TWO

Placing Archaeology within a Unified Science of Cultural Evolution

Alex Mesoudi and Michael J. O'Brien

MESOUDI, WHITEN, and Laland (2006) have argued that culture can be studied within a single overarching evolutionary framework, just as different branches of biology are linked within a similar synthetic framework. Here we explore how archaeology fits into this framework, primarily as a means of studying macroevolutionary patterns. This is illustrated by the use of phylogenetic methods to analyze artifact distributions (e.g., Buchanan and Collard 2008; Jordan and Shennan 2003; O'Brien, Darwin, and Lyman 2001; O'Brien and Lyman 2003; O'Brien et al. 2002; Tehrani and Collard 2002). We argue that macroevolutionary archaeological work would benefit from a more detailed and explicit consideration of microevolutionary mechanisms of cultural transmission, as exemplified by Bettinger and Eerkens's (1999) use of Boyd and Richerson's (1985) cultural-transmission biases to account for geographic differences in artifact variation. This is reinforced by our own experimental work and highlights how a plurality of methods—archaeological, computer modeling, and experimental—and scales—macro- and microevolutionary—can provide a fuller account of past cultural evolution than can any single method or scale. Finally, we point out that archaeology can benefit from comparative studies of social learning in other species and that a "cultural evo-devo" perspective can potentially link ethnographic, psychological, and archaeological theory and data.

ARCHAEOLOGY AS A MACROEVOLUTIONARY SCIENCE

In a recent paper published in *Behavioral and Brain Sciences*, Mesoudi, Whiten, and Laland (2006) argue that we can take advantage of the similarities between cultural and biological evolution (see Mesoudi, Whiten, and Laland 2004) in order to model the structure of a science of cultural evolution after the structure of the science of biological evolution. In essence, if both cultural and biological change are governed by the same underlying Darwinian processes of variation, differential selection, and the inheritance of selected variants, then the cultural and biological sciences should broadly share the same methodological and conceptual divisions. Figure 2.1 shows the resulting structural

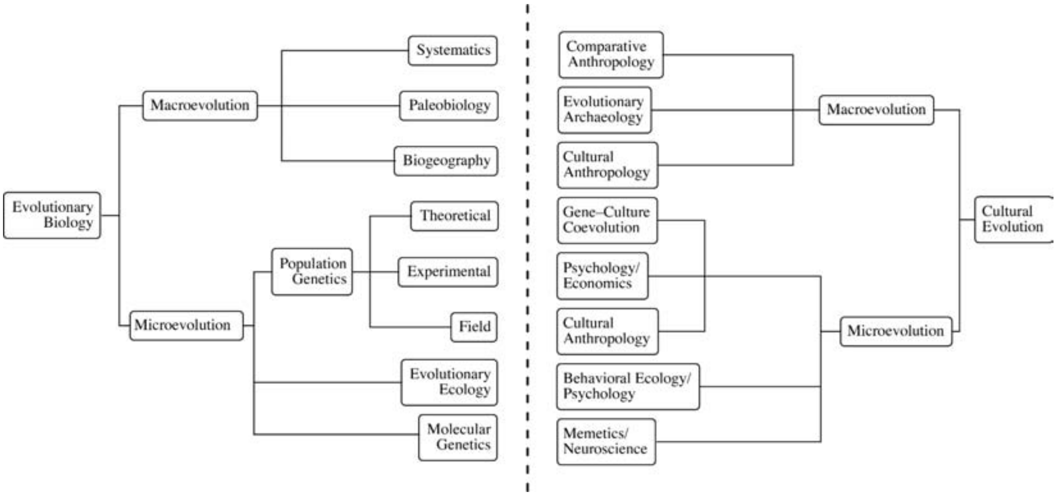

FIGURE 2.1 The structure of a science of cultural evolution (right) mapped onto the parallel branches of evolutionary biology (left) (from Mesoudi et al. 2006).

mapping that links the subdisciplines of evolutionary biology to their existing or potential cultural counterparts.

One of the branches shown in figure 2.1 is evolutionary archaeology (Dunnell 1980; O'Brien and Lyman 2000, 2002), the cultural parallel of paleobiology. In both disciplines, researchers are interested in identifying past biological/cultural forms and reconstructing lineages and clades of those forms, thus revealing evolutionary relationships among the forms. In paleobiology, this has been successfully carried out ever since the Modern Synthesis of the 1930s and 1940s (Huxley 1942), with the principles of genetic inheritance providing the mechanism needed to link evolutionary lineages and clades. In archaeology, it is only recently that lineages of artifacts have been explicitly seen as being causally connected by inheritance, or cultural transmission (see the essays in Lipo et al. 2005). O'Brien and Lyman (2000, 2003) have referred to this as the assumption of *heritable continuity*, distinguishing it from mere *historical continuity*, in which forms are in sequence but are not necessarily causally linked by cultural transmission. The assumption of heritable continuity allows a truly Darwinian evolutionary archaeology (O'Brien and Lyman 2000, 2002; Shennan 2002). Put more forcefully, evolutionary archaeology *demands* such an assumption.

The parallel goals of paleobiology and evolutionary archaeology allow archaeologists not only to adopt similar underlying theoretical or conceptual assumptions as paleobiologists (such as heritable continuity) but also to borrow and adapt specific methodological tools that have been developed by paleobiologists. Perhaps the most important of these are cladistic, or phylogenetic, analyses. Cladistic methods were originally developed and are extensively used by biologists to reconstruct the evolutionary history of species based on their morphological, behavioral, and/or genetic similarities (Harvey and Pagel 1991; Hennig 1966). Only recently have these methods been applied to cultural data sets (e.g., Collard, Shennan, and Tehrani 2005; Gray and Atkinson 2003; Gray and Jordan 2000; Holden 2002; Jordan and Shennan 2003; Mace and Pagel 1994; O'Brien et al. 2001, 2002; O'Brien and Lyman 2003; Rexová, Frynta, and Zrzavý 2003). The main strength of such methods lies in the formal differentiation of homologous traits, which were inherited from a common ancestor, from analogous traits, which evolved independently in unconnected lineages (figure 2.2). This distinction is necessary in order to reconstruct accurate evolutionary

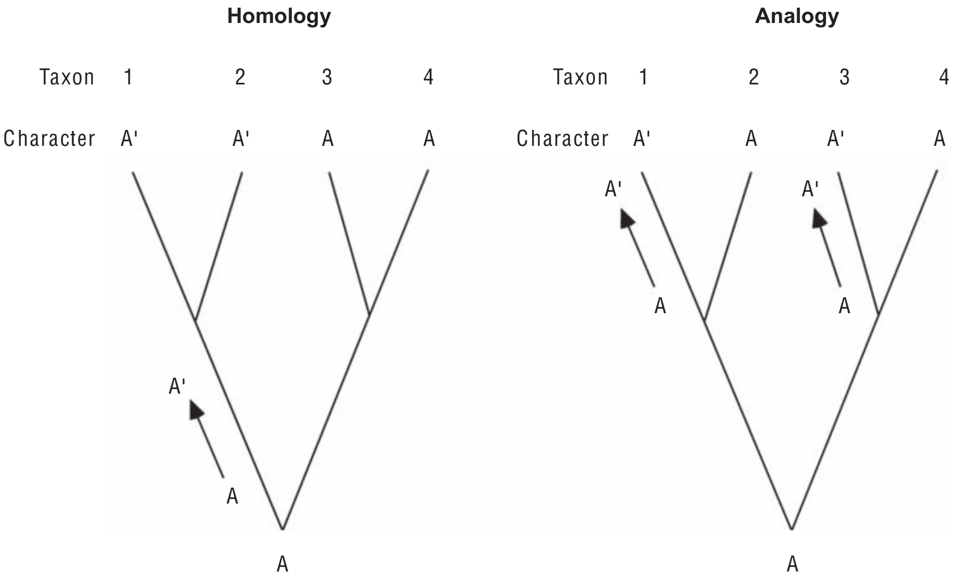

FIGURE 2.2 The difference between homologous characters (attributes) and analogous characters. In the diagram on the left, an ancestor produces two lines, each of which splits into two lines, producing taxa 1–4. Note that one set of descendants (taxa 3 and 4) carries the ancestral character state (A), whereas in the other set, the descendants (taxa 1 and 2) share a derived character state (A'). That derived character state is homologous to taxa 1 and 2, meaning that they share it because their common ancestor had it. In the diagram on the right, taxa 1 and 3 each have the derived state, A', but it is analogous to those two taxa, meaning that they evolved it independently as opposed to inheriting it from a common ancestor.

histories of either biological species or cultural artifacts (Lyman 2001).

For example, O'Brien et al. (2001, 2002; O'Brien and Lyman 2003) performed a phylogenetic analysis of Paleoindian period projectile points from the southeastern United States (figure 2.3), providing a more methodologically and conceptually rigorous understanding of the past spread of projectile-point technology in that region than is obtained using alternative methods that do not distinguish between analogous and homologous features, such as phenetics (numerical taxonomy) or informal verbal arguments made on the basis of supposed "stylistic" similarity. Similarly, Tehrani and Collard (2002) used phylogenetic methods to reconstruct the history of Turkmen textiles based on their patterned designs (figure 2.4), finding an earlier period dominated by phylogenesis, involving the branching of separate lineages, followed by a later period of ethnogenesis, involving crossing between lineages. This finding calls into question the common critique (e.g., Moore 1994; Terrell, Hunt, and Gosden 1997) that phylogenetic methods cannot account for the reticulated structure of cultural transmission because of the assumed prominence of horizontal cultural transmission in human history.

On closer inspection, this dichotomy between a branching, divergent biology and a reticulated, convergent culture is largely illusory. Ethnographic evidence suggests that vertical cultural transmission plays a major role in human culture (Guglielmino et al. 1995; Hewlett, De Silvestri, and Guglielmino 2002; VanPool, Palmer, and VanPool 2007), whereas horizontal cross-lineage transfer of genetic material is common in many biological species (Abbott et al. 2003). Accordingly, Collard, Shennan, and Tehrani (2005) found that twenty-one cultural data sets fit just as well as twenty-one biological data sets to a phylogenetic tree model.

Although trees produced through methods such as parsimony, maximum likelihood (Hall 2001), and Monte Carlo Markov chain Bayesian techniques (Huelsenbeck, Rannala, and Masly

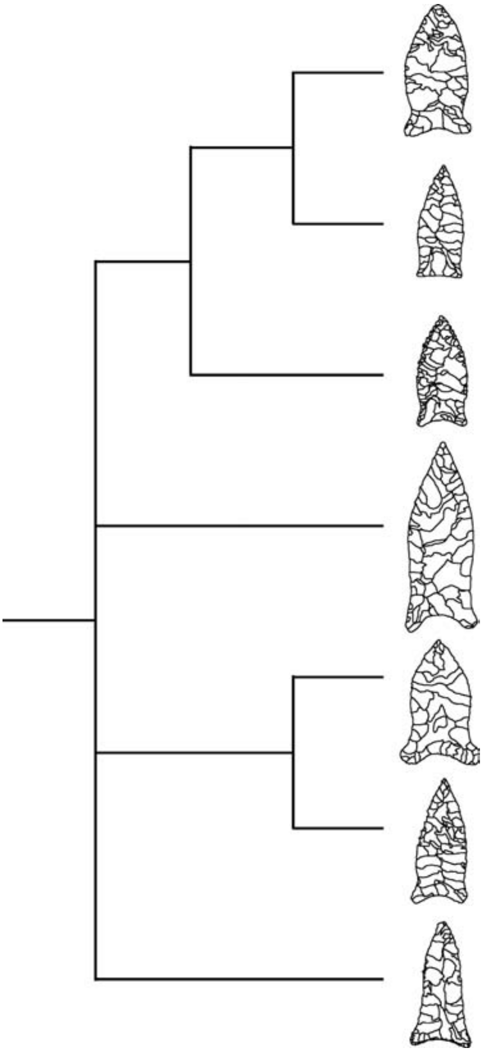

FIGURE 2.3 A portion of a much larger phylogenetic tree of projectile point classes from the southeastern United States, illustrating divergence from a single common ancestor (after O'Brien and Lyman 2003).

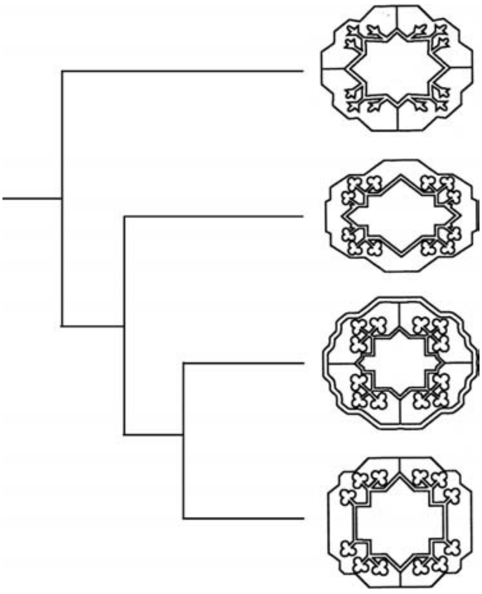

FIGURE 2.4 A phylogenetic tree of Turkmen textile designs prior to the Russian invasion of Central Asia (after Tehrani and Collard 2002).

2000) appear to have considerable promise for phylogenetic ordering, it is important to note that they are but one weapon in the social scientist's arsenal. Other methods—split-decomposition graphs (Bandelt and Dress 1992), tests for serial independence (Abouheif 1999), iterated parsimony (McElreath 1997), network analysis (Lipo 2005), tests for matrix correspondence (Smouse and Long 1992), assessment of hierarchical cluster structure (Pocklington 2005), and seriation (Lyman and O'Brien 2005)—should be used in tandem with tree-producing methods in order to address questions of phylogeny.

Another group of archaeologists has adopted a different tool from evolutionary biology to help explain patterns in the archaeological record. Following Cavalli-Sforza and Feldman (1981), Neiman (1995), Shennan and Wilkinson (2001), and Bentley and Shennan (2003) have applied to archaeological data the neutral-drift model originally developed by population geneticists (Crow and Kimura 1970). Hence, Neiman (1995) demonstrated that random copying can account for changes in decorative patterns found on Illinois pottery, and Shennan and Wilkinson (2001) found evidence for a nonrandom, anticonformist copying bias in Neolithic central European pottery. The latter example highlights how the neutral-drift model can be usefully used as a null hypothesis, so that when artifact frequencies deviate from frequencies expected by random copying, this indicates the operation of other cultural transmission biases, such as conformist, nonconformist, or prestige-based biases.

LINKING CULTURAL MICRO- AND MACROEVOLUTION

Phylogenetic methods such as those just discussed are used to study biological or cultural *macroevolution* (figure 2.1). That is, they are used to identify patterns and trends in long-term change over multiple generations using large samples of specimens. The major advance within evolutionary biology brought about by the Modern Synthesis was that the macroevolutionary patterns observed by paleobiologists (e.g., Simpson 1944) came to be seen as the long-term population-level result of the microevolutionary principles of genetic inheritance discovered by geneticists.

Viewing cultural macroevolution and microevolution within a single overarching framework (Mesoudi, Whiten, and Laland 2006), and recognizing that lineages and clades of artifacts are causally linked by cultural transmission (Lyman and O'Brien 2000), leads us to a similar synthesis for evolutionary archaeology. That is, large-scale patterns observed in the archaeological record can be (partly) seen as the result of specific biases in cultural transmission at the microevolutionary level (Bettinger and Eerkens 1999; Boyd and Richerson 1992; Lyman and O'Brien 2001). For archaeologists, just as for paleobiologists, these past microevolutionary inheritance or transmission processes cannot be directly observed at the individual level. Rather they must be inferred from (often incomplete) historical population-level data. This is not to say that differences in the processes of cultural transmission are the only source of archaeological patterns; environmental factors such as rainfall and climate or features of geography will be important in many cases. Nevertheless, the details of cultural transmission at the individual level likely will play some role in generating measurable patterns in artifact form and variation at the population level.

What does it mean to consider the microevolutionary details of cultural transmission when analyzing macroevolutionary patterns and trends? In a sense, the debate highlighted here over whether culture is branching or convergent is a debate over transmission, with the former assuming vertical cultural transmission and the latter assuming horizontal cultural transmission. As Borgerhoff Mulder, McElreath, and Schroeder (2006) point out, however, there is also an unstated assumption that this transmission is occurring at the level of groups rather than the level of individuals that was originally intended by Cavalli-Sforza and Feldman (1981) when they first used the terms *horizontal* and *vertical* in this context. Vertical transmission at the individual level can produce blending if individuals marry into new groups, whereas horizontal transmission can produce branching if it is restricted within groups. Many of the studies used to justify an assumption of vertical transmission, such as Guglielmino et al. (1995), are ethnographic studies of transmission within groups and may not bear on whether culture as a whole is branching or blending (Borgerhoff Mulder, Nunn, and Towner 2006).

One study that attempted to explicitly link different cultural transmission processes to macroevolutionary patterns is Bettinger and Eerkens's (1999) comparison of projectile-point variation in the western United States. Bettinger and Eerkens observed that different attributes (e.g., width and weight) of projectile points found in eastern California were largely uncorrelated (table 2.1), which they argued was because the designs of points in this region originally spread by *guided variation* (Boyd and Richerson 1985), in which individuals acquire a cultural trait, then modify it through individual trial and error. Hence, each attribute is subject to separate individual trial and error, causing the attributes to vary independently. Conversely, projectile points found in central Nevada, which feature uniform designs with often highly correlated attributes (table 2.1), were argued to have spread by *indirect bias* (Boyd and Richerson 1985), with individuals copying wholesale the design of the single most-successful or prestigious model. If everyone is copying the design of a single model, then point designs in the

TABLE 2.1. *Correlations (Pearson's r) between Different Projectile-Point Attributes from Nevada and California*

		AXIAL LENGTH	MAXIMUM WIDTH	BASAL WIDTH	NECK WIDTH	THICKNESS	DISTAL SHOULDER ANGLE	PROXIMAL SHOULDER ANGLE	WEIGHT
Maximum length	NV	1.00	0.58[a]	0.48[a]	0.51	0.51[a]	–0.19	–0.34	0.86
	CA	1.00	0.24	0.07	0.21	0.15	–0.24	–0.24	0.76
Axial length		NV	0.59	0.49[a]	0.51[a]	0.49[a]	–0.18	–0.33	0.86
		CA	0.22	0.04	0.16	0.14	–0.24	–0.27	0.74
Maximum width			NV	0.44	0.72	0.12	–0.48	–0.53[a]	0.62
			CA	0.54	0.69	0.26	–0.47	–0.08	0.71
Basal width				NV	0.71	0.21	0.11	0.26	0.80[a]
				CA	0.78	0.05	–0.06	0.31	0.14
Neck width					NV	0.23	–0.15	–0.15	0.61
					CA	0.11	–0.06	0.15	0.40
Thickness						NV	0.14	–0.02	0.70
						CA	0.03	–0.02	0.57
Distal shoulder angle							NV	0.53[a]	–0.12
							CA	0.16	–0.38
Proximal shoulder angle								NV	–0.21
								CA	–0.01

[a] Indicates a significantly stronger correlation in the Nevada sample than in the California sample, as predicted by the model (Boyd and Richerson 1985).

SOURCE: Bettinger and Eerkens (1999).

population as a whole will become uniform, and their attributes will correlate. Here Bettinger and Eerkens demonstrated a potential link between individual-level cultural transmission (guided variation vs. indirect bias) and population-level archaeological data (uncorrelated vs. correlated point attributes). We encourage more such studies that test hypothesized links between cultural micro- and macroevolution.

EXPERIMENTAL SIMULATIONS OF CULTURAL TRANSMISSION

Experimental simulations of cultural transmission offer another means of testing hypotheses regarding the effect of transmission biases on macroscale evolutionary change (Mesoudi 2008). Evolutionary biologists are increasingly studying biological evolution experimentally in the laboratory using microorganisms (Cooper, Rozen, and Lenski 2003), often addressing issues regarding biological macroevolution that previously only the fossil record could address, such as punctuated equilibria, long-term adaptation in rugged fitness landscapes, and the evolution of sexual reproduction. The cultural equivalent of such experimental simulations would involve transmitting cultural information—in the form of attitudes, knowledge, behavioral practices, and group norms—along multiple "generations" of participants in the psychology laboratory, and measuring the effect on the transmission of that information of different modes of social learning, different types of information, different social networks, and so on.

Although such studies have been few and far between in the history of psychology, a number of studies in recent years have begun to address such questions. Some have used Bartlett's (1932) linear transmission chain method either to identify cognitive or memory biases that affect the transmission of written texts (Bangerter 2000; Kashima 2000; Mesoudi and Whiten 2004; Mesoudi, Whiten, and Dunbor 2006) or to study the transmission of behavioral strategies among players of economic games (Schotter and Sopher 2003). Others have experimentally tested the predictions of formal mathematical models regarding when people should engage in different strategies of social learning and when they should rely on individual learning (Kameda and Nakanishi 2002, 2003; McElreath et al. 2005). Such methods have the potential to provide important insights into both specific archaeological processes and more general principles regarding cultural transmission that can inform archaeological work.

Experimental methods have several advantages over historical methods, such as the ability to rerun history in multiple replications; to access complete, uninterrupted data; to directly compare fitness or efficacy at different points in time; and to manipulate and control environmental conditions and experimental variables. Although there are several limitations on the use of experimental simulations to study biological evolution, such as the long generation time of some species or the fact that the majority of species in the fossil record are now extinct and cannot be studied, these limitations may not be so severe for cultural evolution. Cultural practices or skills can be acquired within a single generation, and many prehistoric artifacts are still in use by traditional societies or amateur enthusiasts (VanPool, Palmer, and VanPool 2008).

Experimental simulations alone can never definitively answer questions regarding past cultural change. Rather, they can complement existing archaeological methods and computer models to provide a more complete understanding of the past. Accordingly, in past work (Mesoudi and O'Brien, 2008) we conducted an experimental simulation of the patterns observed by Bettinger and Eerkens (1999), in which groups of participants design their own "virtual projectile points" and engage in social and individual learning. These experimental simulations confirm that the transmission biases (guided variation and indirect bias) hypothesized by Bettinger and Eerkens to have generated their archaeological patterns (low and high inter-attribute correlations, respectively) generate similar patterns of variation in our experimental data, thus increasing our confidence in this cultural transmission explanation of Great Basin artifact variation.

CULTURAL TRANSMISSION IN OTHER SPECIES

So far, we have briefly discussed a number of different modes of cultural transmission, such as Cavalli-Sforza and Feldman's (1981) vertical and horizontal transmission or Boyd and Richerson's (1985) guided variation and indirect bias. However, it may be instructive to go beyond these differences by drawing from the wider literature regarding animal social learning, within which there has been extensive debate over the precise underlying social learning mechanisms exhibited by various species in different contexts (e.g., Avital and Jablonka 2000; Fragaszy and Perry 2003; Hurley and Chater 2005; Whiten et al. 2004). Indeed, the transmission biases discussed in the prior sections are a small subset of all possible cultural processes.

Regardless of whether nonhuman species have "culture" (Boesch and Tomasello 1998; Laland and Hoppitt 2003; Whiten 2005; Whiten, Horner, and Marshall-Pescini 2003), humans are likely to share many social-learning mechanisms with other species as a result of either descent from a common ancestor or convergent biological evolution. Note that we treat the terms *social learning* and *cultural transmission* as broadly synonymous, with no connotations as to which mechanisms can or cannot support culture, however culture is defined.

Much of the literature has been concerned with specifying exactly what one individual is learning from another individual and how this learning is achieved. Whiten et al. (2004) identify a number of distinct processes that address these issues, including *imitation*, where an individual copies the motor action of a model; *emulation*, where an individual copies the result or the goal of a model's action; *affordance learning*, where an individual learns from a model about the physical properties of an object; *observational conditioning*, where an individual learns from the model the positive or negative value of an object; and *stimulus enhancement*, where an individual's attention is directed by a model toward an aspect of their shared environment. To these behavioral processes, which were delineated primarily by primatologists, we can add for humans spoken and written language (Christiansen and Kirby 2003), which undoubtedly significantly transformed cultural transmission and cultural evolution in our species.

With respect to archaeology, any or all of these behavioral and linguistic processes may have been operating when people constructed tools, and different processes may have led to different patterns in the archaeological record. For example, Tomasello, Kruger, and Ratner (1993) have argued that of the behavioral processes just listed, only imitation has the necessary high fidelity to sustain the accumulation of cultural modifications over time that appears to typify many archaeological seriations. Anthropologists, on the other hand, have historically stressed the importance of symbolic communication, such as language, in the transmission of culture (e.g., White 1962). Perhaps experimental and computer simulations of such processes might indicate which is necessary for the long-term cultural transmission and evolution of different artifacts.

In addition to these broad processes affecting how information is learned from others, other factors affecting what is learned include when individuals learn from each other and from whom they learn (see, e.g., Laland 2004). Examples of "when" strategies derived from theoretical analyses and experimental studies are the self-explanatory "copy when established behavior is unproductive," "copy when individual learning is costly," or "copy when aspects of the environment are uncertain." The cultural-transmission biases discussed earlier are examples of Laland's "who" strategies: "copy kin" (vertical transmission), "copy unrelated individuals" (horizontal transmission), "copy the majority" (conformist bias), and "copy successful/-prestigious individual" (indirect bias). Finally, cultural transmission can be guided by content biases (Henrich and McElreath 2003), where the intrinsic quality of information affects its likelihood of transmission, or where biologically evolved or culturally shaped features of human cognition bias the acquisition of certain types of information over others. To reiterate, human cultural transmission was likely to have been (and likely still is) a complex interplay among these different processes and biases, and only by using quantitative methods such as gene culture coevolution models or phylogenetic analyses, together with controlled experimental simulations, can we begin to unravel this complexity.

CULTURAL EVO-DEVO

Missing from figure 2.1, but mentioned by some of the commentators in Mesoudi, Whiten, and Laland (2006), is the emerging field of evolutionary developmental biology, or "evo-devo" (Carroll 2005; Müller and Newman 2003). This approach is gaining increasing influence within biology, and there have been several calls for it to be integrated into the evolutionary synthesis (Kutschera and Niklas 2004). In biology, evo-devo concerns how genetically and environmentally influenced developmental processes interact with longer-term evolutionary change. A "cultural evo-devo" in an archaeological context would concern the behavioral processes by which material artifacts are generated by culturally transmitted information stored in the brain and how this process interacts with macroevolutionary change.

It might be useful in this context to treat cultural traits, including and especially artifacts, as "recipes" (Lyman and O'Brien 2003; Neff 1992). These comprise the materials required to construct an artifact (the "ingredients") and the behavioral rules required to construct and use the artifact (the "instructions"). Similarly, cognitive psychologists (e.g., Weber, Dixon, and Llorente 1993) have proposed that people represent artifacts as interlinked, hierarchical knowledge structures, incorporating behavioral scripts governing their construction and use, much like the recipe concept. It is also notable that biologists often use the recipe metaphor to describe the development of organisms from genetic information (Dalton 2000; Ridley 2003). There is real potential here to move beyond the metaphors and incorporate behavioral data from ethnographic studies of artifact construction and use, psychological data regarding the representation of artifact knowledge in the brain, and archaeological data regarding the evolution of artifacts. This is made easier within a single overarching evolutionary framework.

CONCLUSIONS

We have argued that placing archaeology within a larger evolutionary framework, such as the one suggested by Mesoudi, Whiten, and Laland (2006), can provide a more comprehensive and accurate account of the archaeological record than can more traditional nonevolutionary theoretical positions. Darwinian evolution naturally places emphasis on cultural transmission, making explicit the assumption of heritable continuity that links lineages of artifacts. The fact that archaeologists face the same questions as paleobiologists encourages the use of methods developed by biologists, such as phylogenetic analyses or drift models, to be applied to archaeological data. The synthetic nature of the evolutionary framework also encourages a more detailed consideration of the microevolutionary processes of cultural transmission and how they generate macroevolutionary patterns. This can be done using experimental simulations and computer models of underlying transmission processes. Comparative studies of human and nonhuman social learning can usefully inform archaeology, and adopting a cultural evo-devo perspective can potentially link ethnographic, psychological, and archaeological data. These interdisciplinary links naturally follow from placing archaeology within a larger unified cultural evolutionary synthesis.

In closing, we remind readers that there are limitations on what we can and cannot know about cultural transmission, especially when relying on incomplete and ambiguous archaeological data. At the same time, however, we should not be dissuaded from continuing to pursue evolutionary studies in archaeology. While empirical studies of past cultural transmission and evolution are undoubtedly difficult, and the phenomena under investigation are undoubtedly hugely complex, evolutionary biologists face similar difficulties in the face of similarly daunting complexity. For example, geneticists face the same difficulties in defining a unit of biological inheritance as anthropologists do in defining a unit of cultural transmission. Indeed, far from having a single, universally agreed-on definition, the "gene" actually has multiple, often mutually incompatible meanings used at different times by different biologists in different contexts (Stotz and Griffiths 2004).

Paleobiologists work with the same kinds of fragmentary data as archaeologists do, yet evolutionary biology has thrived through the use of simple assumptions and models and an overarching theoretical framework that unites disparate disciplines and methods. Discoveries in genetics and paleobiology have been made that were unthinkable mere decades ago. Perhaps a few decades from now, future evolutionary archaeologists will look back on similarly dramatic progress in their own field.

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