Leaf-cutter colonies must control foraging territories. Scored 2/2/3
Wirth, R., H. Herz, R. J. Ryel, W. Beyschlag, and B. Hölldobler. 2003, *Herbivory of Leaf-Cutting Ants: A Case Study on Atta colombica in the Tropical Rainforest of Panama*: Ecological Studies, v. 164. New York, Springer.

VV.6 Intra-community violence
- 1 = declines
- 2 = stable
- 3 = increases

9 = missing

COMMENTS: Scored 2/2/2

VV.7 Inter-community violence
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: Scored 2/2/3; leaf-cutter colonies compete for resources.

VV.8 Intra-community exchange/ transmission/ diffusion
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: UNCLEAR HOW THIS DIFFERS FROM VV.2, AT LEAST FOR ANTS. Ants lack culture. Information is transmitted across generations genetically except for information about food sources, sources and occurrences of danger, presence of brood, presence of noxious substrates, etc. Leaf-cutting ants are arguably more sophisticated with regard to such information transmission compared to the non-leaf-cutters. Scored 2/2/3.

VV.9 Inter-community exchange/ transmission/ diffusion
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: It's doubtful that any information is exchanged between colonies except perhaps information about territory. Scored 2/2/2.

VV.10 Kinship structure
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: The entire colony ("community") is a closely related family with, in lower attines and non-leaf-cutting higher attines, a single mother and father (deceased but represented by stored sperm). In leaf-cutters it is a family with a single mother and multiple fathers, so it is somewhat less related in comparison. I have therefore scored this 2/2/1, but those scores may be misleading in the intended context of this variable, and perhaps should instead be 2/2/2.

Variables **Comments and references**

VV.11 Size of kin group
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: The size of the kin group is identical to the colony ("community") size, so the answer to this question is the same as for VIV.2 and may be misleading in the intended context of this variable. Scored 2/3/3.

VV.12 Access to and control of resources
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: The abundance/size of resources certainly changes in the evolutionary transition from non-leaf-cutting to leaf-cutting, but individual access to resources probably does not. Scored 2/2/2.

VV.13 Access to and control of reproduction (social and physical)
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: Within a colony, access to reproduction is limited to male (son) and queen (daughter) offspring except that, in many "primitive" ants, including non-leaf-cutting fungus-farming ants, workers can produce haploid (male) eggs. This ability is lost in leaf-cutters, so I have scored this 2/2/1.

VV.14 Access to leadership
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: Irrelevant in ants, which are leaderless.

VV.15 Differential survivorship
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: Some tasks in ant colonies are higher-risk than others. Although this is poorly studied, in lower attine ants and likely in most (but perhaps not all) non-leaf-cutting higher-attine ants, individuals are subject to temporal polyethism, carrying out lower-risk within-nest tasks earlier in life, and carrying out higher-risk outside-nest tasks (e.g., foraging) later in life. There is probably some temporal polyethism in leaf-cutters, too, but there is also morphological caste polymorphism, which means that castes of a certain size are automatically assigned to high-risk jobs, so I have scored this 2/2/3.

VV.16 Cultural evolutionary mechanisms for selection of behaviors and their transmission
- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

COMMENTS: No culture in ants, so 9/9/9.

VV.17 Genetic mechanisms for selection of behaviors and their transmission
- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

COMMENTS: It's all about genetics in ants, so 3/3/3.

VV.18 Diversity of tasks
- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

COMMENTS: The diversity of tasks would appear to increase across my three categories, or at least in the transition from non-leaf-cutting and leaf-cutting higher attines, so it should be scored 3/3/3 or 3/2/3.

VV.19 Specialization of tasks
- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

COMMENTS: Scored 2/3/3.

VV.20 Informal social control mechanisms (religion/ tradition)
- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

COMMENTS: 9/9/9.

VV.21 Genetic social control mechanisms
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: I don't think "control" is the appropriate word here because in ants there is no centralized controlling individual or individuals. That said, one could regard the "controllers" as particular genes/gene complexes that exert control over other genes and over phenotypes. But I interpret the spirit of this question as addressing whether genetically based mechanisms for coordinating social systems are stable, increase, or decrease, and score this 2/2/3..

VV.22 Communal social control mechanisms
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: According to Peter, this addresses traditions that control behavior and is likely irrelevant to ants, so 9/9/9 unless it encompasses behaviors like worker policing.

VV.23 Authoritarian social control mechanisms
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: Absent in ants.

VV.24 Traditional coordination of labor and tasks (ritual/ religion/ mythology)
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: 9/9/9.

VV.25 Genetic coordination of labor and tasks
1 = declines

2 = stable
3 = increases
9 = missing

COMMENTS: Since all behaviors in ants are under genetic control, this variable may be redundant with a number of others. Scored 2/2/3.

VV.26 Authoritarian coordination of labor and tasks
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: 9/9/9

VV.27 Communal decision making
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: 9/9/9, although all "decisions" in an ant colony are in a sense "communal," certainly in contrast to authoritarian.

VV.28 Pheromonal communication
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: 2/2/3

VV.29 Tactile communication
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: 2/2/2

VV.30 Acoustic communication
1 = declines
2 = stable
3 = increases
9 = missing

Variables **Comments and references**

COMMENTS: 2/2/2

VV.31 Visual communication
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: The sister group of the fungus-farming ants is a group of specialized predators, most with large eyes. Fungus-farming ants, in contrast, are not known for their remarkable vision. 1/2/2.

VV.32 Linguistic communication
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: 9/9/9, unless we regard pheromones and stridulation as a form of language. 9/9/9

VV.33 Written communication
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: 9/9/9

VV.34 Environmental information extraction--observation / interaction
1 = declines
2 = stable
3 = increases
9 = missing

COMMENTS: According to Peter, this is about contrasting the ability to monitor and process information about the environment in non-farming and farming ants (and between my other two categories of farming ants). I can't say that lower fungus-farmers are better at monitoring their environments than non-fungus-farmers. It's not even clear that they monitor/analyze different aspects of the environment. Likewise the non-leaf-cutting higher attines. But leaf-cutters have increased abilities to recognize the plants they're attacking, and probably to recognize other environmental features as well. 2/2/3

VV.35 Environmental information extraction--dedicated organic sensors
1 = declines
2 = stable
3 = increases

9 = missing

COMMENTS: Ants have the usual insect sensory apparati as well as extra-good odor receptors. It's not yet clear whether fungus-farming ants are even better at smelling than their non-fungus-farming close relatives, but there is reason to believe they are modified for detecting the odors and tastes of both their fungal cultivars and fungal and bacterial garden pathogens. I am therefore scoring this as state 3/3/3, increasing across all three categories.

VV.36 Environmental information extraction--technological sensors
- 1 = declines
- 2 = stable
- 3 = increases
- 9 = missing

COMMENTS: 9/9/9