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Cultural species and their ecosystems

Commentary on "Do Institutions for Collective Action Evolve?" by Elinor Ostrom

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Abstract The target article was written for a workshop that I organized with Lin Ostrom titled "Rules as Genotypes in Cultural Evolution". In my commentary, I describe the background for the workshop and target article in addition to commenting on the article itself. A compelling case can be made for functionally organized human groups as like species that adapt to their local environments. A cultural inheritance mechanism is required for this to happen, which functions analogously to genetic inheritance, although the mechanistic details need not be analogous. Indeed, a diversity of cultural inheritance mechanisms are possible that need not be mechanistically analogous to each other. In addition, most modern human populations consist of a diversity of functionally organized groups, or cultural ecosystems. The distinction between "species" and "ecosystem" is important because the concept of an inheritance system applies primarily to the former. Finally, positive cultural evolution in modern large-scale society must be engineered and an explicitly evolutionary perspective will add value to the enterprise.

Before I comment on Lin's article, it will be helpful to describe the circumstances that led to its creation. I first met Lin at a 2009 workshop organized by the political scientist Sven Steinmo titled "Do Institutions Evolve?" (Steinmo 2010; Lewis and Steinmo 2012). It was the Darwin bicentennial and this was one of scores of evolution-related forums that had been organized around the world. Some of the participants were distinguished scholars who studied institutional change from a variety of social scientific perspectives (e.g., political science, economics, cultural anthropology) while others, such as myself, employed a more explicit evolutionary perspective. The

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"value added" of an explicitly evolutionary perspective became a major debating point. After all, the evolutionists were grumpily told, smart people have been studying institutional change for a long time without using the E-word or using it only casually. What exactly did modern evolutionary science have to offer that had not already been achieved?

Lin had a foot in both camps. Her background was in political science, she was an early adopter of game theory, and she had assimilated quite a lot of the recent evolutionary literature. As president of the newly formed Evolution Institute, I was in a position to organize my own workshops and I proceeded to engage Lin and her postdoctoral associate Michael Cox in two projects. The first was a multi-year effort to rethink economics from an evolutionary perspective, which resulted in the publication of a special issue of the *Journal of Economic and Behavior Organization* titled "Evolution as a General Theoretical Foundation for Economics and Public Policy". Our article is titled "Generalizing the Core Design Principles for the Efficacy of Groups" (Wilson et al. 2013) and generalizes Lin's work on common-pool resource (CPR) groups in two respects: first, by showing how the core design principles that she derived for CPR groups follow from the evolutionary dynamics of cooperation in all species and our own evolutionary trajectory as a highly cooperative species; and second, by showing how they apply to a much wider range of human groups than CPR groups. Another article in the special issue addresses the "value added" question in general terms (Wilson and Gowdy 2013).

The second project was Lin's choice. Early in our relationship that began in 2009, I asked what topic she would most like to address in a workshop and she replied "Rules as Genotypes in Cultural Evolution". That led to a workshop that was co-sponsored by our respective organizations, the Evolution Institute and the Workshop for Political Theory and Policy Analysis, which was held at Indiana University in April 2012. The target article was written for this workshop and was read by the participants as part of their preparation. Sadly, Lin's cancer was in an advanced stage and she was still devotedly caring for her husband Vince. Nevertheless, she was present and fully engaged during the first day of the workshop.

Like the 2009 workshop organized by Sven Steinmo, ours included scholars from a melting pot of disciplines. Even though we chose the participants ourselves, the dynamics of the workshop was much like the earlier one. The phrase "Tower of Babel" came to mind as clinical psychologists, cultural anthropologists, and political scientists struggled to find common ground, which was a prerequisite for discussing the more refined question of whether cultural evolution requires something analogous to a genotype and the degree to which rules (whatever they are) qualify as cultural genotypes. I am confident that an overarching evolutionary perspective can solve the "Tower of Babel" problem for the human social sciences, as it does for the biological sciences, but the magnitude of the task is still daunting. Our workshop only scratched the surface.

For the rest of this commentary, I will provide my own sketch of what it means for rules to function as genotypes in cultural evolution, drawing upon the workshop as a whole in addition to Lin's article.

1 Human groups are like species

No matter what one's academic discipline, the concept of a human group as a functionally organized unit is inescapable. The tradition of functionalism is founded upon this notion, but even critics of functionalism talk about groups as "corporate units" (e.g., e.g., Evans-Prichard 1965; see Chap. 2 of Wilson 2002) for a general discussion of functionalism). Governments and business corporations attempt to function as corporate units, which is implicit in their names, as do the miniature CPR groups studied by Lin. The question of how functional organization evolves above the level of individual organisms is a deep evolutionary question, regardless of the inheritance mechanism (e.g., genetic, cultural, or computer algorithms). Everyone who studies human groups should be aware of the basic evolutionary considerations, which my article with Lin and Michael attempts to provide for a social scientific audience. The main implication to stress here is that a functionally organized human group is roughly comparable to a biological species that has evolved to survive and reproduce in a given environment (Wilson 2013).

2 Species inhabit ecosystems

Most sizeable human populations consist of many functionally organized groups. The multi-group assemblage is roughly comparable to a multi-species ecosystem. This point might seem obvious but it has important consequences for the concept of rules as genotypes in cultural evolution. Biologists typically employ the concept of genotype for the study of single species but not multi-species ecosystems. The reason is that the concept of genotype is inherently concerned with functional organization. Within a given species, every genotype has a corresponding suite of phenotypes, which are subject to selection, such that the surviving genotypes produce suites of phenotypes that are relatively well adapted to their environments. We can usefully think about the genotypes of wasps and trees, but if we were to arbitrarily combine the genotypes of wasps and trees into a single unit for analysis, more confusion than insight would result. That's why the concept of genotype is employed primarily for the study of species and not ecosystems.

Actually, the situation is more complex than this in ways that are instructive for the concept of rules as genotypes in cultural evolution. The more accurate statement is that the concept of a genotype is most appropriate for a unit of selection, whatever the unit of selection might be. The previous paragraph assumes that individuals are the unit of selection, such that genotypes producing tigers with sharp teeth (for example) are favored over genotypes producing tigers with dull teeth. When groups are the units of selection, it makes sense to talk about a group genotype that includes the genes of all the group members, along with their interactions and associated proximate mechanisms. And when multi-species ecosystems are units of selection, it does make sense to talk about an ecosystem-level genotype. This is not just speculation but has been demonstrated in laboratory experiments (Swenson et al. 2000a,b) . In one experiment (Goodnight 1990a,b), two-species flour beetle communities were selected for the density of one of the species. This procedure resulted in the selection of genes in *both*

species that interacted with each other to increase the density of *one* of the species. In a sense, the species were like chromosomes in a community-level organism. No one would be surprised if the genes for sharp tiger teeth reside on different tiger chromosomes, because all of the chromosomes are selected as a unit. The same goes for genes in different species when all of the species are selected as a unit. Burgeoning interest in the microbial communities that inhabit all higher organisms, called microbiomes, has increased awareness that even conventional individual-level selection might draw upon genes from the microbiome, not the individual organism (e.g., Dethlefsen et al. 2007). Sharp tiger teeth could be caused in part by microbiome genes, for example, because they are "all in the same boat" with respect to the unit of selection (for more on multilevel selection, see Sober 1998; Wilson and Wilson 2007).

These fast-breaking developments in evolutionary biology have analogous implications for the study of cultural evolution. Part of the "Tower of Babel" problem at the "Rules as Genotypes" workshop was due to the fact that the participants were studying cultural change at very different scales. For example, Lin's conception of rules as genotypes in cultural evolution is based on small groups that are manifestly attempting to achieve a certain objective (managing a common pool resource) requiring coordinated action. Another participant at the workshop was Ian Lustick, a political scientist who constructs agent-based models of large geographical regions such as the war-torn Middle East (Lustick et al. 2012). These regions consist of multiple groups that are functionally organized but in conflict with each other, so that the region as a whole is not functionally organized. The concept of "rules as genotypes" might not be appropriate at this scale, even though Lustick must specify rules of sorts in the construction of his agent-based models.

3 Species are impressively adapted to their environments

Robert Boyd, one of the main architects of modern cultural evolutionary theory (Boyd 1985; Richerson and Boyd 2005), made another simple but foundational point at the workshop. Like biological species, human groups are not just well adapted to their environments—they're *really really* well-adapted. The knowledge required to survive and reproduce in harsh environments, such as the arctic or desert, would require an entire library shelf of how-to books, yet somehow it is learned and transmitted across generations without any books at all. Once we appreciate the number and sophistication of cultural adaptations, the need to think explicitly about culture as an evolutionary process, complete with inheritance mechanisms that play the same role as genetic inheritance mechanisms, becomes more compelling.

Boyd's point applies not just to traditional cultures inhabiting harsh physical environments, but to the many cultural groups in our midst. A well-adapted religion, for example, "instructs" its members to behave appropriately across dozens of contexts (Wilson 2002). Lin's lifelong study of CPR groups gave her a sophisticated understanding of how small groups adapt to their local environments, which is evident in her article. One point worth stressing is the *need* for local adaptation. Every environment inhabited by a group is sufficiently different that fine-tuning (and sometimes major tuning) is required to accomplish shared objectives. This is why externally imposed

solutions fail so often and why CPR groups are best qualified to formulate their own rules—as long as they possess the core design principles that enable them to function as cooperative units in general terms. Lin describes the process of CPR groups adapting to their environments as a form of tinkering. There is typically an explicit selection criterion, such as how to monitor work duties or resource use. The potential solutions are not totally random (neither are genetic mutations), but they are sufficiently contingent and haphazard that different groups faced with the same problem frequently adopt different solutions. Thus, the process of tinkering as described by Lin is a variation and selection process that adapts the group to its local environment—cultural evolution in action.

4 The one-to-many relationship between ultimate and proximate causation

In biological species, every trait that evolves requires at least two explanations (Mayr 1961): Why it exists, compared to many other traits that could have existed, often (but not always) based on the winnowing action of natural selection; and how it exists in a mechanistic sense. These are called ultimate and proximate causation, respectively, and they inherently exist in a one-to-many relationship. Just as there are many ways to skin the proverbial cat, any given functional property of an organism (the ultimate cause of its existence) can potentially be caused by many proximate mechanisms. As a recently documented example, the adult ability to digest lactose has evolved by genetic evolution at least twice in human populations that keep livestock, but the proximate genetic and physiological mechanisms are different (Holden and Mace 2009). This is only to be expected, because it is unlikely that exactly the same mutations would arise in geographically isolated populations.

These same considerations apply to cultural "species" In Lin's work, the one-to-many relationship is reflected in her distinction between *design principles* and *their implementations*. There are eight core design principles, which are functional categories such as "monitoring" or "graduated sanctions", but each design principle can be implemented in numerous ways. Lin discovered this distinction the hard way. Originally, she attempted to correlate specific implementations with group performance, without success. The reason is easy to understand in retrospect. If there are ten successful ways to monitor (for example), the correlation between any one way and group success will be weak. Only when Lin grouped implementations into functional categories was she able to demonstrate strong correlations.

When we apply the ultimate-proximate distinction more generally to the concept of rules as genotypes in cultural evolution, we reach a discouraging conclusion. The proximate mechanisms of cultural inheritance might be highly diverse and the mechanisms that play a vital role for some groups might be tangential or absent in other groups. An example from biology will illustrate the nature of the problem. Methylation is a biochemical process that regulates gene expression by attaching methyl groups to DNA nucleotides. It is essential for cell differentiation in some taxonomic groups and it would be easy to assume that it is part of the basic machinery of life, but it turns out to be totally absent in other taxonomic groups (e.g., Drosophila; Bird 2002). It is only one way to skin a cat. This is likely to be true for any product of genetic or cultural

evolution that qualifies as "machinery", which is just another word for "proximate mechanism".

For this reason, one of the least successful aspects of Lin's article is her attempt to provide a taxonomy of rules. Even her preliminary effort is so complex that it results in a combinatorial explosion, as she herself acknowledges. The very word "rule" is probably inadequate to cover the diversity of mechanisms that qualify as the cultural equivalent of a genotype, some of which won't resemble rules at all. For example, Marco Janssen stressed at the workshop that an atmosphere of trust is important for people to cooperate and it is difficult to think of *trust* as a *rule*. As Robert Boyd observed, our understanding of cultural inheritance is comparable to our understanding of genetic inheritance before Mendel. A lot of work is in front of us—but that should be taken as a call to action, not as a counsel of despair.

5 On evolutionary mismatch and the need for cultural "workarounds" to improve the cultural evolutionary process

Part of the evolutionary narrative is that humans are genetically adapted to life in relatively small social groups. When group size increased with the advent of agriculture, some of these adaptations broke down, such as the ability to monitor and punish free-riding and active exploitation. Cultural evolution was required to restore group-level functionality to large groups. The culturally evolved mechanisms act as "workarounds" that interface with our genetically evolved psychology to accomplish functionality at a larger scale. To pick an example with which I am familiar, the city of Geneva in the 1500's was tiny by modern standards (app. 13,000 people) but still much larger than any hunter-gatherer group. It was functioning poorly as a corporate unit prior to the advent of Calvinism, due largely to factionalism, which was called "the Genevan disease". The religion provided by Calvin and his associates caused the city to function much better as a corporate unit and the proximate mechanisms nicely fit the description of "workarounds" that interface with our genetically evolved psychology, including the conception of God in relation to people, the theological interpretation of forgiveness and faith, the division of the city into smaller units overseen by Elders, egalitarian governance by a small group of pastors, and so on (Wilson 2002, Chap. 3).

These general considerations apply to mechanisms of cultural inheritance. Our genetic capacity for cultural evolution evolved in the context of small groups of known individuals with reputations based on their past behaviors. Under these conditions, it is relatively easy to sample alternative behaviors and their consequences or to blindly copy others with good reputations. These mechanisms are likely to break down in larger groups and unless they are restored by cultural "workarounds", cultural evolution will cease to operate as a winnowing process. Good practices will originate but not spread, for example, because there is no mechanism for groups to learn from far-distant groups. Lin provides an example in her article in which the simple procedure of getting CPR groups together to compare notes led to the spread of best practices.

The need to engineer mechanisms of cultural evolution in modern social environments requires a subtle balancing act. On one hand, small groups must be given the authority to manage their own affairs. Social engineering has earned a bad name with

ham-fisted top-down interventions that interfere with cultural evolution at the local scale. On the other hand, some coordination among groups is required for positive cultural evolution to take place at a larger scale. The concept of polycentric governance developed by Vince and Lin Ostrom, along with their colleagues at the Workshop for Political Theory and Policy Analysis, is an attempt to accomplish this balancing act (McGinnis 1999).

Put another way, the distinction between "species" and "ecosystem" demarcates the boundary between functional organization and disorganization. Human cultural evolution will take place whether managed or not. Unmanaged, it will result in lower-level functionally organized units (species) that interact in ways that often lead to dysfunctional outcomes (ecosystems). Appropriately managed, the entire ecosystem can become like a species, although in ways that rely heavily on decentralized processes and therefore don't resemble management in conventional terms. I predict that an explicitly evolutionary perspective will add considerable value to the enterprise (Wilson et al. 2014).

Acknowledgments I join the many others who knew Lin in mourning her passing and I cherish the opportunity that I had to work with her for several years prior to her death. I thank my colleagues at the Evolution Institute for their role in making my collaborations with Lin possible.

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