If we adopt the first option, we see that cultural group selection concerns the fraction of groups within a specific area that are of a specific type. However, this head-counting method of reckoning group selection does not map cleanly to what we would like to call adaptation – the thing that natural selection seeks to explain. For example, we would not want to say that Inuit culture is "less adapted" than Roman culture because there were at one point more Romans.

If we adopt the other option and refer to culture itself as the lineage, then the culture itself can evolve because the replicators are the ideas and practices that exist within that culture. However, if the culture is the lineage, we cannot say that it evolves when it takes more territory, in the same way that a species does not evolve with more individuals. Adaptation is presently understood to be about changes in the frequency of replicators, not about absolute numbers of interactors. In sum, cultural evolution (changes of practices within a group) is necessarily a separate process from cultural group selection (changes of the frequency of group-types at a specific location).

We can illustrate these points with a spatial agent-based model of cultural accumulation of knowledge about food-processing skills (Čače & Bryson 2007). In this model there are two variants of a species: free riders who exploit knowledge but never share it and altruists who communicate knowledge with any other nearby agent (perhaps just by failing to conceal their food-processing skills). Knowledge enters the system at a fixed rate of chance discovery, such that each agent has a small chance of discovering a new food source in its own life. Because of constraints placed on lifespan and on the rate of communication, "communities" of neighbouring agents form with expertise in a small fraction of the available skills the environment affords, though this fraction is still larger than the maximum of one skill any agent might learn on its own. When two communities encounter each other by chance, there is a brief surge in population, as both groups quickly learn about the super-set of their food-processing skills. But this process is not evolution; it is only a temporary advantage from happenstance exchange. Future generations cannot sustain the level of cultural accumulation because there is no meta-behavioural (e.g., deliberate teaching) acquisition of skills, nor any change in the biological factors (e.g., lifespan) that determined the likely number of items that can be transmitted from one generation to the next.

Nevertheless, as with most viscous spatial models of altruistic behaviour, there is adaptation in the biological sense. Altruists outcompete free riders, because they are more likely to know about food sources, because they are more likely to live near knowledge sharers – their relatives. This is a simple function of being born by your mother and taking time to move, a process understood by Hamilton (1964) but sometimes overlooked in simplistic modelling (Sober & Wilson 1998).

The upshot for Smaldino's target article is that we have slightly corrected his use of language, but have largely supported his main claim, including providing evidence in the form of a formal agent-based model.

The collaborative emergence of group cognition

doi:10.1017/S0140525X13003051

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Abstract: We extend Smaldino's approach to collaboration and social organization in cultural evolution to include cognition. By showing how recent work on emergent group-level cognition can be incorporated within Smaldino's framework, we extend that framework's scope to encompass collaborative memory, decision making, and intelligent action. We argue that beneficial effects arise only in certain forms of cognitive interdependence, in surprisingly fragile conditions.

Smaldino rightly distinguishes genuinely emergent group organization from mere aggregation, pointing to the active collaboration of individuals with different capacities as the key form of cooperation. We offer two friendly but important extensions. We incorporate group cognition into Smaldino's framework; and we see the conditions under which structured differentiation is beneficial as more fragile than he acknowledges. These modifications encourage integration of work on the cultural evolution of group-level traits with substantial research traditions on distributed cognition, organizational psychology, and collaborative recall.

On standard views in cognitive science, cognition is strictly an individual-level achievement. "Social" cognition is thought to occur when people think *about* social phenomena or when social stimuli trigger cognitive processes. But cognitive processes are conceived in nonsocial terms. If *group cognition* is countenanced, it is understood atomistically, as the aggregate output of individual cognition plus social processes of combination. Little attention is paid to collaborative interdependence as the hallmark of emergent group-level cognition, as expressed in the Gestalt maxim that "the whole is greater than the sum of its parts."

This attractive but puzzling concept is clarified in a large body of rigorous experimental research on group problem solving in social and organizational psychology (Laughlin 2011) that is surprisingly neglected both in Smaldino's presentation and in cognitive science at large. In one key work, Steiner (1966) distinguished five types of group tasks. In additive and compensatory tasks, group members do not interact in producing an outcome. In additive tasks, the group outcome is indeed the sum of the member contributions. In compensatory tasks, the group outcome is a statistical average of individual solutions. The proper aggregation of estimates or predictions can yield greater information gains than the sum of individual contributions (Bettencourt 2009), as in the "wisdom of crowds" (Surowiecki 2004). But such crowd intelligence is largely aggregative in the sense of Wimsatt (1986), as Smaldino argues.

Although conjunctive, disjunctive, and complementary tasks require interactions among group members, only the latter are collaborative in a richer sense. Conjunctive and disjunctive tasks are end points on a spectrum of how many group members must succeed individually for the group to succeed. A disjunctive task, for example, would be a group working on a sudoku, where the group succeeds if any of its members solves the puzzle. Here, the role of social interactions is a matter only of recognizing and adopting a solution found by any one member. In complementary group tasks, on the other hand, members coordinate and combine their diverse knowledge, abilities, and cognitive resources into a collective, organization-dependent outcome that no individual could have produced alone. Psychological processes studied from this group-level perspective include problem solving (Larson & Christensen 1993), collective induction (Laughlin & Hollingshead 1995), the development of transactive memory systems (Wegner 1986), and creativity (Hargadon & Bechky 2006).

Likewise, the "distributed cognition" framework studies collaborative, dynamically evolving work practices mediated by the use of tools and representational instruments and carried out in environments that provide a rich organizational structure (Hutchins 1995b; Perry 2003; Sutton 2010). It borrows from traditional cognitive science an emphasis on processes of creating, transforming, and propagating representational states, but views them as part of larger cognitive ecologies that involve the coordination

of resources across people, tools, and shared environments. Complex collaborative tasks that have been analyzed as distributed cognitive systems include maritime navigation crews (Hutchins 1995b), emergency rescue management (Garbis & Waern 1999), theatrical practices in Elizabethan drama (Tribble 2005), bioengineering labs (Nersessian 2006), and crime scene investigation (Baber et al. 2006). Expanding Smaldino's framework, we argue that these cases exemplify emergent group-level cognition (Sutton et al. 2010; Theiner 2013; Theiner & O'Connor 2010).

Our concept of emergent group cognition differs from the "assembly bonus effect," when "the group is able to achieve something collectively which could not have been achieved by any member working alone or by a combination of individual efforts" (Collins & Guetzkow 1964, p. 58; cf. Larson 2010). Firstly, an assembly bonus effect can occur without emergent group cognition. The "wisdom of crowds" critically depends on the *lack* of collaborative interdependence. It requires, ideally, that individual decision makers are connected only through suitable information aggregators such as market pricing, but otherwise do not influence each other's judgments.

Secondly, emergent group cognition does not necessarily produce assembly bonus effects. This is why Smaldino's claim that "structured differentiation is often beneficial to group success" (sect. 3, para. 7), while appropriately correcting standard views, needs some qualification. For example, though shared remembering in dyads or groups is a ubiquitous human activity, experimental studies of collaborative recall find that groups often remember *less* than the sum of their parts (Harris et al. 2013; Weldon & Bellinger 1997). The most common explanation for such *collaborative inhibition* is that hearing other people recall disrupts individuals' idiosyncratic mnemonic strategies (Basden et al. 1997). The fact that collaborative facilitation is surprisingly hard to find experimentally (but see Harris et al. 2011; Meade et al. 2009) suggests not that emergent group cognition does not occur, but that the conditions under which it is beneficial are surprisingly fragile. As Smaldino notes, the history of group organization matters, as does the structure of differentiated expertise. A further key factor is the fine-grained nature of the communicative interactions in active collaboration among group members (Sterelny 2012; Sutton 2013). This point can be neglected in *social combination* approaches in small group research, which tend to be output- rather than process-oriented and concerned mostly with intellective tasks where comparison with traditional baseline models (e.g., *truth-wins*, *better-than-best-member*) makes sense. Apart from lacking ecological validity, such narrow focus can lead us to misconstrue the functions of real-world group cognition. An important function of shared remembering, for example, is to reinforce social bonds, by merging disparate memories into a stable rendering of shared past experiences (Barnier et al. 2008; Hirst & Manier 2008; Hirst & Echterhoff 2012). Recognizing the beneficial effects of collaborative interdependence requires that we conceptualize "group success" more broadly.

This concept of emergent group cognition can centrally inform ecologically realistic studies of the coevolution of minds, groups, and cultures.

Coordination, cooperation, and the ontogeny of group-level traits

doi:10.1017/S0140525X13003063

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Abstract: Group-level traits (GLTs) clarify the necessity of cultural multilevel selection theory. We propose a revised definition of the GLT concept. We also highlight the need to better understand the interplay between the dimensions of cooperation and coordination in the ontogeny of GLTs.

We find Smaldino's argument lucid and compelling. His clear delineation of group-level traits (GLTs) pinpoints the sorts of social complexity that cannot be explained by selection of individuals or kin and highlights the importance of *coordination*, in addition to *cooperation*, as a fundamental determinant in cultural evolution. We think the examination of GLTs should be taken further and that by doing so the concept may help catalyze advances in fields that draw on evolutionary theory.

Smaldino's call for a "between-levels perspective" (sect. 7, para. 2) parallels one for a mesoeconomic approach (Dopfer 2011; 2012) from evolutionary economics. Mesoeconomics is often considered as a placeholder for economic studies that do not fit neatly in either micro or macro categories (Dopfer 2011). However, if economics can grow to include Smaldino's culturally transmissible GLTs subject to natural selection, we feel that mesoeconomics could "gain an independent and genuine place in the architecture of economics" (Dopfer 2011).

However, first, GLTs may need to be redefined. Smaldino argues that GLTs are the *phenotypic effect* of social organization, rather than that organization itself. We agree that group-level social organization does have "phenotypic" effects (e.g., the music of a rock band) and that those phenotypic effects are subject to natural selection. However, if we call the *phenotypic effect* of social organization the "trait," how then do we talk about different social structures with similar phenotypic effects, or the multiple phenotypic effects of a single type of social organization? In biology, the concept of pleiotropy refers to the condition in which one gene generates multiple phenotypic effects. Such a thing is surely also possible with social organization. This issue makes the "phenotypic effect" definition of GLT awkward to apply. For example, the music played by the rock band may be recorded and played back. We would all agree that the performance is the phenotypic effect of the rock group's organization, but if we use Smaldino's definition, then the *recording* of the performance would also be considered a GLT. But certainly, the recording is not a group-level organizational trait, but the output of one. Defining GLTs as the details of social organization itself solves a number of issues with the concept.

This redefinition has the benefit of simplifying how we conceptualize institutional selection. If a GLT is an organizational structure, then we can see that group-level phenotypic effects can be the result of individual-level traits, emergent GLTs, aggregate group behaviors, or any combination thereof. Discussions of group selection tend to focus on aggregate group-level effects exerting influence on the prevalence of cooperative individual-level traits within a population. GLTs are behaviors that *cannot* be enacted by a single individual and are built on interdependencies between individuals (e.g., zone defense, a queue, square dance). For this reason, a GLT can only exist when organization matters. Organization is only likely to matter in the context of pre-existing behavioral heterogeneity and/or culturally transmitted differentiated social roles. Smaldino's general insight is that models of cultural evolution stand to be advanced substantially by the addition of these types of heterogeneity. We also believe that such a consideration will necessarily help the study of the development, or ontogeny, of social structures.

In examining the social ontogeny of structures, coordination and cooperation leap out as central dimensions. Smaldino suggests that both are necessary components of GLTs, but he stops short of defining them as hard requirements. Both cooperation and coordination influence the development of a social structure and bear on Smaldino's aggregate versus emergent distinction.

Some social structures may begin their development with a set of differentiated actors and then come to develop cooperation over time. An archetypal example of such a structure is the