

(12/09/2012)

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UNDERSTANDING COLONIAL TRAITS USING SYMBIOSIS RESEARCH AND ECOSYSTEM ECOLOGY

FINAL VERSION PUBLISHED IN

BIOLOGICAL THEORY, 4 (SUMMER 2009) PP. 240-246

[HTTP://WWW.MITPRESSJOURNALS.ORG/DOI/ABS/10.1162/BIOT.2009.4.3.240](http://www.mitpressjournals.org/doi/abs/10.1162/BIOT.2009.4.3.240)

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ABSTRACT: E. O. Wilson (1974: 54) describes the problem that social organisms pose: “On what bases do we distinguish the extremely modified members of an invertebrate colony from the organs of a metazoan animal?” This framing of the issue has inspired many to look more closely at how groups of organisms form and behave as emergent individuals. The possible existence of “superorganisms” test our best intuitions about what can count and act as genuine biological individuals and how we should study them. As we will discuss, colonies of certain organisms display many of the properties that we usually reserve only to individual organisms. Although there is good reason to believe that many social insects form genuine emergent biological individuals, the conclusion offered here is of a slightly different sort. I will argue that to understand some social insects’ interactions and the emergent traits they give rise to, it may be helpful to shift our understanding from a community-level approach to an ecosystem-level approach. I will argue that viewing certain insect colonies (termites) as parts of ecosystems allows us to better understand some of the adaptations that have emerged from their evolution.

Keywords

Biological individuality; Social Insects; Emergence; Adaptation

1. Thinking about Biological Individuality

All organisms are individuals but not all individuals are organisms (for good surveys of these issues see J. Wilson [2007] and R. A. Wilson [2007]). A complete discussion of biological individuality cannot be offered here, but a few points need to be made.

Physical continuity is not an essential property to being a biological individual. Janzen (1977) makes this point explicitly when describing dandelion patches and aphid colonies as counterintuitive cases of emergent biological individuality and coined “evolutionary individuals” to refer to these individuals.

The point about physical continuity is often even more dramatic. As Horvath (1997) describes correctly in the case of slime mold, we get a case where physical continuity is clearly transitory: the spore stage lacks physical continuity between parts of the slime mold, whereas slug stages are completely integrated amoeba colonies.

If physical continuity is not satisfactory to characterize biological individuality, where should

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we look? Many authors (Wilson and Sober [1989]; Janzen [1977] to some extent) emphasize functional integration as a more significant component of biological individuality. Biological individuals are entities that act, perform, and survive as wholes. In contemporary literature of evolutionary transitions and dynamics one finds similar ideas framed in terms of cooperation (an individual emerges if lower-level parts eliminate competition in favor of cooperation). For biological entities, such functional integration is most often seen as the result of natural selection.

Some have attempted to characterize functional integration for colonies. McShea and Venit (2002), in discussing the functional integration between zooids of a colony argue that the degree of “connectedness” can be as simple as the shape of wall (or membrane) or behavioral interactions, and go on to argue that “connectedness between parts” is a fundamental criterion for establishing the individuality of colonies.

If an ensemble of components (these components being in the cases described here distinct organisms) persists or disappears as a whole when faced with pressures from the environment, and if the explanation of their common fate is their mutual interactions, we have an “emergent” individual. This common fate criterion is described in relation to emergent individuals in Wilson and Sober (1989) to argue in favor of studying superorganisms in the context of a richer notion of multilevel selection. As Hamilton et al. (2009) point out, although Wilson and Sober use the term “superorganism,” the argument may be better served by focusing on the term “individual.” Using “superorganism” forces us to focus on an analogy to a specific category, *organisms*, that is already heavily intuition-laden—Hölldobler and Wilson’s (2008) book is an example of some of the interpretative difficulties of using the word “superorganism.” From a discussion on group selection and how social insect colonies could be construed as superorganisms, Wilson and Sober define biological individuality in terms of functional integration and common fate. The functional organization will in most cases be the result of adaptation, and the common fate arises from a common selective pressure. To paraphrase their suggestion, let us offer a provisional definition for biological individuality to guide our discussion: *A biological individual is a functionally integrated entity whose integration is linked to the common fate of the system when faced to selective pressures of the environment.*

Following Wilson and Sober's suggestion we will adopt the view that, arguably, functional organization is a central aspect of biological individuality (see Gould and Lloyd 1999 for criticism of this view).

Although the question obviously has significant ontological implications, the treatment offered here is not necessarily committed to a specific strong metaphysical claim concerning the individuality of said systems. I argue that there is some explanatory benefit in describing some systems as individuals with functional traits, but this does not fully address the ontological question about whether there are in fact emergent individuals. For now, let us agree that there *seems* to be emergent functional integration above the organismal level and see where that takes us. As McShea and Venit suggest, to understand the functional integration within an individual, one has to understand how the various components interact. Such components in organismal biology usually refer to traits.

2. Identifying Emergent Traits

Many disciplines use the term “trait,” and each does so according to its own purposes. The term “trait” itself is not always used, but equivalents are always somewhere in the background. The term “character”, for example, is often used in organismal biology. The difficulty of pinpointing one meaning is not surprising: whole-parts relationships are a classical philosophical relationship that has yet to find a definitive resolution (McShea and Venit 2000). A nice example of the intricacy of the issue in biology is in contemporary work in phenotype ontology research and the attempts to develop a unified syntax to describe organismal traits (Mabee et al. 2007). Part of the difficulty is in figuring out the relationship between trait, phenotype, and adaptation. I cannot solve these issues here (see Brandon 1990 for a primer), but some provisional points can be made.

First, the concept of trait is maybe as crucial to understand how colonies thrive as the concept of individuality. This is not surprising if we adopt Wilson and Sober's notion of biological individuality.

Let us consider a provisional way of identifying traits: a trait is any varying part of a system that affects the fitness (broadly construed) of that system. Here a trait is linked to adaptations. In ecology, the description of the link between trait and adaptation is described somewhat differently: a trait may be what affects, for instance, community assembly. Since community assembly has direct impact on the survival of the organisms in the community, the intuitive link between trait and adaptations remains. But this stance is not uncontroversial. As Gould and Lewontin (1979) famously argued contra pan-adaptationism, issues of functional description, modularity, and adaptations are intertwined when defining what a trait is and, they argue, often lead us to misguided descriptions of how organisms actually function. This broader debate will not be resolved here, but let us assume for a moment that traits are linked to fitness differences. To be safe, we could say that all adaptations are traits but remain agnostic about the converse. We will later see how this applies to colonies.

Instead of agreeing on a complete definition of what a trait is, it may be sufficient to agree on ways to *identify* what some traits may be. Special questions of reductionism arise in the cases of colonies and communities. How can we be sure such traits exist at an emergent colony level and are not merely an aggregate of lower-level individuals? An advantage of identifying traits with adaptations is that an indirect way of identifying a trait is to see whether new selective regimes come into play when a new variation appears in a system. In the case we will be looking at, this links traits to adaptations, and therefore, to trait functions that are identified relative to their evolutionary role and, more importantly, to their potential effect. Although this seems to associate my account to Wright/selected effects contra Cummins/causal role functional accounts, it does not (see Bouchard in press for a discussion of how ecosystem selection warrants functional pluralism).

3. Colonies and Symbiosis

Now that we have briefly highlighted the significance of the concept of individuality and of traits, we can start looking at how they apply to colonial individuals such as eusocial insects and the community they take part in. Many colonies seem to maintain some sort of emergent equilibrium state. Colonial insects such as ants, wasps, bees, and termites can foster what Wilson refers to as “social homeostasis.” Wilson defines social homeostasis as “[t]he maintenance of steady states at the level of the society either by control of the nest microclimate or by the regulation of the population density, behavior, and physiology of the group as a whole” (Wilson 1971: 469). The fact that a hive, say, may maintain a constant internal temperature raises the possibility that this temperature maintenance ability is an emergent trait for the emergent individual that is the hive. Such a hypothesis is often entertained in the colony literature (see Hölldobler and Wilson 2008: 49-50 for an explicit mention of the question).

We will focus on how some species of termites develop similar traits and see what lessons fall out of it. Turner writes eloquently about termite colonies and how they attain some very complex forms of social homeostasis:

I shall use the term colony to describe the assemblage of individual organisms that make up a familial unit. For example, a termite colony represents the descendants of a single queen, as well as the symbionts associated with them. The nest is the structure in which a colony is housed. ... Among termites, the nest often has associated with it ancillary structures, the most spectacular being a mound. (Turner 2000: 180)

This definition of colony is not without problems. First, it does not distinguish between single species, eusocial insect colonies, and eusocial insects involved in broader multi-species communities. Following Hölldobler and Wilson, I would recommend using the word colony to refer only to the single species collective of organisms working cooperatively, and treat multi-species communities as a separate case. Turner melds two ideas in this notion of colony: (1) that collections of same-species individual organisms can act as one emergent individual, and (2) that collections of individuals of different species can act as one emergent individual. Some cases examined by Turner focus on case (1), while others focus on case (2). However, they deserve distinct treatment. After all, is the mound linked primarily to termites or to the symbiotic community in which termite colonies take part? There might be a way to resolve the issue by focusing on the fact that with mounds we are dealing with an abiotic structure (i.e., in this case, dried mud). As we shall see, I view this as a first hint that ecosystem analysis may be more fruitful to understand some emergent traits of some emergent individuals; we must go beyond the colony or the community approach to understand the functioning of the mound. To see this, we must discuss cases where colonies are involved in symbiotic communities.

All biologists agree on the fact that symbioses are enduring associations between individuals pertaining to different species. However, there is no consensus on the way these associations should be defined beyond that (for a detailed history of the field see Sapp 1994). Some researchers consider symbioses as associations in which both partners derive a benefit. This

usage, consistent with the popular understanding of the term, comes down to identifying symbioses to mutualisms. As a result, parasitism is excluded from the purview of symbiosis research. In contrast, other biologists (e.g., Goff 1982; Lewin 1982; Saffo 1996; Paracer and Ahmadjian 2000) favor a broader definition, in which symbiosis is understood independently of the consequences of the interaction. Provided that the association persistently involves individuals of different species, it counts as a case of symbiosis, even if one of the partners derives no apparent benefit from it (commensalism) or is demonstrably harmed by the interaction (parasitism).

Despite this lack of consensus on the definition, there are reasons to prefer the outcome-independent one. Several problems are associated with the definition of symbiosis as mutually advantageous interaction. To name but one, it is often unclear whether both partners really benefit from the interaction, because the exact nature of its consequences for at least one of the symbionts is not well understood. Lichen, say, which is a symbiosis between algae and fungi, used to be categorized as a mutualism. However, the algae seem to derive no benefit from the interaction. Some researchers (e.g., Ahmadjian and Jacobs 1983) have hypothesized that the fungi might parasitize the algae (see Sanders 2001 for review).

For our purposes it is preferable to endorse the broader definition of symbiosis and to conceive of the different categories of interactions (parasitism, commensalism, and mutualism) along a continuum rather than as being sharply distinct. Also, by focusing on the idea of persistence of association to identify symbioses, one gets an idea of symbioses that will be compatible with Wilson and Sober's common fate criterion, which will allow us to understand some emergent individuals as evolving ecosystems.

4. Termite Mound as Ecosystem

Let us now briefly examine a particular case where colonies and symbioses are involved. Turner's work mentioned earlier is an inspiration for the treatment offered here. Turner (2000), examining the notion that organisms could have external physiologies, describes in detail the fungus-growing, mound-building termites *Macrotermes* (he is mostly interested in *Macrotermes michaelseni* but the problem is similar for many related species such as *Macrotermes natalensis*). A succinct description will hopefully be sufficient to give an idea of the broader argument.

Reprising Lüscher's (1961) analysis, Turner explains how the termite colony "breathes," consuming oxygen and producing CO₂. The colony is in a symbiotic relationship with fungus (Termitomyces) that it harvests within the nest. Fungus is often a parasite for social insects, but the slow growing Termitomyces is actually "good for" the termites. Consuming that fungus aids termites' digestion of wood (cellulose), which they are unable to effectively digest by themselves. The slow growth of Termitomyces may also explain why the fungus takes advantage of the shelter of the mound contra other, faster growing species of fungi. (Outside of mounds, Termitomyces are overtaken by most other fungi because of their slow growth rate.)

This mutualistic relationship has allowed both species to explore niches previously unavailable to them (Aanen et al. 2002). At least on the termite side, the symbiosis is now obligate insofar as the termites need to ingest the fungus to be able to digest the cellulose found in their primary food source. In this way, the fungus plays a metabolic function for the termites. To make an imperfect analogy, the termites need the fungus as much as humans need their liver. Individual termites benefit from ingesting the fungus, but it is the colony of termites that does the fungus-growing. Division of labor is a well-studied phenomenon in social insects, and it is important to understand that this primitive agriculture in termites is possible only because some termites are allocated different tasks.

The fungus-harvesting is impressive by itself, but this behavior occurs within a mound constructed by the termites for a very particular function. In order for the colony to grow, it needs to evacuate some of the CO₂ generated by the termites and fungus and let in oxygen from the outside. The impressive spires built by the *Macrotermes michaelseni* (which are three metres high on average and oriented relative to local wind patterns in what seems to be a nonrandom fashion) may contribute to this function. Turner argues (again in an echo to Lüscher's work) that a colony of termites creates a mound in a way that it controls the CO₂ present for the colony. The convection produced by the pressure differential of the mound's spire sucks out CO₂ and sucks oxygen in. The colony, Turner argues, in some sense creates a lung for itself to maintain its social homeostasis.

This homeostasis allows for the system, in this case the colony, to increase its capacity to survive or persist (he also makes this point in Turner 2004). Turner focuses on how the mound is a trait for the termite colony, but this point needs further analysis. As I have pointed out earlier, the distinction between colonies and communities in cases where social insects are involved in symbioses is not trivial: are we identifying a “lung” for the colony *or* for the symbiotic community? However peculiar this question may seem, it obscures a more fundamental point. In either case, the species are interacting with abiotic structures that act for the benefit of the emergent individual level. Whether we have a collection of termites or an assemblage of termites and fungus, they both use the mound (ultimately a dried mud chimney) as a lung.

If, as Turner argues, some physical structures (e.g., mounds) should be understood as external organs built by organisms, then we have to include non-biological materials and structures in our construal of evolving individuals. If an evolving individual may be in part non-biological, then it is possible that its evolution will not be fully accounted for via a populational approach, since the adaptive external structures that Turner describes cannot be passed on genetically.

To fully appreciate this one needs to better understand the difference between communities and ecosystems. As most of the terms defined in this article, there are no agreed-upon definitions of the terms, but a broad consensus has emerged. Odenbaugh (2007) offers a detailed analysis of the concepts and their consequences for ecology.

A *community* corresponds to the assemblage of most or all interacting species (populations) in a given area, ecological niche, or environment. Communities are defined solely by the biotic entities included in it. Proponents of this view include MacArthur and Gleason. Some

(Hutchinson, Clement) think communities need not be functionally integrated, but this view is the minority view in contemporary ecology.

An *ecosystem* corresponds to the functional assemblage of all communities as well as their abiotic (physical, chemical, geological, climatic) environment. This view has been defended by Tansley, Lindeman, Elton, etc.

In short, “community” is a populational term focusing on the demographic distribution of the biotic individuals in a given context (e.g., predator-prey population interactions), whereas “ecosystem” is a functional term focusing on the functional integration between biotic and abiotic subsystems in a given context. I argue that an ecosystem approach is better equipped to encompass fully the functional system that is the termite-fungus-mound system. Dangerfield et al. (1998) make a related claim in describing the termite colony as “ecosystem engineers.” In a basic sense this is true of many species where niche construction is involved. The more radical point is that an ecosystem approach is the best way to understand certain emergent traits of colonies.

5. Emergent Traits and Ecosystems

In the case examined here—the interaction between termites and fungi—I have argued that the emergent individual is the ecosystem: the mound is a trait in the adaptative sense, and it is arguably “good for” the symbiotic community composed of termites and fungus. This system is composed of both abiotic material and communities, which fits the ecosystem view much better than a community approach.

Of course, these are not trivial claims and they need further development (the broader argument can be found in Bouchard 2004, 2008; Turner 2004). But the take-home message is relatively straightforward: If we are to entertain seriously the existence of “superorganisms,” we have to expect emergent traits at the “superorganism” level. Because many social insects are involved in symbiotic communities, these traits may not always be trackable to the allelic frequencies of a single species, making the notion of fitness at the superorganism level complicated at best. Moreover, the fact that, sometimes, abiotic structures can act as fundamental parts of a superorganism means that we need revamped models to think about biological evolution.

There is hope in this regard. Biologists have for a long time studied how multi-species communities interact with their environment. Ecosystem ecology is based on the idea that it is more fruitful to consider the assemblage of biotic and abiotic material in some environments as genuinely integrated systems that perform (or fail) as integrated wholes—a distinct echo of how we discussed biological individuality earlier. Maybe superorganism research would be better served by looking at ecosystem research for inspiration as to how to understand the evolution of complex emergent traits.

The mound is a trait, but a trait for whose benefit? In the case of the association between termites and fungi, it is the trait of a symbiotic community as a whole. But since the trait itself is abiotic and can be passed on from one generation to the next, it may be more appropriate to talk about the trait of an ecosystem instead of the trait of a community. The emergent individual here is the ecosystem of which the colony, the fungus, and the mounds are parts.

For many, there is something awkward about talking about ecosystem traits (or characteristics). There are at least two points of contention here: (1) Are these associations really ecosystems? (2) Can ecosystems be said to have traits? Let us come back to the benefits of answering positively to both questions. The claim is that to understand some apparent adaptations in nature, it is more helpful to focus on how social insects are involved in ecosystems instead of communities. The importance of abiotic structures in the thriving of these communities makes an ecosystem approach necessary. The idea is that it is those ecosystems that are genuine evolutionary individuals, since they are the ones subject to the external selective pressures and they are the ones where a response to selection is displayed. (This does not preclude lower level individuals from continuing to struggle for survival.) The adaptive trait that the mound is exists at the ecosystem level. But how are we to relate this adaptation to fitness?

Fitness is a controversial subject within evolutionary theory (see Rosenberg and Bouchard 2009 for a philosophical survey). Most would agree that fitness has two components—survival and reproduction. For most species, biology has emphasized reproduction over survival, the latter being described as a means to achieve reproductive success (Sober 2001). In the case of insect colonies—or more precisely, as I have argued, colonial ecosystems—thinking solely in terms of persistence is fruitful insofar as it helps us understand adaptive traits such as the mound. Elsewhere (Bouchard 2004, 2008) I defend an account of fitness based on differential persistence (see also Thoday 1953 and Cooper 1984 for a similar idea). Swenson et al. (2000) have shown the possibility of conducting artificial ecosystem selection experiments for small ecosystems, but they do not discuss in detail how to conceive the fitness of these ecosystems. Again, the inspiration from ecosystem ecology may be very fruitful. Ecosystems do not reproduce per se, so defining fitness in terms of differential reproductive success is moot. Understanding how the ability to persist helps us track adaptations is a large part of understanding how ecosystems could be said to evolve. One also notices that focusing on persistence is not only the cornerstone of ecosystem ecology, but of symbiosis research as well.

An alternative to this account is, of course, to reduce the apparent phenomenon in terms of coevolution and extended phenotype (Turner 2000 favors this line of reasoning). Symbiosis in general is often described as such by non-symbiosis researchers. One of many problems with this approach is that the coevolutionary story depends on some kind of competition or, more broadly, struggle between the organisms involved to have some sort of “progressive” arms-race leading to better community assembly. But many symbiotic relationships go back and forth between parasitic and mutualistic relationships, often solely depending on punctual ecological constraints. Thinking only in terms of replicators (genes of termites or fungi genes) may seem more helpful, but the genes alone don't show symbiosis. The ecological context is necessary to tell us whether the genotypes lead to parasitic phenotypes or mutualistic phenotypes. For example, the symbiosis between plant roots and mycorrhizal fungi is an instance of mutualism when the plant grows in a soil poor in nutrients. In this case, the plant gains better access to mineral nutrients and the fungus draws photosynthetic carbon from the plant. However, in other environmental conditions, the fungi may consume much of the photosynthetic carbon of the plant, hence slowing plant growth. Only detailed engineering analysis can explain how and when an organism goes from parasite to symbiont (a fortiori if abiotic subsystems are involved).

This type of analysis is at the core of ecosystem ecology where, regardless of the paradigm, some sort of functional analysis detailing energy transfer or some other resource transformation scheme is always present.

In the case of the termite-fungus assemblage, the phenotype of the emergent individual is in part the shape of the termite mound, in part the structure of the *Macrotermes* colony population structure, and in part the fungus it harvests as a symbiont. But this phenotype is not “passed on” through sole genetic inheritance. (It goes without saying that the mud structure persists without change in allelic frequencies.)

When a mound is passed on from one generation to the next, a colony is getting a lung “for free” this mound is not coded genetically (although the ability to maintain one probably is). The existence of the mound allows for the continued harvesting of the fungi. The system (termites-fungi-mound) is a functional unit with many different types of components (biotic and abiotic), and variations of said components offer various responses to fluctuations in selective pressure.

Considering symbiosis emphasizes the importance of examining the persistence aspect of the interaction. Although persistence and common fate are not synonymous, they track similar phenomena. Focusing on how the mound contributes functions usually maintained by “normal” physiology in the case of individual organisms takes us back to the notion of functional integration. I would argue that termite-fungus-mounds are emergent individuals in a sense close to what Sober and Wilson described. But what kind of individual are they? Because their subsystems are biotic and abiotic, they should be construed as ecosystems. We should not be surprised if many symbiotic associations involved in some sort of niche construction demand a similar type of analysis. Moreover, we should not be surprised if, just as is the case in symbiosis research and ecosystem research, persistence is more significant than reproduction.

In this article, I looked at cases where social insect colonies arguably give rise to emergent biological traits that are not reducible to the mere aggregation of the phenotypes of individual organisms composing these colonies. In a broader sense, the question is not whether the individual is a community *or* an ecosystem, but whether natural selection can really lead to all kinds of overlapping evolutionary individuals. My claim is that in the case of termite-fungus interactions *one* of the evolutionary individuals is a multi-species individual, which functions thanks to abiotic components (in this case, the mound). The best way to frame this type of system is thanks to the theoretical resources of ecosystem ecology.

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