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The Economic Origins of Ultrasociality

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Abstract: Ultrasociality refers to the social organization of a few species, including humans and some social insects, having complex division of labor, city states and an almost exclusive dependence on agriculture for subsistence. We argue that the driving forces in the evolution of these ultrasocial societies were economic. With the agricultural transition, species could directly produce their own food and this was such a competitive advantage that those species now dominate the planet. Once underway, this transition was propelled by the selection of within-species groups that could best capture the advantages of (1) actively managing the inputs to food production, (2) a more complex division of labor, and (3) increasing returns to larger scale and larger group size. Together these factors reoriented productive life and radically altered the structure of these societies. Once agriculture began, populations expanded as these economic drivers opened up new opportunities for the exploitation of resources and the active management of inputs to food production. With intensified group-level competition, larger populations and intensive resource exploitation became competitive advantages and the "social conquest of earth" was underway. Ultrasocial species came to dominate the earth's ecosystems. Ultrasociality also brought a loss of autonomy for individuals within the group. We argue that exploring the common causes and consequences of ultrasociality in humans and the social insects that adopted agriculture can provide fruitful insights into the evolution of complex human society.

Keywords: agricultural transition, division of labor, major evolutionary transitions, multilevel selection, surplus production, totipotency, ultrasociality

> "But the mere fact that organisms and societies evolve by various selective mechanisms is not the whole (superorganism) story, for it does not tell us the fundamental reasons that ants and termites live social rather than solitary lives. Those reasons are to be found in economics—in the science that concerns itself with how resources are utilized and allocated." – Michael Ghiselin (2009, 243-244).

1. Introduction

With the widespread adoption of agriculture some 10,000 years ago human societies took on some important characteristics shared with social insects—ants and termites in particular—that also engage in the production of their own food. These characteristics represented a sharp break in the evolutionary history of these lineages and led to two important outcomes (1) ecosystem domination as a product of a dramatic increase in population size and much more intensive resource exploitation and (2) the suppression of individual autonomy as the group itself became the focus of economic organization. The evolution of agriculture in fungus-growing ants and termites, and in human societies, is an example of convergent evolution—the independent evolution of similar characteristics in species not closely related. In terms of genetics, ants, humans and termites could hardly be more different. Yet in all three lineages similar patterns of economic organization emerge through similar selection pressures. We use the term ultrasociality to refer to these lineages and we address the question of its origin through the fundamental question of evolutionary biology: "where did something come from and what were the selection pressures that favored its spread?" (Blute 2010, 13). We follow Campbell (and Darwin) in insisting that the evolution of human ultrasociality is a consequence of some of the same mechanistic (that is, not consciously directed) evolutionary forces that govern other species. Foley (2008, 164) calls the adoption of agriculture by ants and humans a case of "convergent selection." In the struggle to survive, agricultural ants and agricultural humans face similar problems and selection tends to favor similar solutions. We fully recognize that the details of ultrasociality in humans play out in ways that are mediated by human intentionality and cultural norms.

1.1 What is ultrasociality?

There is no general agreement in the use of the term ultrasociality, partly due to the lack of consensus in the biological and social sciences in classifying social behavior. The many definitions of ultrasociality are conflicting, even among the same authors. For example, Campbell sometimes classifies ants, humans, and termites as ultrasocial (Campbell 1982) but other times refers to ultrasociality as large scale cooperation among unrelated individuals (Campbell 1983; and also Turchin 2013). This seems to restrict ultrasociality to humans but remarkable examples of non-kin altruistic behavior in non-human populations are being documented, for example, the recent discovery of cooperative brood raising by two different species of spiders (Grinsted, Agnarsson & Bilde 2012). E.O. Wilson (1975), although he does not use the term ultrasocial, considers humans to be one of the four pinnacles of social evolution along with colonial invertebrates, social insects and non-human mammals. Richerson and Boyd (1998) use the term ultrasocial to describe humans after agriculture, but do not include social insects in their definition. Following Wilson and Hölldobler (2005, 13368), we reserve the term eusocial to refer to social insects and a handful of other species having an advanced level of colonial existence and a sharp division between sterile and reproductive castes.[1]

We begin with Campbell's (1982, 160) definition of ultrasociality: "Ultrasociality refers to the most social of animal organizations, with full time division of labor, specialists who gather no food but are fed by others, effective sharing of information about sources of food and danger,

[1] To add to the confusion, Wilson (2012, 16) recently classified humans as eusocial: "*Homo sapiens* is what biologists call 'eusocial', meaning group members containing multiple generations and prone to perform altruistic acts as part of their division of labor."

self-sacrificial effort in collective defense. This level has been achieved by ants, termites and humans in several scattered archaic city-states." We confine our discussion of ultrasociality to human, ant, and termite societies that actively manage food production.[2] The extent of differentiation, collaboration, and cohesion of agricultural social species place them in a qualitatively different category. This demarcation is, of course, somewhat arbitrary and we recognize the antecedents of both managed agriculture and the specific characteristics of ultrasocial societies. We argue that the change from foraging wild plants and animals to the active management of agricultural crops was a particularly powerful impetus for the human transition to ultrasociality.[3] To clarify our use of this term, by our classification leafcutter (attine) ants would be both eusocial and ultrasocial. Complex human societies with agriculture would be ultrasocial but not eusocial. Human hunter-gatherer bands are not ultrasocial, although the antecedents of ultrasociality are clearly present in these societies, as we discuss below. A striking difference between insects and humans is the presence of non-reproductive castes in the former.[4]

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[2] Mueller et al. (2005) include ambrosia beetles as having complex agriculture. We do not include them because little is known about their social behavior such as their task-partitioning activities (Mueller et al. 2005, 575).

[3] Precisely defining ultrasociality is difficult partly because of the ambiguity of the transition from "non-ultrasociality" to "ultrasociality". There also exist innumerable gradations from cooperative societies to supercolonies (see the discussion in Moffett 2012). Also, cause and effect can be difficult to disentangle. So "managed agriculture" can be both an impetus for the evolution of ultrasociality and a characteristic of full-blown ultrasocial societies. Turchin (2013, 62) writes of the stages of ultrasociality: "Thus, it is perhaps best to think of multiple transitions instead of a single one."

[4] However, as a reviewer pointed out, a human variation on "non-reproductive" castes is the grandmother hypothesis (Williams 1957; Hawks 2003). Humans are unique among primates in that females live for an unusually long time after menopause. It is hypothesized that postmenopausal women contribute knowledge and skills, including child-rearing, that enhance the fitness of the group.

We recognize that the term ultrasocial is controversial but we insist that human and insect societies that practice managed agriculture are fundamentally different from the small-scale foraging societies from which they evolved.

1.2 Agriculture and Ultrasociality

Mueller et al. (2005, 564) list the defining features of agriculture: (1) habitual planting, (2) cultivation, (3) harvesting, and (4) nutritional dependency on the crop (obligate in insects and effectively obligate in humans). The active cultivation of crops calls forth a similar configuration of production in dissimilar species. The production of crops is a physical process calling forth similar kinds of economic efficiencies. The prime examples of agricultural insect societies are the attine ants of the New World tropics (comprised of about 200 different species) and the fungus growing termites of the Old World tropics (comprised of over 300 species). All the existing species of fungus growing ants and termites apparently arose from a single common ancestor for each line (Aanen & Boomsma 2006; Mueller & Gerardo 2002). Old World termite agriculture arose between 24-34 million years ago, and New World ant agriculture appeared about 50 million years ago. These two independently evolved insect agricultural systems, and human agricultural systems, are examples of mutualistic symbiosis, reciprocally beneficial relationships between genetically distant species. Aanen and Boomsa (2006, R1014) write of the agricultural transition in fungus growing ants and termites: "No secondary reversals to the ancestral life style are known in either group, which suggests that the transitions to farming were as drastically innovative and irreversible as when humans made this step about 10,000 years ago."

Humans made the transition to agriculture in perhaps seven or eight regions of the world at various time after the beginning of the Holocene some 12,000 years ago. Each case was different in terms of the kinds of plants that were domesticated and the kinds of complex societies that evolved. All of them radically altered their surrounding ecosystems compared to the earlier hunter-gatherer presence. Those agricultural transitions that evolved complex state societies showed a remarkable similarity. The convergent evolution of state societies after agriculture is nothing short of astonishing. Wright (2004, pp. 50–51) describes the results of parallel evolution from hunter-gatherers to civilization in Europe and the Americas:

> What took place in the early 1500s was truly exceptional, something that had never happened before and never will again. Two cultural experiments, running in isolation for 15,000 years or more, at last came face to face. Amazingly, after all that time, each could recognize the other's institutions. When Cortés landed in Mexico he found roads, canals, cities, palaces, schools, law courts, markets, irrigation works, kings, priests, temples, peasants, artisans, armies, astronomers, merchants, sports, theatre, art, music, and books. both sides of the earth.

In broad outline, the same cultural patterns and institutions also evolved in the Indus Valley, the Far East and the Middle East. This suggests the existence of some common underlying forces driving the evolution of human ultrasociality—the transformation of hunter-gatherers into agriculturalists—that transcend human intentionality and the specific characteristics of pre-agricultural cultures (Gowdy & Krall 2014).

1.3 Evolutionary convergence driven by the economics of production

A key evolutionary innovation that led to ultrasociality was a change in the economic organization of production, namely, the move from foraging-for-livelihood to managed agriculture (Gowdy & Krall 2013, 2014). Ultrasociality as expressed in the active management of crops is a reconfiguration of society around a cohesive and internalized dynamic of intensive resource exploitation and, where environmental conditions permit, expansion. The active management of the supply of food offers a species the opportunity for expansion and engages interconnected and mutually reinforcing economic drivers that give a common structure and dynamic to agricultural societies. These include: (1) actively managing inputs to food production, (2) capturing the advantages of a complex division of labor, and (3) capturing the competitive advantages of larger scale and larger group size. Selection pressures favored groups with the potential to reconfigure themselves to take advantage of economic efficiencies associated with agriculture. The new group dynamic was not simply a larger aggregation of individuals that comprised the group. The economic organization of the group itself more rigidly defined the role of individuals within it and came to constitute a cohesive whole with a unique evolutionary dynamic. In this transition economic life was restructured in similar ways in very dissimilar species. Although ultrasociality is a well-established field of study, to date the importance of the evolution of the economic configuration of ultrasociality has not been adequately explored.

1.4 The consequences of ultrasociality

The consequences of the ultrasocial transformation are strikingly similar in human and social insect societies. The first similarity is the dominance of the world's ecosystems by ultrasocial species, what Wilson (2012) refers to as "the social conquest of earth." In only a few thousand years, humans made the transition from being just another large mammal living within the confines of local ecosystems, to a species dominating the planet's biophysical systems. Similarly, social insects dominate the ecosystems within which they occur. One of the most complex social insects, leaf cutter ants, live in large cities of millions of individuals devoted to a single purpose—the cultivation of a specific kind of fungus that feeds the entire colony (Hölldobler & Wilson 2011).

A second similarly is the reduction in individual autonomy that occurs with the differentiation of individuals around agricultural production. Members of ultrasocial societies become profoundly interdependent and a large proportion of the day-to-day lives of individuals is spent in specialized productive activities. In this sense individual autonomy is suppressed for the good of the ultrasocial agricultural group. In ultrasocial ant societies, compared to non-ultrasocial ants, individuals have less flexibility in the tasks they perform, they have a limited repertoire of tasks compared to all those present in the group, and they apparently have a loss of individual intelligence (Anderson & McShea 2001). Although less extreme than with social insects, a loss of individual autonomy is also seen in human societies after the adoption of agriculture. With the advent of large-scale agriculture, individuals were designated to a more narrowly defined role in the material reproduction of society. They were born into distinct and rigid castes that determined their life trajectories and occupations. The subjugation of human individuals is, of course, mediated by culture and, unlike insects, humans often resist this subjugation. Ant and termite castes are based on different phenotypes while the human division into castes and occupational classes is based on culture, customs, and social institutions.[5]

It is difficult to appreciate the enormity of the break with the past that ultrasociality represents. Biologists rightly note that population explosions are common as new species move into new territories with exploitable resources thereby increasing their biotic potential. Populations rise and fall regularly, sometimes dramatically, as resources wax and wane. But ultrasociality is unique—it is characterized by an expansion of biotic potential which is more than simply moving into a new geographic area with a new source of food. Rather it is the active harnessing of the inputs to food production and a reconfiguration of the group in order to do so. Ultrasocial species are configured to actively produce and expand their food supply rather than wait for nature to provide it. With the onset of ultrasociality, economic factors emerged and

[5] But see Cochran and Harpending (2009) who argue that the development of agriculture greatly accelerated the rate of human biological evolution.

coalesced in such a way that the social/economic development of the diverse species that practiced it shared a similar group pattern and dynamic—a new mode of production that gave them a decisive evolutionary advantage.

In the following pages we first discuss the general characteristics of the major evolutionary transition to ultrasociality with agriculture in the context of current controversies about multilevel selection (MLS). Section 3 is a general discussion of ultrasociality in terms of the radical changes in human and insect societies, focusing in on the common economic drivers behind ultrasocial transitions. Section 4 focuses specifically on the human agricultural transition. In section 5 we discuss the social consequences of ultrasociality—ecosystem domination and the suppression of individual autonomy. We end in section 6 with some reflections on the implications of the ultrasocial transition for current human society.

2. Ultrasociality and Multi-Level Selection

Ultrasociality is both extremely rare and extremely successful. It is difficult to explain in terms of individual selection. Why should individuals sacrifice their own interests for the good of the group? A growing number of authors argue that traditional explanations, kin selection and reciprocal altruism, cannot adequately account for the numerous examples of cooperation among unrelated individuals and even unrelated species (Grinsted, Agnarsson, & Bilde 2012; Nowak, Tarnita & Wilson 2010).[6] These traditional explanations are challenged to explain the extreme interdependence and coordination that occurs with agriculture. It is problematic (in the case of humans) to make the claim that the extreme cooperation among individuals to the point of loss of individual autonomy is connected to the survival of genes over generations. MLS is especially

[6] Turchin (2013, 70) writes: "Although other approaches are certainly possible, I believe that the most fruitful avenue of resolving the puzzle of ultrasociality is provided by the theoretical framework of cultural group (or, better, multilevel) selection."

important in expanding the currency of evolution beyond the gene to include economic configuration. This is essential when it is clear that the economic configuration of diverse species around agriculture looks the same and clearly gives each species a competitive advantage. MLS theory argues that the basic principles of Darwinian evolution—variation, selection, and retention—operate at different levels. Darwinism can be generalized to explain the evolution of genes, individual organisms, or groups of organisms. MLS provides a framework to understand why ants, termites and humans developed similarly as groups once they began the transition to agriculture and how this created evolutionary paths that led these diverse species in similar directions. Unraveling the commonality of the evolutionary processes that bring diverse species to a similar place allows us to use MLS to examine the importance of economic drivers operating at the group level as a different currency of evolution. We are not discounting the importance of the play of evolution on the gene we are simply adding another element to the complex matrix of evolution.

2.1 Multilevel section and group-level traits

Despite some resistance to MLS, there is a growing interest in applying the concept more broadly to include human social evolution (Boehm 1997, 1999, 2012; Gowdy & Krall 2013, 2014; Hodgson & Knudsen 2010; Reeve 2000; Boyd and Richerson, 2002; Richerson & Boyd, 2005; Smaldino 2014; Turchin 2013; van den Bergh & Gowdy 2009; Wilson 1997; Wilson & Gowdy 2013, 2014). Boyd & Richerson (2002) argue that social learning in humans leads to gene-culture co-evolution and selection for group-level traits. Social scientists and biologists have acknowledged the importance of the co-evolution of genes and culture (Richerson & Boyd 2005; Wilson 1997). Smaldino (2014) has explored the emergence of group-level traits through, among other things, evolutionary competition between groups. Caporael (1997) and Caporael &

Garvey (2014) use the concept of "core configuration"—the scaffolding of smaller to larger social and economic units—to examine the emergence of group-level traits. The group selection approach has been fruitfully applied to the evolution of cooperation (Sober and Wilson 1998), the evolution of state societies (Spencer 2010), and the role of warfare in early agricultural societies (Choi & Bowles 2007; Turchin 2006). Campbell (1982, 161) provides guidance as to how group selection works in human societies:

> Much hypothesized cultural evolution must achieve a kind of "group selection" precluded among vertebrates at the purely biological level and achieved by invertebrates only through caste sterility. The models of cultural evolution of Boyd & Richerson (1980) help here. Non-linear, multiple-social-parent transmission, with a majority amplifying effect, pushes face-to-face groups to internal unanimity in the absence of selection. This provides the raw material of within group homogeneity and group-to-group heterogeneity prerequisite for group selection. Such selection would come through differential group success, differential growth, conquest with cultural imposition, voluntary attraction of converts, imitation etc.

While it is clear that culture can promote homogeneity and cohesion within groups, it leaves ambiguous the common evolutionary process at work for both humans and insects. One cannot reasonably argue that insects have culture in the way that humans do. The explanation for homogeneity and cohesiveness of the insect colony is usually attributed to genetic relatedness while that of humans is most often attributed to culture. A more complete parsing of the MLS literature with regard to the common evolutionary matrix at work for both social insects and humans who become ultrasocial is warranted.

2.2 MLS1 and MLS2

The multilevel selection literature divides selection into two types, multilevel selection one (MLS1) and multilevel selection two (MLS2). As described by Okasha (2006) multilevel selection one (MLS1) is a case where certain traits (such as altruism, to use D.S. Wilson's trait group example) may decrease individual fitness but enhance the competitiveness of groups that practice it. Therefore groups having many altruists have a competitive advantage over groups that have few and altruism gets reproduced (Okasha 2006, 178). Altruism is an individual (particle) level trait but the group dynamic enhances the probability that it will be reproduced. With MLS1, natural selection still operates at the individual level and also at a group level, but both levels of selection work on "a single evolutionary parameter"—in this case altruism (Okasha 2006, 178). With MLS1 altruism is still an advantage to the individual because by enhancing group survival it also enhances individual survival.[7] Most examples of group selection in the literature fall into the MLS1 category –"traits that can be easily measured in individuals but require group selection to evolve because they are locally disadvantageous" (D.S. Wilson 2010, section XIX).[8]

2.3 Emergent characteristics in humans and social insects

The evolutionary picture becomes more complicated when the play of selection at the group level is not on a single trait but on a cluster of emergent characteristics that define the group and make it a whole. Okasha (2006, 178) says it succinctly: "In MLS2, individuals and groups are both 'focal' units, and the two levels of selection contribute to different evolutionary changes, measured in different currencies." According to Okasha (2006, 112): "Emergent characters are often complex, adaptive features of collectives, which it is hard to imagine evolving except by

[7] Technically, the fitness of an altruist in a group of altruists is higher than the fitness of a non-altruist within a group of non-altruists. A non-altruist could still have an advantage in a group of altruists.

[8] This level of selection might be used to describe the nature of the group-individual tradeoff in hunter-gatherer societies (see the essays in Gowdy 1998). Individuals are altruistic because this enhances the survival of their group, and thus their own survival. The fitness of the group can be characterized by the average fitness of its members (Michod 2005, 970). Moreover, each individual within hunter-gatherer societies is important for the well-being of the group. For example, in small hunter-gatherer bands the loss of an individual hunter or gatherer represents a significant loss to the group. The good of the individual is clearly integrated with the good of the group.

selection at the collective level." Okasha (2006, 229-230) accepts the standard view of MLS2 but points out that it applies only to the later stages of an evolutionary transition (after the collective units have formed and are replicating). In the early transitional stages cooperation must spread among the particles so that they will eventually give up their individuality and form discrete collectives. Thus the "emergent characters" present difficulties for multilevel selection because it is a chicken and egg problem. This is described by Okasha (2006, 113) in reference to work by Williams (1992), and Sober and Wilson, (1998): "…the emergent character requirement conflates product with process." This may be true, but it does not constitute an intractable problem if sufficient attention is paid to both process and product, that is, the emergence and configuration of the group-level trait. MLS2 needs to capture the process that forms an altered group that then has sufficient cohesion and force to become a focal point of selection. The process must account for the emergent characteristics which configure the group that then becomes a unit of selection.

The commonality in the structure and dynamic of ant, human, and termite societies that develop large scale agriculture is not merely coincidental. MLS2 does not sufficiently sort through the process/product problem and it delineates the fitness criteria as successful collectives producing more offspring collectives. This does not capture a basic attribute of the fitness of a food producing group, namely, its internal expansionary dynamic. Fitness is not simply that more new colonies form. It is that any single colony can grow to an enormous size.[9] With agriculture the collective is extended over generations. Some ultrasocial social insects develop new collectives from existing collectives when a queen flies away and starts a new nest. The

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[9] One "supercolony" of Argentine ants in California possibly contains a trillion individuals (Moffett 2012, 925). We should point out that deciding which ants depend on agriculture is not an easy matter. Argentine ants manage scale insects whose droppings (honeydew) provide about 70% of the ants' diet, but they are also opportunistic foragers.

cumulative effect is different for humans who do not start new colonies with the same ease and sharp delineation as agricultural insects. Again, we argue that, although the details of expansion may differ between humans and social insects, the economic drivers of that expansion are similar.

Smaldino has expanded the discussion of group selection with his refinement of MLS2. His discussion helps guide our thinking about the common evolutionary story of insect and human ultrasociality. The group is defined by Smaldino by the emergence of group level traits that "involve organized collections of differentiated individuals" (Smaldino 2014, 243). These within-group traits constitute between-group differences that become the focus of selection. Smaldino (2014, 249) is clear: "In order to explain group level traits, the emergence of differences among individuals within a single group, and the subsequent organization of those differentiated individuals and their coordinated behavior must be accounted for." In this framework we must identify the commonalities in both the process of differentiation and the commonalities in the reconfiguration of that differentiation into a whole if we are to explain the common structure and dynamic of societies of ants, humans, and termites. The configuration of the whole then defines its group level trait and the unit of selection.[10]

Smaldino (2014, 248) specifically discusses the homogeneity of the group using the example of social ants: "interdependent collaboration of workers, soldiers, drones and queens" is promoted through genetic relatedness … the colony is in some sense an extended phenotype of the queen." The conclusion is that differentiation within the colony comes about through environmental stimuli that trigger phenotypic differences and cohesion is a largely a matter of

[10] We recognize that the claim that group-level traits are units of selection is controversial. See Santana and Weisberg's (2014) commentary on Smaldino (2014). But we believe that "strong" group level traits are a legitimate focus of analysis. See Smaldino's reply (2014, 282-283) and the excellent commentaries on the group selection controversy by Wilson (2010) and Lloyd (2012).

genetic relatedness, although positive assortment through group structure may also play a role. He contrasts this to the situation found in humans where between-group differences, and within-group cohesiveness, are "triggered culturally rather than genetically requiring different explanations for their emergence and evolution." Differentiation and cohesion is culturally mediated, but placing too much emphasis on the different mechanisms in social insects and humans that bring about differentiation and cohesion is a diversion from identifying the commonality among these diverse lineages. The organization of agricultural production promotes a more elaborate differentiation of individuals (division of labor). In a sense it does not matter how species attain differentiation as long as they do so. In all cases the extensive division of labor around the active management of food production creates a profound interdependence. The extreme differentiation of occupations brings about a much greater cohesion and co-dependence in production and rewrites the boundaries between the individual and the group.

3. Agriculture and the economic drivers of ultrasociality

The common evolutionary story of ultrasociality, that is, the emergence of group level traits leading to agricultural societies can be understood as a matter of economic organization. The importance of economic organization has been noted but has not been developed in a systematic way. With control of the production of food, there came a tremendous potential to expand the subsistence base, thereby expanding the potential for population growth.[11] In the transition to agriculture a common recipe or program took hold and led very different species in the same direction. Human and insect agricultural societies exhibit both a complex interdependence and a

[11] This potential is obviously limited if resources are limited in a particular place. The expansion of human agriculture, for example, was limited in Papua New Guinea because of topography and the reliance on root and tree crops rather than cereals (Diamond 1997a, 148).

dynamic of expansion.[12] When these lineages started managing food production some basic economic laws gave them such an evolutionary advantage that they came to dominate the planet. We separate our discussion of economic drivers for purposes of highlighting them but we acknowledge that in reality they are mutually reinforcing and intertwined. For example, the division of labor is both a characteristic of ultrasocial systems and a preadaptation that enabled ultrasociality. The division of labor and economies of scale are intimately connected.

3.1 Actively harnessing the inputs to food production

With agriculture it was possible for humans, ants, and termites to interject themselves directly into the food production process. Humans could actively capture solar energy in crops that replaced other vegetation and tap into stocks of agricultural inputs like fertile soil and water for irrigation. The economist Georgescu-Roegen (1976) pointed out that stocks of inputs like the nutrients in fertile soil have an advantage over flows because they can be used at any rate and can therefore make possible a larger and more complex production process (Georgescu-Roegen 1976).[13] More energy and other resources can be directed to food production. E. O. Wilson (1987, 6) points out the importance to ant agriculture of tapping into resource stocks: “What unusual or unique biological traits have enabled the ants to remain abundant and relatively unchallenged morphologically for over 50 million years? The answer appears to be that the ants were the first group of predatory eusocial insects to both live and forage primary in the soil and

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[12] In terms of the increase in size and complexity, human and insect societies differ. Insect ultrasocial species expand their territories by duplicating colonies. So that, past a certain point, total growth of numbers comes from duplicating identical modules without an increase in the social complexity of individual models. Human institutions such as markets and trade call forth increases in complexity as total populations increase.

[13] Georgescu-Roegen is best known for his work for his work on the dependence of industrial societies on stocks of scarce and finite fossil fuels, but he also wrote extensively about the unsustainable use of fertile soil.

rotting vegetation on the ground." This gave them an almost unlimited supply of nutrients to support their agriculture. Hölldobler & Wilson (2011, 2-3) write: "The leafcutter ants are partly comparable in their achievement to that of human agriculturalists. And they have attained a breakthrough of organic evolution: by utilizing fresh vegetation on which to grow their crops, they have tapped into a virtually unlimited food source." Perhaps forest floor vegetation is not technically a stock but it essentially amounts to a stock for ant agriculturalists. Attine ants commandeer vegetation away from species that would otherwise use it.

Tainter et al. (2006, 52) in discussing energy transformations in complex societies argue that the evolution of ant agriculture shows two major resource transitions. The first was the adoption of agriculture itself—based on actively growing fungus on high-quality insect droppings. This transition was highly successful but the size of the colonies was limited by the scarcity of quality insect droppings. The second transition was a shift from collecting droppings to growing fungus on much more abundant leaves and other organic material. Each step in ant social evolution not only paved the way for the next step, it also came with increasing complexity and regimentation of ant society which itself enhanced the ability to tap into the stock.

3.2 The complex division of labor

An important economic driver of ultrasociality and its evolution is the expansion and sharpening of the division of labor. Both biologists and economists have extensively studied the division of labor. Biologists have identified the benefits of division of labor in social insects (Beshers & Fewell 2001; Franks 1987; Oster & Wilson 1978; Wilson 1971). Hölldobler & Wilson (2009, chapter 5) give numerous examples describing its advantages. In the case of ants, the number of total tasks increases with the total number of ants sampled in a colony (Hölldobler & Wilson

2009, 125). Holbrook, Barden, & Fewell (2011) and Hölldobler & Wilson (2009) found that the division of labor (the number of distinct roles) increases with colony size although it is hard to separate cause and effect. Phenotypic variation enables ants to differentiate according to their productive role or their role in supporting productive activity (as in defense).

It should be acknowledged that the division of labor is common in the animal world, and is not by itself a distinguishing characteristic of ultrasociality. For example, a division of labor based on care of the young is common among animals. It spontaneously appears in normally solitary queen ants when the queens are forces to associate (Fewell & Page Jr. 1999) and similarly in normally solitary bees. Solitary sweat bees alternately dig nesting holes and guard the nest. When two are put together one will specialize in excavation and the other will guard the nest entrance resulting in efficiency gains in both tasks. According to Holbrook et al. (2009, 301): "Paired individuals performed more per capita guarding, and pairs collectively excavated deeper nests than single bees—potential early advantages of social nesting in halictine bees." Even in a simple society of two individuals there is an advantage to a larger scale (from one to two) permitting a division of labor. The spontaneous appearance of the division of labor in these simple cases is remarkable and may hold keys to its development in ultrasocial societies. But the extent of the division of labor in ultrasocial species is unique in its complexity and interdependence.

The active management of agricultural crops is a particularly powerful impetus for a more complex division of labor. Consider the differences between a eusocial honeybee colony and an ultrasocial attine ant colony. Honeybees survive by foraging for pollen from plants but they do not actively manage the sources of pollen. Honeybees have a division of labor, for example, cleaning, feeding the brood, receiving the nectar, foraging, and defense depending on the age of the individual bees (age polyethism). Yet there are only three physical castes, workers, drones and queens. Workers are of only one physical type. Some attine ants, by contrast, have many castes who actively manage the production of various species of fungi which feed the colony. There are castes are based partially on size which "coarse-tunes" rather than "fine-tunes" the phenotypes to perform a wide variety of tasks (Oster & Wilson 1978). Ants within each size caste can perform a number of further-refined highly specialized tasks. For example, there is a caste of tiny attine ants whose job it is to ride atop the much larger leaf carriers and defend them from attacks by parasitic flies (Hölldobler & Wilson 2011). Large soldier ants have jaws so specialized for defense that they cannot feed themselves. There are even "untouchable" ants whose job it is to remove wastes and pathogens from the fungal gardens. The point is that the active management of food production, and the defense of food surpluses, calls forth a much more complex division of labor requiring many more tasks and a much greater degree of coordination than does mere foraging. Ferguson-Gow et al. (2014) found a significant positive relationship between the complexity of agriculture systems in attine ants (from lower attines to leafcutters) and complexity of the divison of labor.

Another factor facilitating the division of labor under agriculture is mutualism. The fungi ants and termites live on could not survive without active management by the ant colony. This requires complex tasks including using antibodies to control the bacteria that attack the fungus (Aanen & Boomsa 2006; Mueller & Gerardo 2002). It is true that flowers are pollinated by (non-agricultural) honeybees but there exist other pollinators and the plants could survive without the presence of honeybees (as they are now doing in many areas because of honeybee dieoff).

The advantages of a division of labor are a central tenet of economic theory. They were recognized by Adam Smith (1937 [1776], Book 1, 2-3) in *The Wealth of Nations* where he presented his well-known pin factory example of the role of the division of labor in rationalizing the production process. One person working alone, he wrote, could scarcely make one pin a day. But when the enterprise is divided into several sub-tasks, productivity increases dramatically.

> One man draws out the wire, another straights it, a third cuts it, a fourth points it, a fifth grinds it at the top for receiving the head; to make the head requires two or three distinct operations; to put it on, is a peculiar business, to whiten the pins is another; it is even a trade by itself to put them into the paper…I have seen a small manufactory of this kind where ten men only were employed…Those ten persons…could make among them upwards of forty-eight thousand pins in a day.

Smith also pointed out that the division of labor is limited by the extent of the market. The larger the market, the more specialization is possible, which enlarges the market still more in a kind of "virtuous circle." Although he was writing about market capitalism, Smith was onto something more fundamental in the sense that he clearly saw that there is a system at play that places a premium on capturing the efficiencies inherent in expanding the division of labor.

Active intervention in food production called forth a more extensive and interdependent division of labor in humans as well as social insects. In hunting and gathering societies the division of labor was relatively simple, primarily based on gender. A more interdependent and extensive division of labor began to take form in pre-agricultural societies with the harvesting of wild grains. There were more kinds of tasks to perform. Access to the good stands of wild wheat was essential and it is likely that defense became more important in order to lay claim to a prime spot. As the active cultivation of crops increased so did the necessity for coordination of production in planning, preparing soil, planting, cultivating, harvesting, processing, storing, and distributing the agricultural output. As well, reproductive rates changed in humans so there was more work to be done in birthing and child rearing. Women's roles became more narrowly circumscribed around these activities. Thus agriculture expanded the division of labor and increased the interdependence between people for day-to-day sustenance.

The division of labor in humans does not entail the same phenotypic (morphological) differentiation as in ants and termites because humans have greater recourse to cultural, institutional, and technological extensions of themselves. But occupational differentiation in humans is also made possible to some extent by genotype-phenotype plasticity. Human brain plasticity allows for a remarkable degree of differentiation in terms of the ability of individuals to adapt to different cultures and behavioral patterns (Frith and Frith 2010; Wexler 2006). This is not to say that specific instances of occupational differentiation are genetically determined, but brain development plasticity gives humans the flexibility to perform a variety of functions. The extent of the detailed division of labor becomes so great in ants and in humans that individuals become tied to a very narrow productive role in society. This creates an interdependence that secures and strengthens the group as a self-referential entity.

3.3 Increasing returns and the competitive advantage of larger group size

Larger group size may also be more metabolically efficient because of economies of scale in energy use. Hou et al. (2010) and Shik et al. (2012) demonstrate this in ant colonies and use Kleiber's Law (the rate at which an organism processes energy increases at a rate that is to the ¾ power of that organism's body mass) as the explanation. Larger colonies have lower rates of per capita energy use (Bruce & Burd 2012). But there seems to be an upper limit on leaf cutter ant colony size due to the fact that colonies will eventually reach a limit where the returns to increasing foraging territory reach the point where further expansion is not profitable (Bruce & Burd 2012).

Among the many tasks that developed with agriculture, defense was one that gave an advantage to larger group size. In human agricultural societies, because of the need to lay claim to property and because of the time lag between planting and harvesting, there was a need to defend property. Although defense may have been necessary even while harvesting wild grain, it took on added importance with the investment in managed agriculture. Human societies that were larger and better able to organize warfare, and develop war-making innovations, outcompeted others and expanded rapidly (Matthew & Boyd 2011; Turchin 2006). Eventually warfare became prevalent as larger scale state societies began to form. As Larsen (2006, 17) puts it: "The record strongly suggests that population size increases associated with food production provided conditions conducive to the rise of organized warfare and increased mortality due to violence."

There are other advantages to larger size and scale. Unlike solitary insects, social insects can perform a number of tasks *in parallel* as opposed to *in sequence,* an advantage described in Adam Smith's pin factory example. As Georgescu-Roegen (1965) pointed out for the human economy, if the scale of operation is large enough idle factors of production can be eliminated and thus larger scale systems can entail a more efficient and productive use of resources as long as they are abundant enough to support the larger scale. Also, time is not lost in moving from one task to another. An ultrasocial society can also take advantage of a spatial distribution of labor allowing for more risk taking in foraging than would be possible for individuals acting alone.[14] In general, larger scale and the division of labor are mutually reinforcing. A larger scale of operation can also take advantage of a spatial distribution of labor allowing for more risk taking

[14] This is striking in the eusocial mammal, the naked molerat. Colonies of these animals live by foraging for a kind of tuber scarce in the deserts where they live. One molerat searching alone would likely starve before a tuber was found. But when one molerat finds a tuber, it makes a call to attract the others which can live for weeks on the find (Judd & Sherman 1996).

in foraging than would be possible for individuals acting alone. Also, with a larger scale individuals can specialize and become more proficient in their task. In general, larger scale and the division of labor are mutually reinforcing.

Human hunter-gatherers lived off the flows of nature—from the solar energy directly captured by living plants and indirectly present in the flow of animals feeding on those plants. They had limited control over these subsistence flows. If hunter-gatherers, like any large carnivore, took too many animals or harvested too many wild plants this created immediate shortages and this tended to keep human societies in ecological balance. These societies also had leveling mechanisms to promote an egalitarian distribution of wealth and power. With the adoption of agriculture, human society and the relationship between humans and the natural world changed dramatically.

4. Agriculture and the human transition to ultrasociality

Anatomically modern humans appeared in Africa about 200,000 years ago. Thus for more than 95 percent of human history we lived as hunter-gatherers in small, mobile groups. Judging from studies of present day and historical hunter-gatherer societies these groups were highly cooperative, egalitarian, and lived within the confines of local ecosystems (Boehm 1997, 2012; Gowdy 1998; Lee 1968, 1984; Pennisi 2014; Ryan and Jethá 2010). Quite suddenly, within just a few thousand years, the vast majority of Homo sapiens were members of populous agricultural societies with complex economies, technologies, and social organization. With the advent of ultrasociality, the human population exploded from around 6 million 10,000 years go to over 200 million by the beginning of the Common Era (CE) 2,000 years ago (Biraben 2003; Bocquet-

Appel 2011; Cox et al. 2009).[15] At the same time, the role of the individual in human society changed radically. With agriculture, there was a loss of individual autonomy, rigid social hierarchies were firmly established, and there was a general decline in the well-being of the average person (Diamond 1997b; Lambert 2009; Larsen 2006). This raises the question of individual choice in the agricultural transition. Why would people accept the significant costs of poorer nutrition, shorter lifespans, and the diseases that came with sedentary existence and dense settlements? The adoption of agriculture most likely was not a choice, but rather a gradual, cumulative process perhaps imperceptible within the lifetime of a single individual. There were likely marginal payoffs that iterated society toward further embracing agriculture. Yet certainly humans could not have anticipated where agriculture would lead them—to hierarchy, regimentation of productive life, ecological degradation, patriarchy, slavery and poor health. Once in place the growth in population it facilitates can then only be supported by sustained agriculture.[16] Humans did not consciously choose agriculture.[17] This again underscores the

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[15] Hunter-gatherers expanded into new areas (like North America) which significantly increased the total human population before agriculture, but this is not the same as the unprecedented population exposition in limited areas that characterized the agricultural transition. Surprisingly, claims are made that the human population explosion after agriculture is not unique (Caspermeyer 2013). It is certainly true that there were periods before the Neolithic where the human population expanded. But a closer examination reveals that these early expansions were not unusual and not of the same order of magnitude as the population explosion after agriculture.

[16] Mueller and Gerrardo (2002, 15428) write of fungus-growing insects: “Evolutionary reversal back to a nonfungus-farming lifestyle has apparently not occurred in any of the nine known, independently evolved farmer lineages (one termite, one ant, and seven beetle lineages). This supports the view, formulated first for humans [Diamond 1997a] that the transition to agricultural existence is a drastic and possibly irreversible change that greatly constrains subsequent evolution.”

[17] The attitude of recent hunter-gatherers to agriculture is instructive. When a !Kung man was asked why he did not grow crops he replied "Why should we plant when there are so many mongongo nuts in the world." (quoted in Lee 1968).

difficulty in understanding transitions themselves rather than before and after characteristics (Okasha 2006).

A basic question raised here is whether human cultural evolution is the result of conscious choice or the blind unfolding of natural laws? There are really two questions. The first is whether human agents act purposefully in pursuing chosen ends. The answer to this seems certainly "yes". But the more interesting question is whether or not the cumulative outcome of individually chosen activities can be explained as the result of human design (see Vanberg 2014). We argue that for some of the most important cultural transitions in human history (agriculture, civilization, market capitalism) the answer is no. Choices small in scale and time—even choices that are perfectly rational from the point of view of an individual acting at a point in time—can lead inexorably to outcomes that are not only unanticipated but actually detrimental to the individual. The economist Alfred Kahn (1966) calls this "The Tyranny of Small Decisions." As we argue above, the transition to agriculture took place through a series of incremental decisions made by innumerable individuals over thousands of years. The outcome of these decisions was a number of hierarchical agricultural civilizations within which the average individual was worse off.

4.1 The origins of human agriculture

There is no consensus as to the origins of agriculture. Price and Bar-Yosef (2011, S168) summarize: “There is as yet no single accepted theory for the origins of agriculture, rather, there is a series of ideas and suggestions that do not quite resolve the questions.” Our intention here is not to provide the definitive explanation for this transition (which likely varied from place to place, McCorriston & Hole, 1991) but rather to offer in broad outline a plausible story for the transition from hunting and gathering to settled agriculture and the concomitant social and environmental consequences. Agriculture gave our species the ability to control and expand its supply of food and this was an evolutionary advantage (as measured by total population) even though it apparently made the average individual worse off. According to Larsen (2006, 12): “Although agriculture provided the economic basis for the rise of states and development of civilizations, the change in diet and acquisition of food resulted in a decline in quality of life for most human populations in the last 10,000 years.” The archeological record substantiates Larson’s claim. Humans after agriculture became shorter and suffered from more debilitating diseases from leprosy to arthritis to tooth decay than their hunter-gatherer counterparts (Cohen & Crane-Kramer 2007; Lambert 2009). It is only in the last 150 years or so that longevity once again reached that of the Upper Pleistocene. The average human life span in 1900 was about 30, and for Upper Pleistocene hunter-gatherers it was probably about 33 years.[18] Only in the last century or so has the well-being of the majority of humanity improved dramatically. It remains to be seen whether or not these improvements can be maintained. Care must be taken not to see the achievements of the very recent past as representative of the consequences of the agricultural transition.

Humans had extensive knowledge of wild plants long before the adoption of agriculture (Cohen l977; Zvelebil & Rowley-Conway l986) so there must have been some experimentation with planting during our lengthy hunter-gatherer history. Flannery (1968, quoted in Bowles & Choi 2012) observes: “We know of no human group on earth so primitive that they are ignorant of the connection between plants and the seeds from which they grow.” Yet understanding and observing and collecting wild plants is one thing, domestication is another. What pushed humans

[18] The Upper Pleistocene estimate is based on the Kaplan et al. (2000) estimate for contemporary hunter-gatherers. Life expectancy estimates are notoriously difficult to compare because of differences in infant mortality, the effects of wars and epidemics, etc.

to adopt agriculture? Convincing arguments have been made that the Holocene provided a period of climate stability that was necessary for successful agriculture. Richerson, Boyd and Bettinger (2001) demonstrate that the possibilities for agriculture were severely limited before the Holocene because of unpredictable climate fluctuations. There were several periods of warming after the evolution of modern humans but none except the Holocene led to agriculture. Climate data indicate that prior to the Holocene, changes in temperature as great as 8^{0}C occurred over time spans as short as two centuries (see Bowles & Choi, 2012, supporting on-line material, page 4). Ice core and pollen records indicate that centuries-scale abrupt climate events occurred regularly during the Pleistocene and that it was not until the Holocene that a protracted period of warming occurred. In the late Pleistocene plant productivity was low because of reduced CO_2 levels (about 180 ppm compared to 250 ppm at the beginning of the Holocene (Shakun et al. 2012). Beerling (1999) estimates that the total amount of stored organic land carbon was 33% to 60% lower in the late Pleistocene compared to the Holocene.

One popular argument is that population pressure drove the adoption of agriculture (Binford 1968; Cohen 1977). But others point out that there is little evidence for population pressure in the areas where agriculture first appeared (Price and Bar-Yosef 2011). However, the Holocene warming may be related to population pressures in some areas. McCorriston and Hole (1991, 49) point out that the effect of the Holocene warming in the Levant was to prolong summer aridity and that this would have affected the availability of agricultural inputs. This likely affected the availability of viable locations for groups of humans. The drier climate also put more pressure on access to water and probably concentrated human and animal populations in areas with ample water. The population picture is further complicated by the fact that even incipient agriculture may have resulted in a more sedentary life which increased fertility rates.

Even the gradual and marginal use of wild grains might have altered population dynamics if it made people more sedentary and more fertile, thus creating a positive feedback path reinforcing the need for more agriculture as pressure on wild food sources and hunting became more challenging.

4.2 A plausible story of the human agricultural transition

A plausible scenario of the human agricultural transition can be sketched out (Gowdy & Krall 2014). Mobile hunter-gatherers moved through places where wild grains thrived, and these grains provided a significant portion of hunter-gatherer diets. As the climate warmed and became more stable, wild grains became more reliable and more important as a food source. People began to sow wild seeds to enhance grain growth and they began to store the grain they collected. As they sowed they also selected for desirable characteristics. Storage, especially amenable to annual grains was a good subsistence strategy since there was variability in production from year to year. This enhanced and concentrated food supply led to a more concentrated population. Perhaps a portion of the population began to stay behind in the seasonal migrations in order to manage the wild crops. Selective planting and harvesting of crop varieties eventually led to managed agriculture and populations more and more dependent on intentional food production.[19]

This plausible story fits with what we know of the agricultural transition in the Levant (which includes parts of modern Palestine, Syria, Israel and Jordan) beginning around 10,000-

[19] The phenomenon of step-by-step evolutionary lock-in has been much discussed. See for example Nanay's (2005) discussion of cumulative evolution and Tennie, Call & Tomasello's (2009) concept of the ratchet effect.

12,500 years ago (Bar-Yosef 1998, 162; McCorriston & Hole 2000b).[20] The Levant is the area of the world where the advent of agriculture is the best documented. A key feature of the Holocene warming in the Near East was that it created conditions favorable to the development of annual grains. The climate of the Levant became more stable and seasonal differences became greater. Around 10,000 years ago the pre-agricultural Natufians began to rely more heavily on wild grains like wheat and barley (McCorriston & Hole 2000a, 2000b). McCorriston and Hole claim (1991, 61): "In our view, the wild annual plants had never been available in densities comparable to those of the early Holocene when seasonality reached unprecedented extremes and favored annual over perennial adaptation." Annuals have an advantage in places with enhanced seasonality especially where there are hot dry summers and strong seasonal rainfall variation. Annuals store their reproductive ability in seeds which can wait (sometimes years) for rain to germinate. Annuals also have unique characteristics that may allow rapid co-evolution to develop between humans and plants (Cox 2009). Annual grains can also be stored and so a greater reliance on them meant a greater capacity to secure a surplus. Evidence exists for food storage at about 11,000 BP, about 1,000 years before domestication and large-scale settlements, in the form of purposely built granaries (Kuijt & Finlayson 2009).

One mutation of wild wheat that would have been important was non-shattering, a mutation that allows for seeds to hang on and not fall to the ground as quickly. This is apparently a rare mutation but might have been noticed by those seed gatherers who were accessing wild

[20] We do not claim that the transition to settled agriculture in the Levant is a universal story. Agriculture arose several times after the beginning of the Holocene, in different climates with different plant ancestors. Nevertheless, the transition in the Levant from the earlier hunter-gatherer Kebaran to the pre-agricultural Natufian to the later fully agriculturalist Pre-Pottery Neolithic is the most well-documented agricultural transition and it is consistent with the story we outline here.

stands of early wheat varieties. The time period for harvesting wild wheat was short---three days to a week before shattering occurs depending on weather conditions. After seeds shatter they must be harvested from the ground which is more time consuming. If people reached a stand of wild wheat after shattering had taken place the only seeds still standing would have been the mutants which would have been noticed. Also, using a sickle would have been a particularly good technology for non-shattering seeds. In this way mutations in wheat interfaced with human intervention to create a selection bias for non-shattering seeds or any other trait that was noticeable and desirable.

Domestication of grains may have initially been unintentional in the sense that wild varieties would have been eliminated and replaced more systematically with plants that required human intervention (Bar-Yosef 1998, 167). With cultivation there gradually developed a specialized active management of grains where control of production was more concentrated within human groups (Flannery 1968; McCorriston & Hole 2000b; Rindos 1984). Active management also required more complex and integrated tasks (in both humans and insects) and thus there is a connection (mutualism) between the characteristics of the crops and the species managing the crops.

As the climate improved and stabilized with the Holocene, wild grains such as *triticum monococcum*, a wheat-like grass, became more plentiful. Evidence suggests that the Natufians intensively harvested wild cereals using sickles (Bar-Yosef 1998, 164-165). There is also evidence of heavy wear of teeth which is presumed to be due to consuming coarsely ground cereals (Smith 1972, 236-237). To reiterate, annuals might have been increasingly abundant and amenable to the climate conditions of the Holocene. Hunting did not cease as the use of wild grains increased but there is likely a shift in strategies of hunting and the importance of hunting in diet. Hunting may have become less reliable as the climate change of the Holocene would have changed the range and concentrations of wild animals (McCorriston & Hole 1991).

Some mention should be made of the effect of the Younger Dryas—a sudden cooler and drier period occurring between 12,800 and 11,500 years ago—on the cultures of the Near East. Belfer-Cohen and Bar-Yosef (2000) argue that it was the stress of the Younger Dryas that that pushed the adoption of agriculture. But others point out that there is no evidence for more intensive resource us or food stress in the late Natufian (Munro 2003). In fact, during this period the population densities and settlement patterns of early Natufian culture reverted back to pre-Natufian levels. It may be that the Younger Dryas interrupted the transition to agriculture rather than encouraged it.

The Natufians were followed by the fully agricultural cultures of the Neolithic, referred to as Pre-Pottery Neolithic A (PPN-A). PPN-A sites are much larger than the Natufian sites, with storage bins for grains, ceremonial structures, and a rich lithic industry. The best known PPN-A settlement is Jericho (about 10,000BP), thought to be the world's first known town, with a population of about 2,000-3,000 people. The Jericho site shows the first known domesticated cereals, emmer wheat and two-row hulled barley (McCorriston & Hole 1991, 51). Storage technology is found abundantly in PPNA and PPNB sites. Makarewicz (2012, 217) writes: "The Pre-Pottery Neolithic A marks a major shift in human approaches to subsistence from plant gathering to the consistent practice of plant cultivation, where wild plant resources were augmented by a more predictable food source in the form of managed plants, particularly cereals and legumes." Eventually the point was reached where the human population in the Levant could not survive without the grains, and the grains could not survive without human intervention.

4.3 Managing crop production: the economic drivers kick in

The active management of crops fundamentally altered human economic organization. Like our ant and termite distant relatives humans began to actively engage in the primary production of their food supply. Economic life was no longer a matter of living off the day-to-day flows from nature. It now involved a direct intervention into food production.[21] Many species use social organization to get food, as in cooperative hunting, for example. But direct intervention in producing food is categorically different and the economics of production take center stage.

First of all, actively producing food requires a more complex and interdependent division of labor. This increase in complexity had its beginnings in the harvesting of wild stands of grains. Harvesting must move quickly or most of the grain may be lost. Protecting access to the good stands of wild grain was essential and it is likely that defense became more important in order to lay claim to a prime spot and may also have increased the likelihood of staying in one place longer and arriving early. As the active management of crops increased, so too did the necessity of coordinating production—planting, cultivating, harvesting, processing, storing, and distributing agricultural output. Supplementing food with wild animal protein became more difficult the more sedentary people became. As well, reproductive rates changed and there was more work to be done in birthing and child rearing. Women's roles became more narrowly circumscribed around these activities. The reward was a greater control over food supply for the group as a whole but the repercussions if things failed were formidable. As long as storage was possible, production of surplus was an insurance against lean times.

A second feature of emergent agricultural society is an impetus to expand because of the productive advantage of larger group size. More food allows expansion, and expansion captures

[21] It is true this interjection can happen indirectly without agriculture as is the case when intentional use of fire to change habitat but even here the interjection is limited and the organizational demands do not extend over time.

the efficiencies of a greater division of labor and economies of scale. Also, many tasks are required that do not directly contribute to food production itself. Those who directly produce food must provide for those not actively engaged in agricultural production. Part of the dynamic of agriculture is the increased reproductive rates caused by sedentary life. Increased reproductive rates also provided one of the most important resources for successful agriculture, a large supply of laborers. But for a time at least this requires some investment in nonproductive individuals, that is, young children who cannot yet work. The result is again that those engaged in the direct provisioning of food must produce enough to feed more nonproductive individuals. Greater population creates a greater need for agricultural output and greater agricultural output creates a greater need for population.

Turchin (2013) points to increasing returns to scale in warfare as a major driver of ultrasociality. Turchin et al. (2013) argue that agriculture increased the payoff for aggression which, in turn, necessitated more food production to feed the expanding military. Groups with more soldiers eliminated or absorbed smaller groups. Warfare has been suggested as a key to the development of state societies (Carneiro 1970; Tilly 1992; Turchin 2006). By contrast, a strong case has been made that "warfare did not exist in hunter-gatherer societies (Culotta 2013). Violence certainly existed in these societies but most lethal events resulted from personal disputes (Fry and Söderberg 2013).

Finally the ecological consequences of annual grain agriculture may have also encouraged the expansionary dynamic. Annuals had a greater capacity for seed production and the rewards of active management were greater, but they also had a greater potential for ecological damage, especially soil erosion and soil disturbance during planting (Cox, 2009). Expansion was also one way out of the ecological problems caused by grain agriculture although in the long run they exacerbated the ecological problems as agriculture expanded into forested areas and deforestation brought down silt.

4.4 Surplus and hierarchy

Surplus production was perhaps initially a response to the favorable climate of the Holocene in the Near East but surplus production and expansion increasingly became necessary to accommodate population growth, the growth of the proportion of nonproductive individuals, the problems of seasonal variation and to counter the ecological degradation of grain agriculture. Because of the premium placed on maximizing output it was important to control production and maximize the output of individual laborers. During key periods such as planting and harvesting work was necessarily intensive and repetitive. The regimentation of work and the productive benefits of a division of labor and attendant economies of scale promoted the success of agriculture but also increased the bureaucracy necessary to manage the complexity, the distribution of surplus and the associated ecological problems. In this environment, relying on stored surpluses to carry societies over seasonal periods of low production made maximizing surplus production in any given year all the more critical. It also increased the stakes associated with management of production and with dissemination of the surplus.

With storage of surplus, complex technology, and the ability to physically control food surplus also came hierarchical societies. Control itself took on added importance moving society increasingly in the direction of hierarchy and property. Year-round storage also meant that early farmers could settle in larger groups throughout the year, and had more flexibility to support specializations like craftspersons, administrators, warriors, and religious leaders (McCorriston & Hole 2000b). The need for efficiency and control set up a more mechanistic and interdependent configuration of production and distribution. The survival of the society depended on the payback from the management of production. Those at the top benefitted from pushing the envelope of agriculture intensification. The successful production of agricultural surplus expanded the material and cultural possibilities of society. But the fact that most individuals had no other option to secure the material necessities of their lives other than to participate in directly producing food placed the human propensity to cooperate at the disposal of both direct and indirect coercion.

Antecedents to hierarchical organization exist in non-agricultural societies and these give credence to the importance of the management of surplus and the active control of production in the creation of hierarchy. Woodburn (1982) distinguished between "immediate return" and "delayed return" hunter-gatherer societies, with the latter possessing a more elaborate technology (capital) such as nets and boats, and showing some evidence of social stratification. In delayed return hunting and gathering societies people have rights over valued assets of various kinds. A commonly given example of a hierarchical culture without agriculture is that of the original inhabitants the northwest coast of North America. A village on Keatley Creek in northwest Canada, was occupied between 2500-1100 years ago by hunter-gatherers who lived on the abundant seasonal salmon runs. The village consisted of more than 115 pit houses and other structures with log and earth roofs. The peak population of the village was about 1500 people. Evidence indicates wide disparities in living standards which may have originated in unequal access to prime fishing grounds (Prentiss 2012; Pringle 2014). Richerson, Boyd and Bettinger (2001) point out that the transition from the beginning of agriculture to the development of state societies took around 2000 years. Thus a dynamic that started out modestly and benignly locked early agriculturalists into a perhaps irreversible process that led to hierarchical state societies.

5. The consequences of ultrasociality

Ultrasociality had two striking consequences for humans and insects. The first is the domination by ultrasocial species of the ecosystems in which they occur in terms of both sheer numbers and in the way those ecosystems are organized to meet the requirements of ultrasocial societies. The second is the loss of individual autonomy in these societies. In this section we discuss the similarities in these two evolutionary outcomes in insects and humans, and perhaps even more interestingly, the dissimilarities due to the differences in genetic (insect) and social (human) evolution, and in the fact that humans, compared to ants and termites, have only very recently started down the path to ultrasociality.

5.1 The social conquest of earth: ecosystem domination, sustainability, and collapse

Ultrasociality evolved in only a handful of species, yet those species dominate the ecosystems within which they occur and indeed the entire planet (Wilson 2012). Sanderson et al. (2002) calculated that over 80 percent of the global terrestrial biosphere is under direct human influence. Astonishingly, the total dry weight human biomass (about 125 million metric tons) is over 12 times the weight of all other vertebrates combined (Smil 2013). Social insects also dominate their ecosystems to an amazing degree. In a survey of a patch of rainforest in the Brazilian Amazon, social insects comprised about 30% of the entire animal biomass and 75% of the insect biomass (Fittkau & Klinge 1973; Wilson, 2008, 6). Wilson (2012, 116-117) "crudely" estimates the total number of ants to be 10^{16}, or ten thousand trillion. If one ant weighs one-millionth of the weight of a human, the total weight of the world's ants is about the same as the total weight of all humans. In subtropical and tropical ecosystems, termites can make up as much as 95% of the soil insect biomass (King, Warren & Bradford 2013; Korb 2007, R998).

Ants, in effect, have re-engineered the ecosystems they are a part of. Folgarait (1998) discusses some of the major functional roles of ants including soil modification through physical and chemical changes, changes in nutrient and energy fluxes, and changes in vegetation. Other species have co-evolved to accommodate themselves to the presence of the numerically dominant ant and termite colonies. By contrast, humans after agriculture have had a predominately negative impact on ecosystems and biodiversity.[22] The archaeological and historical record of early agricultural societies is characterized by rapid expansion followed by collapse and social disintegration (Diamond 2005; Weiss & Bradley 2001; Weiss et al. 1993). Examples include the Akkadian empire, Old Kingdom Egypt, the Classic Maya, and the Harappan of the Indus valley. These civilizations disintegrated from a variety of factors including the loss of soil fertility, erosion from reliance on annual plants, soil salinization, water mismanagement, and the inability to withstand prolonged droughts. Climate change in particular is increasingly accepted as a driver of past societal collapse and disruption (Weiss & Bradley 2001; Rosen & Rivera-Collazo 2012). The basic problem is that ultrasocial societies are expansionary; that is, they have a constitutional proclivity to expand and because of the tremendous interdependence they are particularly difficult to disengage before they reach the point of collapse either due to ecological limits (that might be exacerbated by climate change) or due to internal conflicts between classes in the case of humans as to the distribution and use of surplus.

Of course, social insects have had tens of millions of years of evolutionary trial and error to hone sustainable cultures. It is quite possible that the early history of ultrasocial ants and

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[22] We do not mean to imply that pre-agriculture hunter-gatherers were innately more ethical in their use of the environment. Their cultures were sustainable because they had to be since they lived directly off the day-to-day flows from nature. Grayson and Meltzer (2003) argue that the hunter-gatherer overkill hypothesis is not supported by evidence and that it represents a convenient "evil human nature" worldview supported both by environmentalists and those who advocate the exploitation of nature.

termites is also littered with unsuccessful experiments with agriculture. Can humans learn something about sustainability from insect farmers? Aanen and Boomsa (2006, R1014) write:

> The farming insect societies had tens of millions of years of natural selection to solve many of the challenges that are also well known to human farmers. They have conveyer belt substrate processing, produce their own pesticides and antibiotics, and practice active waste management. Neither the ants not the termites, however, have been able to overcome the fundamental laws of host-symbiont conflicts, which imply that only monoculture farming is evolutionarily stable. Our own farming practices evolved culturally by frequent exchange of crops, and learning and copying innovative practices. The problem is that, on the larger scale that we apply today, many of these practices are unlikely to be sustainable, even on an ecological time scale.

Ants and termites have practiced monoculture successfully for tens of millions of years while the short history of human management of a few crops shows a pattern of recurring instability (Benckiser 2010). One reason social insects have achieved sustainable agriculture is that their agriculture has more successfully harnessed the benefits of mutualism—the advantages of cooperation between ants and termites and the fungus they raise and feed on. Our mutualism around annuals is more ecologically problematic due to soil erosion, pest control, and a number of other challenges. Cooperation between unrelated agents can have great benefits, but there is always tension between the benefits of cooperation and the benefits of defecting—the classic Prisoner's dilemma (Trivers 1971). Social insects have largely overcome Prisoner’s dilemma type reproductive conflicts by developing mutualism because one-to-one cooperation is more stable (easier to enforce) than cooperation among several agents. Ant feces provide critical nutrients (especially nitrogen) without which the fungus could not survive. Not only is mutualism between agriculturalists and their crops taken to the point where one could not survive without the other (as with humans), in ants it is taken to the point where their physical bodies have adapted to the physical needs of the fungus. Foster and Wenseleers (2006) show that three key factors are important to mutualism evolution (1) high benefit to cost ratio, (2) high within-species relatedness and (3) high between species fidelity. The economic drivers behind the success of managed agriculture likely raised the benefit to cost ratio of mutualism.

Regarding sustainability, an important difference between human and insect societies is social instability. Unlike insect societies, human groups are characterized by recurrent and sometimes calamitous within-group conflicts. Georgescu-Roegen, following Lotka, attributes this to the difference between "endosomatic" and "exosomatic" organs (Georgescu-Roegen 1977; Lotka 1925). The occupations of social insects is determined in large part by their phenotypes—for example, door keeper ants have large heads (endosomatic) which serve no other purpose than to block the entrance holes to the colony. Humans, by contrast, depend on the objects of material culture (exosomatic) which can be appropriated according to cultural rules that may or may not be accepted. An ant is born to be a soldier, a human is not. There is no biological reason for one human to be homeless and another a billionaire.

5.2 The loss of individual autonomy in ultrasocial societies

Another basic feature of ultrasociality is the subjugation of the individual for the evolutionary success of the group. Subjugation can be understood partly as an artifact of the division of labor in agricultural societies. An important commonality in human and ant division of labor in ultrasocial agricultural systems is that *individual* behavioral complexity and flexibility is in general not as great compared to those societies relying on hunting and gathering. The behavior of individuals, in the context of an elaborate division of labor, is simpler in ultrasocial societies even as the society grows more complex. In the case of ants, increasing social complexity is not associated with increasing individual behavioral complexity (Holbrook, Barden & Fewell, 2011). Adam Smith (1937 [1776], 734): recognized the danger for humans of labor specialization and the mental toil on individuals who endlessly perform the same tasks:

> The man whose whole life is spent in performing a few simple operations, of which the effects are perhaps always the same, or very nearly the same, has no occasion to exert his understanding or to exercise his invention in finding out expedients for removing difficulties which never occur. Her naturally loses, therefore, the habit of such exertion, and generally becomes as stupid and ignorant as it is possible for a human creature to become.

Commenting directly on Smith's observation, Moffett, in reference to ants (2010, 70) writes: "This deficiency can be observed for large ant societies as well, in which specialized workers are incapable of accomplishing much without the cooperation of nestmates." Likewise, Anderson and McShea (2001, 211) find that "individuals of highly social ant species are less complex than individuals from simple ant species." They find that individual ants in more complex ant societies with a high degree of division of labor exhibit "low individual competence" and "low individual complexity."

Increasing social complexity in ants is associated with a loss of brain size. Riveros, Seid and Wcislo (2012) tested the association between brain size and sociality across 18 species of fungus growing ants and found that increased colony size was associated with decreased relative brain size.[23] With agriculture human brain size began to decrease dramatically. According to Hawkes (2011) the decrease in brain size during the last 10,000 years is nearly 36 times the rate of *increase* during the previous 800,000 years . There is an important distinction between the "social brain" and "social intelligence" and "collective intelligence." We fully agree with the "social brain" hypothesis that human intelligence evolved to facilitate within-group cooperation, empathy, and mind reading (Frith & Frith; Wexler 2006). Collective intelligence, on the other

[23] The brain of leafcutter ants is remarkably large, accounting for 15% of their body mass compared to 2% for humans (Seid, Castillo & Wcislo 2011). Darwin (1871) noted that "the brain of the ant is one of the most marvelous atoms of matter in the world, perhaps more marvelous than the brain of man." (quoted in Wcislo 2012, 1419)

hand, refers to the ability of groups to solve complex problems far beyond the capabilities of any individual within the group. Collective intelligence can increase while individual intelligence declines.

Individual simplicity may be an advantage in collective decision making. In fact, the standard economic model of extreme rationality may apply more to ant colonies than to humans. For example, a number of experiments show that humans are susceptible to the fallacy of irrelevant alternatives. A choice between alternatives **A** (a fully paid 10 day vacation to Paris) and **B** (a fully paid 10 day vacation to Rome) should not be influenced by the inclusion of an irrelevant unrelated choice **C** (a paid vacation to your least favorite nearby city). Humans are consistently susceptible to this fallacy (Ariely 2008), but ants are not. Edwards and Pratt (2009) in an experiment involving the choice of an ant colony between nesting sites showed that the colonies are not influenced by irrelevant alternatives. They surmise: "We suggest that immunity from irrationality in this case may result from the ants' decentralized decision mechanism. A colony's choice does not depend on the site comparison by individuals, but instead self-organizes from the interactions of multiple ants, most of which are aware of only a single site." (Edwards and Pratt 2009, 3655) In some species of ants, the colony solves very complex problems of economic organization and in fact it may outperform humans (Edwards and Pratt (2009). Collectively, ants have developed complex strategies to manage agricultural production. Like humans, they have developed a number of herbicides to control weed molds that attack the fungus they rely on, they have elaborate manuring regimes that maximize harvests, and cultivars are shared between distantly related ant colonies (Mueller, Rehner and Schultz 1998).

The social insects demonstrate that collective intelligence can be quite impressive without a corresponding level of individual intelligence. Off-loading of tasks in complex human societies is one explanation given for the decline in human brain size after the Pleistocene (Geary & Bailey 2009). People may not have to be as smart to stay alive. Cognitive scientist David Geary refers to this as the "idiocracy theory" after the 2006 film (McAuliffe 2011). Geary and Bailey (2009) and Mithen (2007), among others, argue that the complex material culture that came with agriculture allowed humans to offload some cognitive requirements, allowing the energy-expensive human brain to decrease in size.[24] Offloading individual intelligence to the "environment", "technology" or the "social brain" is not necessarily a good thing from the point of view of an individual human. Social intelligence increased but individual intelligence may have declined (see Barrett, Henzi, & Rendall 2007). This hypothesis fits nicely with our point that a major consequence of ultrasociality is a loss of individual autonomy and possibly, cognitive capabilities. According to Mithen (2007, 705) even the social brain may have deteriorated with agriculture and civilization:

> This development [sociality and social intelligence] has nothing to do with *Homo habilis* or handaxes, bipedalism or brain size. It is the origin of farming at, or soon after, 10,000 years ago. It is only with the economic basis that farming provides that writing mathematics and digital technology could be invented and it is these that effectively define the nature of our cognition today. The brain is important, of course, but it now plays a mere supporting role to a cognitive system that is primarily located in materials entirely outside the body—books, computers, paintings, digital stores of data and so forth. There are, of course, our capacities for empathy, mind reading and social interaction that not digital computer is ever likely to replace. But I doubt if these today are very different to those of our early human ancestors living several million years ago (Mithen 1996). Indeed, if anything, I suspect they have deteriorated through lack of use as we have become dependent on material items as the source of information.

[24] The relationship between human brain size and intelligence is controversial. But in a meta-analysis of the relationship between in vitro brain volume and intelligence McDaniel (2005, 337) concluded: "For all ages and sex groups, it is clear that brain volume is positively correlated with intelligence."

A basic categorical mistake is to conflate the collective accomplishments of civilization with the understandings and intelligence of the average human—as in "we" formulated the theory of relativity, or "we" put a man on the moon. Scientific understanding of the origins of the universe and our species, the works of Shakespeare and Mozart, space exploration etc. are equated with human intelligence even though most people on the planet are unfamiliar and little affected by these achievements.

Intelligence, both social and collective, may be related to group size. Dunbar (1993, 681) suggests that cognitive constraints imply a consistent group size for effective human communities: "There is a species-specific upper limit to group size that is set by purely cognitive constraints." Effective group size is limited by the maximum number of individuals with whom a person (or animal) can maintain social relationships by personal contact. For humans this maximum number is somewhere around 150-200 individuals. Naroll (1956) presented evidence for a "critical threshold at a maximum settlement size of 500, beyond which social cohesion can be maintained only if there is an appropriate number of authoritarian officials." (quoted in Dunbar 1993, 687) The size of the neocortex increases with group size – but only up to a point.[25] Dunbar's argument does not contradict the evidence that human brain size, and by implication cognitive ability, decreased after agriculture.

5.3 Control without hierarchy[26]

Ultrasociality channeled the existing propensity to cooperate in a new direction (Gowdy & Krall 2014). For example, sociality, caring for others, and cooperation with non-kin are defining

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[25] In their commentary on Dunbar's paper, Falk and Dudek (1993) point out that a number of factors, including total brain size, can be correlated with larger group size. They also argue that there is nothing remarkable about the size of the human neocortex compared to other apes.

[26] This phrase is taken from Gordon (2007).

characteristics of the human species (Frith & Frith 2010). These traits not only made it possible for humans to flourish and survive the extreme environmental changes of the Pleistocene, they fostered sustainable use of environmental resources and equalitarian social arrangements (Boehm 1997; Pennisi 2014). In non-ultrasocial groups, these traits worked both for the benefit of the group and for individuals within the group. Small scale human societies have developed myriad forms of social organization to minimize group conflicts and to insure that one individual or one small group of individuals cannot dominate (Boehm 1997; Wilson, Ostrom & Cox 2013). Woodburn (1982, 438) writes of immediate return (simple technology and material culture) hunter-gatherers:

> Without seeking permission, obtaining instruction, or being recognized as qualifies (except by sex) individuals in these societies can set about obtaining their own requirements as they think fit. They need considerable knowledge and skill but this is freely available to all who are of the appropriate sex and is not, in general, transmitted by formal (or even informal) instruction: rather it is learnt by participation and emulation. In most, but not all, of these societies neither kinship status nor age is used as a qualification to obtain access to particular hunting and gathering skills or equipment.

But sociality and cooperation take on a different character with ultrasociality. Cooperation and coordination of activities in ultrasocial societies subjugate the individual to further the needs of the ultrasocial entity. The emergence of ultrasociality leads directly to a loss of autonomy at the individual level because autonomy interferes with the coordinated functioning of the group (Anderson & McShaea 2001, 219). There is general recognition that selfish behavior can subvert the common good. In evolutionary terms, adaptation at any given level in the MLS hierarchy tends to be undermined by what happens at lower levels (Wilson 2013). What is not generally recognized is that what is good for the higher level may be not be good for entities at the lower level. For humans, the most social of human activities is the reproduction of material life but the productive configuration of society changed with the active management of crops. In a sense cooperation was coopted with agriculture and rigidly structured around narrowly defined productive roles (Gowdy and Krall 2013). With human ultrasociality the terms “pro-social” and “contrasocial” lose definition. When food production becomes the organizing principle of a society, the “good of the group” becomes “the good of the ultrasocial entity” not the good of the average member of the group. What is good for the higher level entity may be bad for individuals at the lower level. Of course, "good" and "bad" are human value judgments that cannot be applied to ant societies.

When the evolutionary leap to ultrasociality is made, individual survival (and by extension to humans, individual well-being) becomes secondary to the survival of the group as an evolutionary entity. The selective “pull” of the group over the individual becomes greater with increasing complexity. In an ultrasocial system there is no reason why *specific individuals* should be more likely to survive. Like cells in a body or bees in a hive, particles are there to serve the collective. In ants and termites, serving the collective has implications for reproductive fitness. In the most extreme examples there are sterile castes. In humans the implications are different because sacrifice for the group is not expressed reproductively.[27] Rather it is measured in the extreme interdependency that delineates and reduces individual life to the role that enables the system itself to be reproduced. When the group begins to take on a life of its own and actively begins to shape its environment[28], individuals are expendable. The group *is* the organism subject

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[27] A reviewer pointed out that in human societies, unlike insect societies, human reproduction remains at the level of the individual organism. But for women, enhanced reproduction more narrowly defined their lives. Women in agricultural societies had many more offspring than hunter-gatherer women but their lives were shorter and arguably less satisfying. Women have been fighting for many generations not to be narrowly defined by their reproductive roles.

[28] There exists large literature on niche construction, a process whereby organisms selectively modify their environments and influence evolution (Laland & Brown 2006; Laland, Odling-Smee & Feldman 2001). Examples abound in nature, from beaver dams to nests and burrows. In

to the imperative to survive. Bees sting to defend the nest, thereby sacrificing themselves for the good of the group. In some species of ants, soldiers have such large mandibles they cannot feed themselves. Individuals are expendable for the good of the group.[29]

In both ultrasocial human and insect societies there is a loss of *totipotency*, defined as "the potential, throughout life, to express the full behavioural repertoire of the population (even if never actually expressed)…" (Crespi & Yanega 1995, 110). The term is meant to capture the range of behavior in a society (occupations, for example) compared to the range of behaviors available to a particular individual. It has been noted that workers in complex insect societies tend to be less totipotent (Anderson & McShea 2001). Studies of social insects and colonial marine invertebrates (reef shrimp) show a negative correlation between colony size and totipotency (Burkhardt 1998). Jaffe and Hebling-Beraldo (1990) find evidence to support the hypothesis that "individuals of highly social ant species are less complex than individuals from simple ant societies." In humans the loss of totipotency is more complex. It is expressed in the more extreme specialization that attends ultrasocial social organization but it is also expressed by the fact that for the majority of humans agricultural life became narrowly focused around a single economic purpose.

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ants, humans, and termites niche construction certainly accelerated with agriculture resulting in city states for these species (Campbell 1982).

[29] Some ants only live a few hours although the colony can persist for years. The loss of individuality is taken to extremes in ant societies that function as superorganisms. Flannery (2009, 2) writes: "In explaining what a superorganism is, Hölldobler and Wilson draw up a useful set of "functional parallels" between an organism (such as ourselves) and the superorganism that is an ant colony. The individual ants, they say, function like cells in our body, an observation that's given more piquancy when we realize that, like many of our cells, individual ants are extremely short-lived. Depending on the species, between 1 and 10 percent of the entire worker population of a colony dies each day, and in some species nearly half of the ants that forage outside the nest die each day." We do not suggest that humans have become ants in a colony but we may have taken that evolutionary path.

Interestingly, Adam Smith (1937 [1776], 735) also discussed the loss of what might be called human totipotency in complex societies as compared to what he called “barbarous” societies:

> Though in a rude society there is a good deal of variety in the occupations of every individual, there is no a great deal in those of the whole society. Every man does, or is capable of doing, almost every thing which any other man does, or is capable of doing. Every man has a considerable degree of knowledge, ingenuity, and invention: but scarce any man has a great degree. The degree, however, which is commonly possessed, is generally sufficient for conducting the whole simple business of the society. In a civilized state, on the contrary, though there is little variety in the occupations of the greater part of individuals, there is an almost infinite variety in those of the whole society.

Agriculture entailed an altered organization of economic life that changed the relationship among individuals within the group and the relationship of both the individual and the group to the biophysical world. Once in place, the economic factors driving efficiency in production gave a competitive advantage for those species that could best capture them. The evolution of state societies was reinforced by a process of “downward causation” (Campbell 1974; Sperry 1969). Campbell (1974) writes: “Where natural selection operates through life and death at a higher level of organization, the laws of the higher-level selective system determine in part the distribution of lower-level events and substances . . . *All processes at the lower levels of a hierarchy are restrained by and act in conformity to the laws of higher levels.”* Those societies having group traits most favorable to surplus production outcompeted other groups. The needs of the higher-level entity began to mold the behavior, organization and functions of lower-level entities. Some possible consequences of this for present human societies are discussed in the next section.

6. Summary and final speculations

We argue that with the widespread adoption of agriculture as the basis for human and insect societies, a transition was made to ultrasociality and that this transition was propelled by economic forces. With the transition, the group begins to function as a single organism and coalesces around the active management of the food supply. With this transition an altogether different group dynamic takes hold; an economic revolution becomes an evolutionary force of extraordinary proportions.

To summarize:

● The shift from hunting and gathering to agriculture was a major evolutionary transition to ultrasociality. The active management of food production is a transformational change in the configuration of productive life that propels greater interdependence and expansion. Agriculture harnessed the driving forces of a complex division of labor, increasing returns to larger group size, and the intensification of resource use by tapping into stocks of productive inputs and this encouraged growth and accumulation. Group selection favored those societies that were larger, more specialized and more aggressive in resource exploitation.

● Major bioeconomic characteristics common to insect and human agriculturalists are: a population explosion, dominance of ecosystems, and the subjugation of individuals to the group and its dynamic.

● Ultrasociality sets into motion processes of self-reinforcing downward causation so that lower levels in the system are at the service of the higher level collective. In the post-agriculture human economy, economic institutions, political systems, religions, and other moral systems fall in line to promote the goal of producing economic surplus.

● Evolutionary systems cannot see ahead. The ultrasocial system cannot see if it is locked into an unsustainable resource use pattern. The system works as a mechanical evolutionary process and will not self-correct until negative feedbacks begin to curtail surplus production. Early agricultural societies were characterized by overshoot and collapse of local ecosystems. In recent history, negative feedbacks affecting the human economy, from climate change, biodiversity loss, and fossil fuel exhaustion for example, have so far been minimal. Forces driving the exploitation of nature and of human labor will continue to work to keep economic output flowing.

These observations have important implications for two current human predicaments—the accelerating degradation of the earth's ecosystems and the generation of inequality. The general message from human ultrasociality is negative—the human enterprise is driven by a mechanical evolutionary process working against individual well-being and environmental sustainability. Humans have also evolved to be a cooperative species. But compassion and cooperation at the individual or even community level may not be sufficient to alter the growing imbalance between humans and the rest of the Earth. Indeed to address the imbalance it may be necessary to fundamentally change the mode of production on a larger scale. This will require changing the dynamic of expansion and the extensive interdependency of labor that is now characterized by extreme inequality. What seems clear from our analysis is that unless the expansionary tendency of the system can be controlled it will likely continue to grow. If this happens it is likely that the earth's life support systems will be destabilized in irrevocable ways (Barnossky et al. 2012; Pimm et al. 2014; Steffen et al. 2011). It would be well to concentrate on all the benefits that might ensue if we successfully change the structural dynamic of this system.

Changing the expansionary dynamic of the system will not be an easy task. The extent of the scaffolding of ultrasociality in our current market society is remarkable. In this economic world human societies have come to look more and more like colonies of ultrasocial ants. A new light is thrown on the idea of the competitive market as an "invisible hand" and Smith's notion that humans have a natural propensity to "truck, barter and exchange." An invisible hand is at work but it is very different than the benign, bottom-up conception of Adam Smith that individual self-interest will lead to the common good (Wilson & Gowdy 2014; Gowdy & Krall 2013). The propensity toward markets is the result of the invisible algorithms that have evolved through the play of natural selection on the group rather than an innate predisposition to create markets. Dominant religious, political, and institutional "cosmologies" (Gowdy et al. 2013; Sahlins 1996) reinforce the drive for production of surplus and a "leave the system alone" approach to public policy. Examples abound, of course, of societies resisting the worst aspects of the world economic order. Resistance has no analytical equivalent in ants (except perhaps attempts by workers to reproduce), but it is central to the human story.

Evidence is accumulating that our day of reckoning with our ultrasocial evolutionary legacy will soon arrive (Barnosky et al. 2012; Steffen et al. 2011). Ant and termite supercolonies are finely tuned entities that evolved over tens of millions of years to be dominant but sustainable players in the ecosystems in which they occurs. Humans are not ants or termites. Our very recent ultrasocial legacy is imperfect—it is far from being efficient and stable. Insects do not face the problems of unemployment and occupational discontent, nor are they disrupted by volatile financial markets, the problems associated with capital accumulation and the class conflict it engenders. The imperfect human ultrasocial system creates openings for change not presented to ants and termites. Perhaps the important question is how to tap these opportunities to gain control of the human ultrasocial system so that our species may once again have a sustainable and equitable way of life.

The human economy has now evolved into one worldwide socio-economic system, the global market economy—interdependent, highly complex and driven by economic forces of capital accumulation and the profit motive. If human society becomes a single entity there is no “selection” pressure. For example, now there seems to be no currently viable competing economic alternatives to market capitalism. The ultrasocial entity, whether ant or human, is a finely tuned and interlocked system defined by growth and accumulation, and the extreme material interdependence of its members. The ability of individuals to alter such systems is problematic. It is hard for us to see this control over our lives because we are so embedded in the system and because the control is invisible. Can we resist leaving a valuable productive resource like fossil fuel in the ground any more than an ant can resist exploiting a pile of sugar? The answer may be “no”. Unless present global trends quickly reverse themselves the human experiment with ultrasociality will likely end disastrously. Unlike the cases in the past where civilizations collapsed and the survivors moved on to other places, with a global overshoot and collapse surviving humans will have no place to go. E.O. Wilson (2014, 95) writes "Nothing at all can be learned from ants that our species should even consider imitating." The social insects are instructive, not as positive models of efficiency, but as a mirror showing the negative consequences of social organization based on the economics of surplus production. We evolved economic structures similar to ants and termites because the same general evolutionary forces drove our economic organization along similar paths. “Human nature” did not cause the dilemmas of inequality and environmental unsustainability. Humans are not naturally rapacious, hierarchical, and competitive any more than they are cooperative and egalitarian. Solving the daunting problems we face requires structural changes in the human economy, not merely changing individual values.

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REFERENCES

Aanen, D. & Boomsma, J. (2006) Social-insect fungus farming. *Current Biology* 16 (24): R1014-R1016.

Anderson, C. & McShea, D. (2001) Individual *versus* social complexity, with particular reference to ant colonies. *Biological Reviews*, 76: 211-237.

Ariely, D. 2008. *Predictably Irrational.* HarperCollins.

Bar-Yosef, O. (1998) The Natufian culture in the Levant, threshold to the origins of agriculture. *Evolutionary Anthropologist* 6:59–177.

Barnosky, A. et al. (22 authors) (2012) Approaching a state shift in earth's biosphere. *Nature* 486: 52-58.

Barrett, L., Henzi, P. & Rendall, D. (2007) Social brains, simple minds: Does social complexity really require cognitive complexity? *Philosophical Transactions of the Royal Society* B 362: 561-575.

Beerling, D. J. (1999) New estimates of carbon transfer to terrestrial ecosystems between the last glacial maximum and the Holocene. *Terra Nova* 11: 162–167.

Belfer-Cohen, A. & Bar Yosef, O. (2000) Early sedentism in the Near East - A bumpy ride to village life. In: *Life in Neolithic Farming Communities. Social Organization, Identity, and Differentiation,* ed. I. Kuijt, pp. 19-37. Kluwer Academic/Plenum Publishers.

Benckiser, G. (2010) Ants and sustainable agriculture. A review. *Agronomy for Sustainable Development* 30: 191-199.

Beshers, S. & Fewell, J. (2001) Models of division of labor in social insects. *Annual Review of Entomology*, 46: 413-440.

Binford, L. (1968) Post Pleistocene adaptations. In L. Binford & S. Binford (Eds.), *New Perspectives in Archaeolog*y. Aldine.

Biraben, J-N. (2003) The rising numbers of humankind. *Population & Societies* 394 (October): 1-4.

Blute, M. (2010) *Darwinian Sociocultural Evolution*. Cambridge University Press.

Bocquet-Appel, J-P. (2011) When the world's population took off: The springboard of the Neolithic demographic transition. *Science* 333: 560-561.

Boehm, C. (1997) Impact of the human egalitarian syndrome on Darwinian selection mechanisms. *American Naturalist* 150: 100-121.

Boehm, C. (1999) *Hierarchy in the Forest*. Harvard University Press.

Boehm, C. (2012) *Moral Origins: The Evolution of Virtue, Altruism, and Shame*. Basic Books.

Bowles, S. & Choi, J.-K. (2012). Holocene revolution: The co-evolution of agricultural technology and private property institutions. Santa Fe Institute.

Boyd, R. & Richerson, P. (1980) Effect of phenotypic variation on kin selection. *Proceedings of the National Academy of Sciences (USA*) 77: 7506-7509.

Boyd, R. & Richerson, P. (2002) Group beneficial norms spread rapidly in a structured population. *Journal of Theoretical Biology* 215: 287-296.

Bruce, A. & Burd, M. (2012) Allometric scaling of foraging rate with trial dimensions in leaf-cutting ants. *Proceedings of the Royal Society of London B* 279: 2442-2447.

Burkhardt, J. F. (1998) Individual flexibility and tempo in the ant, *Pheidole dentate*, the influence of group size. *Journal of Insect Behavior* 11: 493-505.

Campbell, D. (1974) Downward causation in hierarchically organized biological systems. In: *Studies in the Philosophy of Biology: Reduction and Related Problems.* F. Ayala & Dobzhansky, T. (eds.), MacMillan.

Campbell, D. (1982) Legal and primary-group social controls. In M. Gruter and P. Bohannan, Eds., *Law, Biology and Culture: The Evolution of Law*. Pp. 59-171, Bepress.

Campbell, D. (1983) The two distinct routes beyond kin selection to ultrasociality: Implications for the humanities and social sciences. In D. L. Bridgeman, Ed., *The Nature of Prosocial Development: Theories and Strategies*. Pp. 11-41, Academic Press.

Caporael, L. (1997) The evolution of truly social cognition. *Personality and Social Psychology Review* 1: 276-298.

Caporael, L. & Garvey, C. (2014) The primacy of scaffolding within groups for the evolution of group-level traits. *Behavioral and Brain Sciences* 37: 255-256.

Carneiro, R. L. (1970) A theory of the origin of the state. *Science* 169: 733–738

Caspermeyer, J. (2013) Genetic study pushes back timeline for first significant human population expansion. Molecular Biology and Evolution Press Office.

Choi, J-K. & Bowles, S. (2007) The coevolution of parochial altruism and war. Science 318: 636-640.

Cohran, G. & Harpending, H. (2009) *The 10,000 Year Explosion*. Basic Books.

Cohen, M. (1977) *The Food Crisis in Prehistory: Overpopulation and the Origins of Agriculture*. Yale University Press.

Cohen, M. & Crane-Kramer, G. (2007) *Ancient Health: Skeletal Indicators of Agricultural and Economic Intensification*. University Press of Florida.

Cox, S. (2009) Crop domestication and the first plant breeders. In *Plant Breeding and Farmer Participation*. Edited by S. Ceccarelli, E.P. Guimaraes and E. Weltizien, Food and Agricultural Organization of the United Nations (FAO), Rome, pp. 171-193.

Cox, M., Morales, D., Woerner, A., Sozanski, J., Wall, J. D., et al. (2009). Autosomal resequence data reveal late stone age signals of population expansion in sub-Saharan African foraging and farming populations. *PLoS ONE 4*(7): e6366.

Crespi, B.J. & Yanega, D. (1995) The definition of eusociality. *Behavioral Ecology and Sociobiology* 6: 109-115.

Culotta, E. (2013) Latest skirmish over ancestral violence strikes blow for peace. *Scienc*e 341: 244.

Darwin, C. (1871) *The Descent of Man, and Selection in Relation to Sex*. John Murray,

Diamond, J. (1997a) *Guns, Germs, and Steel: The Fates of Human Societies*. W.W. Norton.

Diamond, J. (1997b) The worst mistake in the history of the human race. *Discover Magazine*, May: 64-66.

Diamond, J. (2005) *Collapse: How Societies Choose to Fail or Succeed*. Viking Press.

Dunbar, R. (1993) Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences* 16: 681-735.

Edwards, S. & Pratt, S. (2009) Rationality in collective decision-making by ant colonies. *Proceedings of the Royal Society B* 276: 3655-3661.

Falk, D. & Dudek, B. (1993) Mosaic evolution of the neocortex. *Behavioral and Brain Sciences* 16: 701-702.

Ferguson-Gow, H., Sumner, S., Bourke, A. & Jones, K. (2014). Colony size predicts division of labor in attine ants. *Proceedings of the Royal Society B* 281: 2014.1411.

Fewell, J. & Page, R.E. Jr. (1999) The emergence of division of labor in forced associations of normally solitary ant queens. Evolutionary Ecology Research, 1: 537-548.

Fittkau, E. & Klinge, H. (1973) On biomass and tropic structure of the central Amazonian rain forest ecosystem. *Biotropica* 5: 2-14.

Flannery, K., (1968) Archaeological systems theory and early Mesoamerica. In *Anthropological Archaeology in the Americas* (ed. Meggers, B.) Anthropological Society of Washington, Washington, D.C., pp. 67-87.

Flannery, T. (2009) The superior civilization. Review of *The Superorganism* by B. Hölldobler and E.O. Wilson. *New York Review of Books*. Available on-line at: http://www.nybooks.com/articles/archives/2009/feb/26/the-superior-civilization/?pagination=false

Foley, R. (2008) The illusion of purpose in evolution. In Simon Conway Morris (ed.) *The Deep Structure of Biology* Templeton Foundation Press, 161-177.

Folgarait, P. (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation* 7: 1221-1244.

Foster, K. & Wenseleers, T. (2006) A general model for the evolution of mutualisms. *Journal of Evolutionary Biology* 19: 1283-1293.

Franks, N.R. (1987) The organization of worker teams in social insects. *Trends in Ecology and Evolution* 2: 72-75.

Fry, D. & Söderberg, P. (2013) Lethal Aggression in mobile forager bands and implications for the origins of war. *Science* 341: 270-273.

Frith, U. & Frith, C. (2010) The social brain: Allowing humans to boldly go where no other species has been. *Proceedings of the Royal Society of London B* 365: 165-176.

Geary, D. & Bailey, D. (2009) Hominid brain evolution: Testing climatic, ecological, and social competition models. *Human Nature* 20: 265-279.

Georgescu-Roegen, N. (1965) Process in farming versus process in manufacturing: A problem of balanced development. In U. Papi and C. Nunn, (Eds.) *Economic Problems of Agriculture in Industrial Societies.* MacMillan.

Georgescu-Roegen, N. (1976) Energy and economic myths. In *Energy and Economic Myths,* N. Georgescu-Roegen, (ed.), pp. 3-36., Pergamon Press.

Georgescu-Roegen, N. (1977) Inequality, limits, and growth from bioeconomic viewpoint. *Review of Social Economy* 35: 361-376.

Ghiselin, M. (2009) Review of *The Superorganism* by Bert Hölldobler and E.O. Wilson. *American Scientist* 97: 240-244.

Gordon, D. (2007) Control without Hierarchy. *Nature* 446: 143.

Gowdy, J. (ed.) (1998) *Limited Wants, Unlimited Means: A Reader on Hunter-Gatherer Economics and the Environment.* Island Press.

Gowdy, J., Dollimore, D., Wilson, D. & Witt, U. (2013) Economic cosmology and the evolutionary challenge. *Journal of Economic Behavior and Organization* 90S: S11-S20.

Gowdy, J. & Krall, L. (2013) The ultrasocial origins of the Anthropocene. *Ecological Economics* 95: 137-147.

Gowdy, J. & Krall, L. (2014) The transition to agriculture and the evolution of human ultrasociality. *Journal of Bioeconomics* 16(2): 179-202.

Grayson, D & Meltzer, D. (2003) A requiem for North American overkill. *Journal of Archaeological Science* 30: 585-593.

Grinsted, L., Agnarsson, I. & Bilde, T. (2012) Subsocial behaviour and brood adoption in mixed-species colonies of two theridiid spiders. *Naturwissenschaften* 99:1021–1030

Hawks, J. (2011) Selection for smaller brains in Holocene human evolution. http://johnhawks.net/research/hawks-2011-brain-size-selection-holocene

Hawks, K. (2003) Grandmothers and the evolution of human longevity. *American Journal of Human Biology* 15: 380-400.

Hodgson, G. & Knudsen, T. (2010) *Darwin's Conjecture: The Search for General Principles of Social & Economic Evolution.* University of Chicago Press.

Holbrook, T., Clark, R., Jeanson, R., Bertram, S., Kukuk, P. & Fewell, J. (2009) Emergence and Consequences of Division of Labor in Associations of Normally Solitary Sweat Bees. *Ethology* 115: 301-310.

Holbrook, T., Barton, M. & Fewell, J. (2011) Division of labor increases with colony size in the harvester ant *Pogonomyrmexcalifornicus*. *Behavioral Ecology* 22: 960-966.

Hölldobler, B. & Wilson, E.O. (2009) *The Superorganism*. W.W. Norton.

Hölldobler, B. & Wilson, E.O. (2011) *The Leafcutter Ants*. W.W. Norton.

Hou, C., Kaspari, M., Zanden, H. & Gillooly, J. (2010) Energetic basis of colonial living in social insects. *Proceedings of the National Academy of Sciences* 107: 3634-3638.

Jaffe, K. & Hebling-Beraldo, M. (1990) Respirometry and the evolution of order: negentropy criteria applied to the evolution of ants. In Proceedings of the 11th conference of the International Union for the Study of Social Insects, Bangalore, India. G. Vereesh, B. Mallik, C. Viraktamath. Oxford Press.

Judd, T. & Sherman, P. (1996) Naked mole-rats recruit colony mates to food sources. *Animal Behaviour* 52: 957-69.

Kahn, A. (1966) The tyranny of small decisions: market failures, imperfections, and the limits of economics. *Kyklos* 19: 23-47.

Kaplan, H., Hill, K., Lancaster, J. & Hurtado, M. (2000) A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology* 156-185.

King, J., Warren, R. & Bradford, M. (2013) Social insects dominate eastern US temperate hardwood forest macroinvertebrate communities in warmer regions. *PLoS One*. DOI: 10.1371/journal.pone.0075843.

Korb, J. (2007) Termites. *Current Biology* 17: R995-R999.

Kuijt, I. & Finlayson, B. (2009) Evidence for food storage and predomestication granaries 11,000 years ago in the Jordon Valley. *Proceedings of the National Academy of Sciences* 106: 10966-10970.

Laland, K. & Brown, G. (2006) Niche contruction, human behavior, and the dapative-lag hypothesis. *Evolutionary Anthropology* 15: 95-104.

Laland, K., Odling-Smee, F. & Feldman, M. (2001) Niche construction, biological evolution, and cultural change. *Behavioral and Brain Sciences* 23: 131-175.

Lambert, P. (2009) Health versus fitness. *Current Anthropology* 50: 603-608.

Larsen, C. S. (2006) The agricultural revolution as environmental catastrophe: Implications for health and lifestyles in the Holocene. *Quaternary International* 150: 12–20.

Lee, R. (1968) What hunters do for a living, or, how to make out on scarce resources. Reprinted in Gowdy, 1968, pp. 43-63.

Lee, R. (1984) *The Dobe Ju/'hoansi* (4th ed.). Wadsworth.

Lloyd, E. (2012) Units and levels of selection. *The Stanford Encyclopedia of Philosophy* (Winter 2012 Edition), Edward N. Zalta (ed.), URL = <http://plato.stanford.edu/archives/win2012/entries/selection-units/>.

Lotka, A. (1925) *Elements of Physical Biology*. Baltimore: Williams and Wilkins. Reissued in 1956 as *Elements of Mathematical Biology*, Dover.

MacDaniel, M. (2005) Big-brained people are smarter: A meta-analysis of the relationship between in vivo brain volume and intelligence. *Intelligence* 33: 337-346.

Makarewicz, C. (2012) The Younger Dryas and hunter-gatherer transitions to food production in the Near East. In Eren, M. (ed.) *Hunter–Gatherer Behaviour—Human Response During the Younger Dryas.* Pp. 195-230, Left Coast Press.

Matthew, S. & Boyd, R. (2011) Punishment sustains large-scale cooperation in prestate warfare. *Proceedings of the National Academy of Science USA*, 108: 11375-11380.

McAuliffe, K. (2011) If modern humans are so smart, why are our brains shrinking? *Discover Magazine,* January 20.

McCorriston, J. & Hole, F. (1991) The ecology of seasonal stress and the origins of agriculture in the Near East. *American Anthropologist* 93: 46-69.

McCorriston, J. & Hole, F. (2000a). Barley. *The Cambridge World History of Food. Vol. 1*, K. Kiple and K Ornelas (eds), pp. 81-90, Cambridge University Press.

McCorriston, J. & Hole, F. (2000b). Wheat. *The Cambridge World History of Food. Vol. 1*, K. Kiple and K Ornelas (eds), pp. 158-174, Cambridge University Press.

McDaniel, M. (2005) Big-brained people are smarter: A meta-analysis of the relationship between in vivo brain volume and intelligence. *Intelligence* 33: 337-346.

Michod, R. (2005). On the transfer of fitness from the cell to the multicellular organism. *Biology and Philosophy* 20: 967-987.

Mithen, S. (1996) The prehistory of the mind: a search for the origins of art, science and religion. Thames & Hudson.

Mithen, S. (2007) Did farming arise from a misapplication of social intelligence? *Philosophical Transactions of the Royal Society B* 362: 705-718.

Moffett, M. (2010) *Adventures among the Ants*. University of California Press.

Moffett, M. (2012) Supercolonies of billions in an invasive ant: what is a society? *Behavioral Ecology* 23, 925-933.

Mueller, U. & Gerardo, N. (2002) Fungus-farming insects: Multiple origins and diverse evolutionary histories. *Proceedings of the National Academy of Science* 99(24): 15247-15249.

Mueller, U., Gerardo, N., Aanen, D., Six, D. & Schultz, T. (2005) The evolution of agriculture in insects. *Annual Review of Ecology, Evolution, and Systematics* 36: 563-95.

Mueller, U., Rehner, S. & Schultz, T. (1998) The evolution of agriculture in ants. *Science* 281: 2034-2038.

Munro, N. (2003) Small game, the younger dryas, and the transition to agriculture in the southern levant. *Mitteilungen der Geseelschaft für Urgeschichte* 12: 47-71.

Nanay, B. (2005) *Can* cumulative selection explain adaptation? *Philosophy of Science* 72: 1099-1112.

Naroll, R. (1956) A preliminary index of social development. *American Anthropologist* 58: 687-715.

Nowak, M., Tarnita, C. & Wilson, E.O. (2010) The evolution of eusociality. *Nature* 466: 1057-1062.

Okasha, S. (2006) *Evolution and the Levels of Selection*. Oxford University Press.

Oster, G.F. & Wilson, E.O. (1978) *Caste and Ecology in the Social Insects*. Princeton University Press.

Pennisi, E. (2014) Our egalitarian Eden. *Science* 344: 824-825.

Pimm, S., Jenkins, C., Abell, R., Brooks, T., Gittleman, J., Joppa, L, Raven, P., Roberts, C. & Sexton, J. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344: 987-996.

Price, D., & Bar-Yosef, O. (2011). The origins of agriculture: New data, new ideas. *Current Anthropology* 52 S163-S174.

Prentiss, A. (2012) The cultural evolution of material wealth based inequality at Bridge River, British Columbia. *American Antiquity* 77: 542-564.

Pringle, H. (2014) The ancient roots of the 1%. *Science* 344: 822-825.

Reeve, H.K. (2000) Multi-level selection and human cooperation. Evolution and Human Behavior, 21: 65-72.

Richerson, P. & Boyd, R. (1998) The Evolution of human ultra-sociality, In: *Ideology, Warfare, and Indoctrinability.* In I. Eibl-Eibisfeldt & F. Salter (eds.) pp. 71-95, Berghan Books.

Richerson, P. & Boyd, R. (2005) *Not By Genes Alone: How Culture Transformed Human Evolution.* University of Chicago Press.

Richerson, P., Boyd, R. & Bettinger, R. (2001) Was agriculture impossible during the Pleistocene but mandatory during the Holocene? A climate change hypothesis. *American Antiquity* 66: 387-411.

Rindos, D. (1984) *The Origins of Agriculture: An Evolutionary Perspective.* Academic Press.

Riveros, A., Seid, M. & Wcislo, W. (2012) Evolution of brain size in class-based societies of fungus-growing ants (Attini). *Animal Behavior* 83: 1043-1049.

Rosen, A. & Rivera-Collazo, I. (2012) Climate change, adaptive cycles, and the persistence of foraging economies during the late Pleistocene/Holocene transition in the Levant. *Proceedings of the National Academy of Sciences* 109: 3640-3645.

Ryan, C. & Jethá, C. (2010) *Sex at Dawn*. Harper Perennial.

Sahlins, M. (1996) The sadness of sweetness: The native anthropology of Western cosmology. *Current Anthropology* 37: 395-428.

Sanderson, E., Jaith, M., Levy, M., Redford, K., Wannebo, A. & Woolmer, G. (2002) The human footprint and the last of the wild. *BioScience,* 52: 891-904.

Santana, C. & Weisberg, M. (2014) Group-level traits are not units of selection. *Behavioral and Brain Sciences* 37: 271-272.

Seid, M., Castillo, A. & Wcislo, W. (2011) The allometry of brain miniaturization in ants. *Brain, Behavior, and Evolution* 7: 5-13.

Shakun, J., Clark, P., Marcott, S., Liu, Z. & Otto-Bliesner, B. (2012) Global warming preceded by increasing carbon dioxide concentrations during the last deglaciation. *Nature* 484: 49-54.

Shik, J., Hou, C. Kay, A., Kasari, M. & Gillooly, J. (2012) Towards a general life-history model of the superorganism: Predicting the survival growth, and reproduction of ant societies. *Biology Letters.* doi: 10.1098/rsbl.2012.0463

Smaldino, P. (2014) The cultural evolution of emergent group-level traits. *Behavioral and Brain Sciences* 37:243-295.

Smil, V. (2013) *Harvesting the Biosphere*. MIT Press.

Smith, A. (1937 [1776] *An Inquiry into the Nature and Causes of the Wealth of Nations*. Modern Library.

Smith P. (1972) Diet and attrition in the Natufians. *American Journal of Physical Anthropology* 37: 233–238.

Sober, E. & Wilson, D.S. (1998) *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Harvard University Press.

Spencer, C. (2010) War and early state formation in Oaxaca, Mexico. *Proceedings of the National Academy of Science USA*, 100: 11185-11187.

Sperry, R. (1969) A modified concept of consciousness. *Psychological Review*, 76: 532-536.

Steffen, W., Grinevald, J., Crutzen, P. & McNeill, J. (2011) The Anthropocene: conceptual and historical perspectives. *Philosophical Transactions of the Royal Society A* 369: 842-867.

Tainter, J., Allen, T.F.H. & Hoekstra, T.W. (2006) Energy transformations and post-normal science. *Energy* 31: 44-58.

Tennie, C., Call, J., & Tomasello, M. (2009) Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364, 2405-2415.

Tilly, C. (1992). Coercion, Capital, and European States, AD 990-1992. Blackwell.

Trivers, R. (1971) The evolution of reciprocal altruism. *Quarterly Review of Biology* 46: 35-57.

Turchin, P. (2006) *War and Peace and War: The Life Cycles of Imperial Nations*. Princeton University Press.

Turchin, P. (2013) The puzzle of human ultrasociality: How did large-scale complex societies evolve? In *Cultural Evolution*, Richerson, P. & Christiansen, M. eds., pp. 61-73, MIT Press.

Turchin, P., Currieb, T., Turner, E. & Gavrilets, S. (2013) War, space, and the evolution of Old World complex societies. *Proceedings of the National Academy of Sciences* 110(4): 16384-163-89.

van den Bergh, J. & Gowdy, J. (2009). A group selection perspective on economic behavior, institutions and organizations. *Journal of Economic Behavior and Organization* 72: 1-20.

Vanberg, V. (2014) Collective action, institutional design and evolutionary "blindness". *Journal of Bioeconomics* 16: 99-104.

Wcislo, W. (2012) Big brains, little bodies. *Science* 338: 1419.

Weiss, H. & Bradley, R. (2001) What drives societal collapse? *Science* 291: 609-610.

Weiss, H., Courty, M.A., Wetterstrom, W., Guichard, F., Senior, L., Meadow, R. & Curnow, A. (1993) The Genesis and collapse of third millennium North Mesopotamian civilization. *Science* 261: 995-1004.

Wexler, B. E. (2006) *Brain and Culture.* MIT Press.

Williams, G. (1957) Peiotropy, natural selection, and the evolution of senescence. *Evolution* 11: 398-411.

Williams, G. (1992) *Natural Selection: Domains, Levels, Challenges*. Princeton University Press.

Wilson, D.S. (1997) Human groups as units of selection. *Science* 276: 1816-1817.

Wilson, D.S. (2010) Truth and Reconciliation for Group Selection. Available at: http://evolution.binghamton.edu/dswilson/wp-content/uploads/2010/01/Truth-and-Reconciliation.pdf

Wilson, D.S. (2013) A good social Darwinism. *Aeon Magazine*, on-line. July 4.

Wilson, D.S. & Gowdy, J. (2013) Evolution as a general theoretical framework for economics and public policy. *Journal of Economic Behavior and Organization* 90S: SS3-S10.

Wilson, D.S. & Gowdy, J. (2014) Human ultrasociality and the invisible hand: Foundational developments in evolutionary science after a foundational concept in economics. *Journal of Bioeconomics,* Under review.

Wilson, D.S., Ostrom, E. & Cox, M. (2013) Generalizing the core design principles for the efficacy of groups. *Journal of Economic Behavior and Organization* S90: S21-S32.

Wilson, E.O. (1971) *The Insect Societies.* Harvard University Press.

Wilson, E.O. (1975) *Sociobiology: The New Synthesis.* Harvard University Press.

Wilson, E.O. (1987) Causes of ecological success: The case of the ants. *Journal of Animal Ecology* 56: 1-9.

Wilson, E. O. (2008) One giant leap: How insects achieved altruism and colonial life. *BioScience* 58: 17-25.

Wilson, E.O. (2012) *The Social Conquest of Earth*. W.W. Norton.

Wilson, E.O. (2014) *The Meaning of Human Existence*. W.W. Norton.

Wilson, E.O. & Hölldobler, B. (2005) Eusociality: origin and consequences. *Proceedings of the National Academy of Sciences* 102(38): 13367-13371.

Woodburn, J. (1982). Egalitarian societies. *Man* 17: 431–451 (reprinted in Gowdy 1998).

Wright, R. (2004). *A Short History of Progress.* House of Anansi Press.

Zvelebil, M., & Rowley-Conwy, P. (1986). Foragers and farmers in Atlantic Europe. In M. Zvelebil (Ed.), *Hunters in Transition.* pp. 67–93, Cambridge University Press.