

precise (cf. Okasha 2006). After all, *any* group trait is presumably ultimately dependent on the traits and behaviours of the constituent individuals in the group, in the sense that once the individuals' traits are fixed, this then fixes the group trait. (Philosophers call this a relationship of "part-whole supervenience.") In cases where the pattern of dependence is particularly complicated, or where the underlying individual traits are heterogeneous, it may be natural to think of the group trait as "emerging" from them, but this is inevitably a matter of degree; thus, "emergent traits" do not constitute a sharply defined category.

Secondly, the question of how best to understand the evolution of a group trait, be it emergent or not, depends heavily on how the group trait gets transmitted down the generations. This in turn depends on whether reproduction occurs at the individual or the group level. In a human group, however functionally organized it is, the constituent individuals all retain reproductive capacities; so presumably, the group trait gets transmitted via individuals transmitting, to their descendants, the individual-level traits on which the group-level trait supervenes. ("Descendants" can be understood to include cultural, as well as genetic, descendants.) I say "presumably" because in principle, one could imagine a process of "group-level reproduction" in which some groups beget other groups, for example, by fission, and directly transmit the group trait to their (group) offspring. However, such a process seems rather unlikely in the case of human groups, and Smaldino does not appear to envisage it.

If it is right that the group traits in which Smaldino is interested are ultimately dependent on individual traits, and if no process of "group-level reproduction," decoupled from individual-level reproduction, is being envisaged, then in principle it must be possible to understand the evolution of the group trait in an individualistic way, by tracking the evolutionary dynamics of the underlying individual trait(s) on which the group trait depends. Thus, I am unconvinced by Smaldino's argument that an individualistic approach is in principle impossible.

Thirdly, I do not entirely agree with Smaldino that extant theories of multilevel selection and kin selection are silent about emergent group traits. The modelling approach known as "contextual analysis," for example, introduced by Heisler and Damuth (1987), explicitly treats an individual's fitness as a function of its own traits and the traits of the group to which it belongs, which can include "emergent" traits that are not mere aggregations of individual-level traits (cf. Frank 2013; Okasha 2006). However, Smaldino is right that the majority of models of multilevel selection do not explicitly incorporate emergent group-level traits into their formal analyses; the "group traits" that feature in such models are typically the frequencies of individual traits (or genes) within the group. But because all group traits, emergent or not, must ultimately depend on individual traits, one cannot assume that such models are incapable of shedding light on the evolution of the group traits that interest Smaldino.

Finally and relatedly, Smaldino argues against the widespread view that multilevel selection and inclusive fitness (or kin selection) models are essentially equivalent because the evolution of any (individual) social trait or gene can be expressed using either. Smaldino argues that this equivalence breaks down when a "between-levels" perspective is adopted, which takes suitable account of emergent traits. I remain unconvinced by this for the reasons given above, but I agree with Smaldino that social evolution theorists have been too quick to endorse the equivalence of multilevel and kin selection. Although it is true that the two are formally or predictively equivalent, in that both yield identical conditions for an allele to increase in frequency, it does not follow that they are causally equivalent. In forthcoming work, I argue that in some cases, multilevel selection yields a better causal representation of social evolution, which in other cases kin selection does better (Okasha, in press).

These critical points notwithstanding, Smaldino's article offers many valuable insights into what an improved theory of human cultural evolution might look like.

## Explaining group-level traits requires distinguishing process from product

doi:10.1017/S0140525X13002975

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**Abstract:** Smaldino is right to argue that we need a richer theory of group-level traits. He is wrong, however, in limiting group-level traits to units of cultural selection, which require explanations based on group selection. Traits are best understood when explanations focus on both process (i.e., selection) and product (i.e., adaptation). This approach can distinguish group-level traits that arise through within-group processes from those that arise through between-group processes.

We agree with Smaldino's thesis: many important aspects of human behavior are best described as group-level traits, emergent properties of social groups characterized by differentiation and organization. Crowdsourcing provides a vivid and contemporary illustration. Wikipedia is the product of an immense collaboration of specialists organized into different roles like author and editor. Such a work cannot be expressed by or reduced to any one of its millions of contributors. How should we make sense of group-level properties like this? According to Smaldino, theory leans too heavily on the *N*-person prisoner's dilemma model in which groups do best when everyone contributes but individuals do best by withholding contributions. This model forces us to think about social groups and behavior in terms like "cooperation," "freeriding," and "altruism." Many group-level properties, especially those with emergent, rather than additive properties, do not fit into this framework.

Although sympathetic to Smaldino's call for a richer theory of group-level traits, we disagree that group-level traits necessarily constitute "a unit of cultural selection that is not encompassed by selection on individuals" (sect. 1, para. 2). This assertion seems to yoke together group-level traits and group-level selection. As we will argue, this need not be the case. The deeper problem is that Smaldino does not clearly distinguish selection from adaptation. Making sense of phenotypic evolution (including group-level traits) is best done by focusing on both process (i.e., building models of selection to determine why one phenotype results rather than another) and product (i.e., studying adaptations to infer the historical selective pressures). Focusing on group-level traits without explicitly modeling selection processes results in a phenomenological approach that obscures and confuses alternative mechanistic explanations. Smaldino gets caught in this trap when discussing caste differentiation in eusocial insects: "the trait [caste differentiation and social organization] does not *emerge* from the collection of individuals possessing those properties, but is merely a statistical description of their organization" (sect. 3, para. 5). It is not obvious why a Roman Legion (discussed in sect. 2) represents a group-level trait, while an insect colony does not. What would help is an understanding of both the consequences of the traits and how they evolve.

To illustrate our point, let us imagine a group of individuals stranded on an island, isolated from the rest of the world. For the sake of argument, we endow these individuals with the capacity for division of labor and trade (as Smaldino notes, a crucial ingredient in the emergence of group-level traits). Capacities like these emerge over evolutionary timescales. Because we are interested in the emergence of group-level traits over historical timescales, we can take these capacities as given. Though capable of division of labor, our hypothetical islanders do not practice it. Instead, they embody Marx's

manifesto: no one is a specialist; everyone is a generalist. During the day, all are fisherman; at night, all philosophers.

Suppose now that some individuals specialize, exclusively fishing or philosophizing. With increasing returns to specialization, these innovators produce more fish or more knowledge than their comrades. If the islanders value leisure—and who does not?—they can have more of it by trading with each other. Fishers trade their surplus catch to philosophers in exchange for knowledge (or whatever it is that philosophers produce). And both parties enjoy more leisure. Specialization-and-trade will quickly spread throughout the community. The benefit of division of labor has transformed our society into one that is differentiated. An outside observer might argue that the economy should be understood as an emergent, group-level trait. But what process caused this trait? Surely not group selection, as there were no competing groups. Instead, the emergent, group-level trait resulted from within-group forces in which individuals made choices to maximize utility.

The observer might then object that this hypothetical fishing-and-philosophizing economy does not, in fact, constitute a group-level trait. After all, the products of labor flow to individuals; they are not properties of groups. Fair enough. Suppose now that fishermen discover that they can catch more fish by working together in collaborative teams, complete with differentiated roles and social organization. (As with division of labor, we are assuming the capacity for collaboration, not explaining it.) These groups fish together for some time, reap profits that are then split among group members, and then individuals go their separate ways. Smaldino argues that ephemeral co-ops like this constitute trait groups but are not “consistent enough over time to constitute a unit of selection” (sect. 3, para. 5). Maybe so. But in our example, the group-level trait results from individuals maximizing utility, not group selection.

Finally, let us suppose that the island is bridged to other islands. People are free to move to whichever island they so desire. On some islands, philosophizing is an individual affair, and so knowledge systems are limited. On other islands, philosophers long ago founded academies in which knowledge could be shared and therefore grows further and faster. Islands with academies are far more attractive to immigrants than islands without them. When migrants vote with their feet, group-level traits can spread through a group-level process (Boyd & Richerson 2009b). In addition, philosophically starved islanders might emulate their more successful neighbors by founding academies, representing another form of group selection (Boyd & Richerson 2002). In both cases, a group-level trait spreads because of group-level selection.

Although we agree with Smaldino that more attention must be paid to group-level traits, we want to stress that this focus on adaptation must be combined with a focus on selection. Group-level traits, as defined by Smaldino, may arise through group selection, but they may also arise through within-group processes. When multiple processes operate simultaneously, it is all the more crucial to understand how they interact in generating adaptation.

## The substance of cultural evolution: Culturally framed systems of social organization

doi:10.1017/S0140525X13002987

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**Abstract:** Models of cultural evolution need to address not only the organizational aspects of human societies, but also the complexity and

structure of cultural idea systems that frame their systems of organization. These cultural idea systems determine a framework within which behaviors take place and provide mutually understood meanings for behavior from the perspective of both agent and recipient that are critical for the coherence of human systems of social organization.

Smaldino advances an argument similar to that of Lane et al. (2009) regarding the need to make “a shift in perspective, from population thinking to *organization thinking*” (2009, p.12, emphasis in the original) by arguing that models of cultural evolution have not taken into account contextualization of human behavior through systems of organization that make human behavior more complex than just as epiphenomena of individual level traits. This leads Smaldino to consider three levels for modeling selection acting on traits: (1) individual traits, (2) multilevel traits (traits aggregated over behaviors engaged in collectively by interacting group members), and (3) group traits expressed through the institutionalized organization of role-differentiated individuals (sect. 1, para. 3). Group traits are, in Smaldino’s view, distinguishable by making use of the “specific organization of [role] differentiated individuals” (sect. 2.2, para. 2), with selection acting on systems of organization that maintain internal differentiation of individuals, hence acting on emergent group behavior (sect. 2, para. 5) rather than on individual behavior expressed collectively, as is the case for multilevel selection.

Although valid questions can be raised about Smaldino’s characterization and differentiation of these three different levels, especially with regard to his thesis that group success in human societies largely comes from “the organization of a well-defined collection of differentiated individuals all participating in a group-level behavior” (sect. 3, para. 4), my focus here is on the phylogenetic trend going from solitary to structured groups and from individual to emergent to culturally framed behavior as we evolutionarily move toward our species, *Homo sapiens*, with its subdivision into highly differentiated societies. The picture drawn by Smaldino, using his wording for the limitations of multilevel selection, “is not incorrect, but it is incomplete” (sect. 3, para. 4).

The evolution of human social systems centers around the development of systems of organization that incorporate, rather than suppress, individual differentiation (Read 2012). Briefly, the phylogenetic trend toward increased individualization of behaviors that we see when we traverse the primates toward *Homo sapiens* is paralleled by social complexity increasing exponentially with the number of individualistic group members (Read 2012, Fig. 4.3). This increase was accommodated not only through neurological changes (Dunbar 1998), but by changes in the structural organization of social units that culminated, from a biological perspective, in reduction of the size of chimpanzee social units (Read 2012)—where chimpanzees’ social organization is often taken as a model for our ancestral lineage when it diverged from the other primates (Chapais 2008)—as a way to accommodate social complexity arising from highly individualized behavior (Read 2012, Fig. 4.4). The social complexity introduced through increased individuality (what Smaldino calls “individual differentiation”), was eventually accommodated within the hominin ancestry of *Homo sapiens* by shifting from social systems based on face-to-face interaction that characterize the non-human primates (which also leads to within-group, aggregated behavior upon which multilevel selection can operate) to relational based systems of social organization (Smaldino’s institutionalized organization of differentiated individuals) that are culturally framed (Read 2012). The framing through cultural idea systems is not included in Smaldino’s argument and is critical to our understanding of human systems of social organization (cf. Leaf 2009).

There is marked change in the ontological level at which selection operates and fitness is measured concomitant with the sequence going from genetic traits expressed individually and in isolation to traits expressed culturally and collectively. The sequence begins with fitness measured by the number of reproducing progeny, then when behavioral interaction among progeny is