Chapter 2
Introduction to Cultural Microevolutionary Research in Anthropology and Archaeology

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Introduction

Evolutionary perspectives in anthropology and archaeology have come a long way since Binford (1962, p. 224) observed that archaeologists could “be among the best qualified to study and directly test hypotheses concerning the process of evolutionary change, particularly processes of change that are relatively slow, or hypotheses that postulate temporal-processual priorities as regards total cultural systems.” Over the last few decades, scholars concerned with the evolution of culture—although by no means only anthropologists and archaeologists—have weighed in with numerous insights on the relationships between biological and cultural evolutionary processes in general and the cultural evolutionary process in particular. Here we offer an overview of biological microevolution processes and discuss how these are approximated in evolutionary studies of material culture in archaeology and cultural anthropology. The goal is to clarify common terms and definitions and to explore microevolutionary processes as they are used in sociocultural perspective. We hope to provide a foundation from which to better understand these concepts and their applications to method and theory in cultural evolution as further developed throughout this section.

The recognition of cultural developments as the consequence of complex and diverse histories as opposed to rungs on a teleological, stage-oriented step ladder out of the darkness of prehistory into the light of civilization is a critically important note in the history of anthropological evolutionary thinking, as is the revelation that cultural evolution can at least be understood through the larger framework of Darwinian evolution and associated forces and processes (Boyd and Richerson 1985; Richerson and Boyd 2005, 2010; Mesoudi et al. 2006). Despite early efforts by pioneering archaeologists in the nineteenth and early twentieth century to link evolutionary theory as then understood with observations of culture change (see Riede 2010), it is only in the last four decades

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A. M. Prentiss (ed.), *Handbook of Evolutionary Research in Archaeology*,
https://doi.org/10.1007/978-3-030-11117-5_2

or so that the field of evolutionary anthropology and archaeology has begun to emerge in a coherent fashion. To date, anthropological evolutionary theory has far eclipsed the earlier presumptions and ideas as to the nature of cultural evolution, such as those espoused by Lewis Henry Morgan (1877) and Herbert Spencer, for example (see Tehrani 2010). Over the last few decades, the field has also developed well beyond the neoevolutionary concepts of mid-twentieth-century thinkers such as Julian Steward (1955), Leslie White (1949, 1959), and other early contributions to the subject as, for example, presented in Sahlins and Service (1960). But, as O'Brien and Lyman (1998, p. 132) point out for evolutionary studies in archaeology, "the words evolution, selection, adaptation, and drift appear regularly in evolution-based studies, but in delving into both the biological as well as the archaeological literature, one soon gets the feeling that there is considerable diversity of opinion," and this holds true even in self-proclaimed Darwinian theoretical contexts. Likewise, other evolutionary terms such as variation, mutation, inheritance, and transmission are often brought to bear in discussions of cultural change without clarifying their meaning in regard to cultural phenomena.

When it comes to studying the evolution of material culture in general and in the past in particular, microscale perspectives can be tricky to tease out of the archaeological record. Even at the scale of the single artifact, feature, or assemblage, we are generally left only with the option of saying something about macroscale contexts rather than their microscale components (see Gould and Eldredge 1986; O'Brien and Lyman 2000, p. 130). There are two main reasons for this. First, it is nearly impossible to archaeologically discern, much less track, descent with modification between *individuals* as opposed to such changes occurring in *populations*. For the latter, ethnographers are perhaps the closest to being able to achieve this, as they have the opportunity to observe the interactions of their informants at the scale of individuals. To a degree, the combination of ethnographic, ethnohistoric, and detailed material culture study can bridge the inferential divides between these different scales of observation, as Jordan's (2015) recent attempt has demonstrated for one Siberian group. Yet, for most archaeologists, such records are not available, and judicious ethnographic analogues have to be combined with theoretical and perhaps mathematical models and a close reading of the archaeological record in order to strengthen inferences about general transmission modes (Tehrani and Riede 2008).

Archaeologists cannot directly observe the individual interactions and behaviors that result in the archaeological record. We can certainly infer as to what may likely have taken place (e.g., by drawing insights from ethno-archaeological analogy or from behavioral studies, sensu O'Connell 1995) or through diligent fieldwork under conditions of extremely favorable preservation (e.g., Assaf et al. 2016; Donahue and Fischer 2015; Högberg 2008). Indeed, this latter approach has recently been placed in a cultural evolutionary and life-history perspective framed within niche construction theory; Riede et al. (2018) have argued that play objects take on a critical role in the cognitive niche of maturing individuals in relation to innovation later in life. This study tried to unpack the microevolutionary mechanism that generates novelty—creativity—rather than framing it strictly analogous to mutation, i.e., as effectively random. Still, microevolutionary processes are most commonly inferred with reference to mathematical and/or ethnographic models. Even when instances of teaching and learning can be excavated and identified with some degree of confidence, linking these up with the bulk of the archaeological record, which represents time-averaged and usually poorly constrained population-level patterns of cultural macroevolution, relies on inferences.

Yet, archaeologists have long been wary of the fact that getting at the singular instances or events that make up units (or moments) of change is tenuous, as is also supported by recent formal modeling that has cultural evolutionary inferences in mind (Porčić 2015; Premo 2014). This was one of the major issues at the heart of the processual movement and the development of middle-range theory (e.g., Binford 1977, 1981, 2001). Conversely, the time depth that archaeology can provide is tailor-made for producing macroscale discussions about change over time in the past, but it also makes getting at the details of interchange extremely problematic.

Second, and related, cultural processes of selection, adaptation, drift, and mutation—while acting on individuals—only become discernable in broad, retrospective view. They are observable as processes only when we see them as patterns at the population scale. Here, we must explicitly understand that microevolution is generally reserved for those processes of change over time within a species, while macroevolution represents "change at larger, more inclusive scales in the taxonomic hierarchy" (O'Brien and Lyman 2000, p. 302). There are certainly more mundane but fundamental reasons as well: a third, less-broad critique could be definitional—that we tend to dwell on and define our evolutionary concepts strictly in their biological contexts, repeatedly attempting to force the square block of biological process into the round space that is culture change. Social scientists concerned with evolution have long recognized this problem also but rarely have attempts been made to operationalize solutions. In the last few decades, evolutionary anthropologists have taken strides toward addressing these, and other, critical issues in the investigation of human evolution (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Jordan 2015; Lipo et al. 2006; O'Brien and Lyman 2002; Prentiss et al. 2009; Richerson and Boyd 2005; Shennan 2002, 2009). This chapter aims to (1) harmonize efforts in cultural anthropology and archaeology that have contributed to building the synthetic evolutionary framework from which to view and investigate cultural change over time at the microscale and (2) outline some of the theoretical and methodological tools utilized to explore microevolution in studies of culture. Structured more or less chronologically, we begin by reviewing early attempts at capturing cultural microevolution and by reflecting on how microevolutionary dynamics play out in the context of cultural phylogenetics and human behavioral ecology studies. We then discuss issues of study design: the selection of traits to be analyzed and the thorny issue of reconciling micro- and macroevolutionary *scales* of analysis. Thereafter, we reflect on the various *mechanisms* impacting on microevolutionary patterns and seek to provide cultural counterparts to the mechanism active in the biological domain. According to Mesoudi et al.'s (2006) classification of cultural evolutionary studies, archaeology belongs firmly to the macroevolutionary branch (Fig. 2.1); archaeological data are simply not well-suited to the study of microevolutionary patterns. By the same token, this chapter ultimately provides more questions than answers but also offers a challenge to future cultural evolutionary studies that through a judicious combination of approaches may well be better able to bridge the gap between cultural evolution at the smallest and the largest of scales.

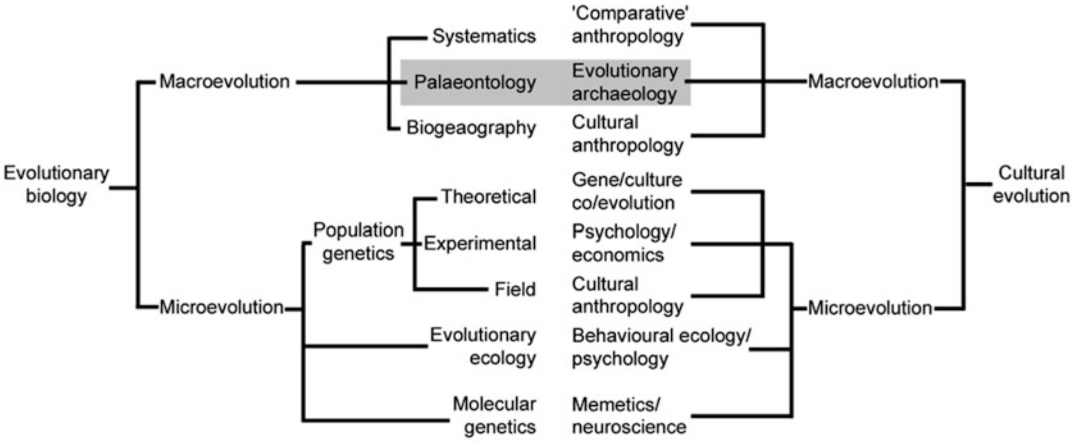

Fig. 2.1 Mesoudi et al. (2006) place archaeology on the macroevolutionary branch of the field of cultural evolution. Drawing on methods and insights from the sister clade may allow us to bridge this bifurcation

Cultural Evolution Evolves

Reviews of the history of evolutionary studies in anthropology and archaeology adequately cover developments in the field to date as they relate to macroevolutionary processes (e.g., see reviews in Barton and Clark 1997; Dunnell 1978, 1986, p. 166; Hodder 2012; Johnson 2010; Lyman 2008; Lyman and O'Brien 1997; O'Brien 1996; Prentiss et al. 2009; Shennan 2008; Trigger 2006). The challenge of this chapter is to illuminate some of the implications of *micro*scale processes of change on culture and in particular on cultural evolution by descent with modification. Considering evolution as what Dunnell (1980, p. 37) so aptly defined as "the differential persistence of variability," this is perhaps more difficult than it sounds. This is because getting at persistent variability requires a temporal aspect in order to see persistence and a population aspect in order to observe variability, which necessitates viewing diversity across multiple spatial and temporal scales. Methodologically, evolutionary research in anthropology and archaeology has swung from early foci on the development of diversity among societies or essential "types" (e.g., Sahlins and Service 1960) to studying changes in material culture traditions by way of seriation studies (Lyman and O'Brien 2006; O'Brien and Lyman 2002) to applications of evolutionary ecology and optimal behavior modeling (see, e.g., Bettinger 2009; Broughton and O'Connell 1999; Cronk 1991; Nettle et al. 2013; Winterhalder and Smith 1981; see also Davies et al. 2012 for broad applications in nonhuman ecology) to a growing contemporary range of phylogenetic applications to studies of material culture (see reviews in Straffon, Chap. 8, this volume; Jordan and Gjesfeld, this volume), as well as even more inclusive views of how cultural phenomena can be studied from an evolutionary perspective (e.g., Kandler and Crema, this volume; Mesoudi et al. 2006; Riede, this volume).

Seriation

As a method of developing lineal evolutionary histories of cultural materials, systematic uses of seriation can offer valuable insights into population-scale developmental trajectories. But the understandings they provide are patently macroevolutionary in scope, as observed in the conceptual definition of taxonomic types that usually have "relatively long temporal (and broad spatial) distributions" (Dunnell 1986, p. 173). However, as Lyman and O'Brien (2006) demonstrate, seriation methods can still be a useful classificatory exercise, for example, as a tool in establishing taxonomies for cladistics analyses. Lipo and Eerkens (2008) provide an excellent example of the utility of seriation in systematically developing culture history chronologies in time and across space. Given an accurate understanding of known material chronologies, seriation can even provide a near microscale perspective on character trait evolution (e.g., Dethlefsen and Deetz 1966).

Human Behavioral Ecology

One analytical framework that comes close to operationalizing processes at the scale of the individual is human behavioral ecology (HBE)/evolutionary ecology and the application of optimal foraging theory and attendant models. HBE is unconcerned with the nature of transmission whether genetic or cultural. Rather, it concerns itself with the overall adaptiveness of behavior and thus decisions made by individuals in response to contextual—most often ecological—circumstances. These studies attempt to predict the decision-making behaviors of *individuals* in specific contexts, thus modeling individual behavioral adaptation under environmental constraints to determine if and how individuals adapt behaviorally to various circumstances and conditions (HBE and OFT, respectively; see Bettinger 2009; Chaps. 11, 12, 13, 14, 15, 16, 17, 18, and 19, this volume; Winterhalder 1981; Winterhalder and Smith 1981 and references therein; and review in Shennan 2008, pp. 82–87).

Phylogenetics

Since Mace and Pagel (1994) suggested that a phylogenetic approach to cross-cultural comparative studies could potentially provide a systematic, statistical framework from which to investigate patterns of hierarchical descent, cultural evolution has increasingly been illustrated through the application of cladistics or tree-based models. Cladistic analyses hypothesize the relational histories of changing trait states within species or groups from a common ancestor. As these models are concerned with identifying the points of divergence over time from earlier ancestral states, they are an exceptional heuristic for thinking about evolutionary relationships of descent within and between units of culture. Applied phylogenetics methods in anthropological studies have become increasingly common, particularly in tracing the development of material culture traditions. For example, Buchanan and Collard (2007), Darwent and O'Brien (2006), Lycett (2009), O'Brien et al. (2001, 2014), Prentiss et al. (2015), and Riede (2008), among others, have utilized cladistic methods to investigate change over time in lithic projectile and core traditions in various temporal and spatial aspects of prehistory. Others have applied phylogenetic methods to studies of, e.g., pottery (Cochrane 2008; Collard and Shennan 2000), historic cutlery (Riede 2009a), clothing, and textile traditions (Buckley 2012; Jordan 2009; Matthews et al. 2011; Tehrani and Collard 2009), and to design elements in various forms of material construction and craft traditions (Jordan 2015; Jordan and Mace 2006; Jordan and O'Neill 2010; Jordan and Shennan 2005, 2009; Marwick 2012; O'Neill 2013; Tehrani and Collard 2013).

While continuing to prove useful to archaeological hypothesis testing to date, phylogenetics explicitly addresses processes of change at the *macro*scale. Thus, microevolutionary studies in the cultural sciences remain somewhat elusive. However, the application of network analyses in conjunction with tree-thinking logic has been used to infer microscale instances of social information transmission within traditions, thus coming close to modeling within-population change over time (e.g., Prentiss et al. 2011; Riede 2008; Jordan 2015). Similarly, recent applications of Bayesian phylogenetic methods have proved effective for identifying some aspects of microscale change, such as frequency rates of change (Atkinson et al. 2008; Pagel et al. 2007) and estimating instances of ancestral state change (Fortunato et al. 2006). Thus far, the most successful applications of Bayesian phylogenetic methods have been undertaken in language-related studies (e.g., Gray and Atkinson 2003; Gray and Jordan 2000; Greenhill and Gray 2005), as the transmission and spread of language have proven to be a close cultural proxy of gene flow since language is a steady delimiter of cultural groups as they have migrated throughout history. However, further applications of a variety of phylogenetics methods appear promising and could theoretically be applied to a wide range of cultural data on diverse cultural traditions, for example, in tracing language descent relationships in broad regional contexts (Gray et al. 2007).

Cultural Microevolution: A Problem of Commensurability

Relatively early in the rocky process of commensuration between Darwinian evolutionary theory and the anthropological sciences, Robert Dunnell (1980, p. 37) observed that "evolutionary biology cannot... be applied unamended and uncritically to cultural phenomena." Dunnell realized that the accepted modes of biological evolution, though clearly at least somewhat analogous to those of cultural evolution, were not the same, but could, if modified and critically applied, “provide the elements of a suitable explanatory structure” for cultural change by way of selection and descent with modification. Dunnell was not the first to point this out, as E.B. Tylor’s (1881, p. 20) observation illustrates:

> On the whole it appears that wherever there are found elaborate arts, abstruse knowledge, complex institutions, these are the results of gradual development from an earlier, simpler, and ruder state of life. No stage of civilization comes into existence spontaneously, but grows or is developed out of the stage before it.

Not much later, the Swedish archaeologist Oscar Montelius linked the typological method directly to the principles of Darwinian evolution as then understood (Montelius 1884, 1899) and actually developed a formal method aimed at tracking patterns of descent with modification (Montelius 1903; see also Riede 2006, 2010). Clearly then, descent with modification of technologies as well as whole cultural systems was a subject of concern to earlier social scientists. However, early qualitative reflections on the subject aside, it was not until the mid-twentieth century that systematic evolutionary thinking began to take hold in anthropology and archaeology in particular.

In 1965, Campbell (1965, p. 26) dissected earlier arguments on sociocultural evolution and processes of variation, selection and retention. He argued that identifying an “analogy between natural selection in biological evolution and the selective propagation of cultural forms” was not only applicable to cultural studies but relevant to the interpretation that culture does in fact evolve through histories of descent from previous forms and as a result of selection pressures. The following year, F.T. Cloak, Jr., presented a brief but insightful discussion of cultural microevolution as it was (and still often is) compared to processes of Darwinian evolution in the biological sciences. Cloak noted that a major deficiency in the utility of using Darwinian evolutionary terms in relation to culture was (and is) that scholars often “have failed to use the proper analogues . . . they have related the wrong biological concepts to the cultural concepts they wish to explicate” (Cloak 1966, p. 7). Cloak observed that the use of cultures as analogous to species breaks down in Kroeber’s (1948, p. 260) traditional “Tree of Culture” schema (Fig. 2.2) because cultures, unlike plants and animals, can potentially continue to exchange traits after they have become speciated or rather widely separated through processes akin to speciation through genetic mutation and drift. In this sense culture evolves unlike a biological entity since biological reproduction is not necessary for cultural inheritance processes to take place. However, the crisscrossing branching pattern in Kroeber’s “Tree of Culture” remains relevant to this day to cultural evolutionary heuristics, as it illustrates remarkably well the combinations of branches, reticulations, and complex interconnectedness evident between disparate cultural phenomena. A further criticism leveled by Cloak lay in the “functionalist” approach to culture in which a single given culture was viewed as directly analogous to a single organism. This, he

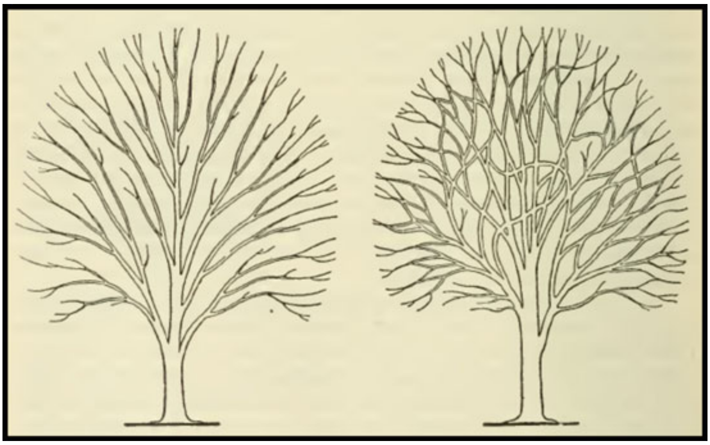

Fig. 2.2 Kroeber’s “Tree of Culture” diagram (1948, p. 260). The “Tree of Life” on the left represents the bifurcating phylogeny of biological organisms. The “Tree of Knowledge” (i.e., culture) on the right represents the braided-stream model (Moore 1994) of weaving and intersecting branches of cultural traditions and their interrelationships

noted, ignored the phylogenetic relationships between cultures—the coherence and congruence within and between cultures that results from the historical contingencies inherent in cultural contact and subsequent change (an issue that has come to be known as "Galton's problem" [Naroll 1965]). As previously observed, this is actually illuminated by the reticulations in Kroeber's more bush-like tree.

Somewhat ironically, Kroeber (1948, pp. 260–261) recognized the importance of this same historicity in his "Tree of Culture" schematic (Fig. 2.2), stating that the branching patterns were meant to illustrate not only how cultures diverge but that reticulations also showed how "it syncretizes and anastomoses too . . . a ramification of such coalescences, assimilations, or acculturations" that are the indelible marks of the historic relationships between cultural traditions. It is these dynamics inherent in cultural lineages that emphasize the importance of recognizing historical contexts as much as possible when hypothesizing about patterns of cultural change. At any rate, contemporary computational methods are able to explicitly integrate potential blending and reticulations (e.g., Bryant et al. 2005).

Cloak went on to present a series of analogies commonly used to juxtapose biological evolutionary concepts with those observed in cultural evolution, namely:

Biological	Cultural
Populations of organisms	Populations of culture bearers
Phenotypic traits	Cultural traits
Gene flow	Diffusion
Natural selection	Natural selection
Biological fixing	Cultural fixing
. . .	Cultural selection

Simply put, Cloak made distinctions between (1) populations of organisms and populations of culture bearers; (2) phenotypic traits and cultural traits; (3) gene flow and diffusion—the ways in which traits move between populations; (4) natural selection and natural selection in biological and in cultural contexts, respectively; (5) fixing processes of introduced traits in receptor populations, biological and cultural "fixing through chance"; and finally (6) not an analogy, but a process that Cloak proposed has no clearly delimited biological analog,[1] cultural selection.

The following discussion treats with each of these somewhat irregular analogues in light of over half a century of further research into processes of cultural evolution, particularly taking into account the extended discussions into the validity of analogies between genetic/biological and cultural/social-learning evolutionary transmission processes (e.g., Claidière and André 2012; Daly 1982; Durham 1982; Durham et al. 1997; Mesoudi et al. 2006; Weingart et al. 1997; see also various chapters, this volume).

Populations: Scale and Commensurable Units of Analysis

At the most general population scale is (1) the individual (the smallest population possible); (2) a given population of closely or relatively closely genetically related individuals; and (3) larger and increasingly unrelated populations that differ from other populations in some distinguishable way

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[1] It should be noted that the field of epigenetics has identified instances where cultural phenomena and sociocultural environmental circumstances precipitate change at the genetic level (e.g., Jablonka and Lamb 2005). Thus, growing evidence indicates that cultural selection has at least some measurable biological consequences.

(e.g., “organisms, species, kingdoms” à la Eldredge 1985, p. 93). In genetics, a population is a straightforward metric—it is made up of interbreeding organisms. In anthropology and archaeology, it is cultural traits which serve as proxies for the behaviors of our informants and the artifacts and assemblages that they create. Each of these can be seen as a single unit of analysis and thus assessed from a microscale perspective, but at any scale that moves beyond the individual, we quickly reach a macroevolutionary imperative that makes discerning between what we define as “micro” and “macro” problematic depending on the overall scale of analysis itself—e.g., localized, regional, or global. The importance of scale becomes most acute when attempting to assess cultures or subgroups within cultures as individual units—e.g., as “organisms” rather than “taxa.” Explicitly in cultural evolution studies, we make generalities based on the scale of our analyses (Binford 1965, p. 203). Because cultural phenomena are prone to such inimitability given high variability in the quality of fidelity of transmitted information between individuals and across time, we can designate commensurable cultural units only so long as we focus on tracing the evolution of cultural traits themselves rather than attempting to trace the “cultural evolution” of populations to which traits are allocated. Cultures, *as such*, do not evolve. What evolves are the ideas and associated behaviors that combine to make identifiable sets of cultural traits empirically observable in specific societies through shared behaviors and practices. It is these behavioral *recipes*—evident as they are in *communities of practice*—that make up what we call “culture” and that evince change over time (cf. Riede 2011). Thus, when it comes to microevolutionary processes of culture change, the size of a population is not as important as the demographic makeup of the population and its pre-existing historical contexts and epistemology that may impose significant effects on how introduced changes are manifest, received, and dealt with. Thus, if we are to say anything about *micro*scale cultural evolution, we must focus on transmission processes that result from mutation, selection (both natural and cultural), gene flow, migration, and drift. Luckily, transmission is something that we *can* observe in anthropology and in the archaeological record, e.g., by way of inferring instances of pedagogy by way of proxies (agent-based modeling has made significant contributions to advancing the accuracy of behavioral computer simulations; see Laue and Wright, this volume).

In any individual, biological ontogeny begins with a pretty straightforward transmission of genetic data from two individuals to a single host individual (or individuals in the case of twins, etc.). Cultural exchange is generally not so straightforward. Even at its closest approximation, for example, vertical transmission of information between parent and offspring, cultural transmission is a complex process. It depends on the nature of the information, its contextual usefulness in the long term (is it adaptive or perceived as in some way fitness enhancing?), as well as the social values in place that may encourage or discourage creativity or innovation or, conversely, that call for conservativism or conformity to the status quo and, of course, any number of existing sociocultural norms that put pressure on the selection of ideas. In cultural evolutionary processes, the transmission of ideas happens at the interindividual level but plays out on the community and population levels. Ultimately, it is vital to appreciate the existing historical, environmental, and social contexts into which cultural traits are introduced in a given population. Thus, within this scenario, we may consider any given cultural unit as a dynamic community of practice or member thereof and prone to change through diverse vectors and dynamically at different relative demographics. Cultural drift, for example, can allow for isolated populations to become increasingly unique over time—effectively micropopulations in a macroscale scenario. In cultural evolutionary processes, transmission isolating mechanisms (TRIMS, Durham 1992, p. 333) precipitate cultural drift in similar fashion to how biogeographical isolation leads to genetic drift in populations of biological organisms (see Chap. 3, this volume).

Traits

In biological terms, a phenotypic trait is one that is expressed as a result of variations in allele frequencies. It is an empirically observable, measurable expression of genes (i.e., variant(s) of alleles), for example, those that determine hair or eye color or that cause diastema or any other observable genetic variation in an individual. A cultural trait is similar in that it could be any number of expressed variants of cultural concepts thus reflected in behavior or material culture. Anthropologists (and archaeologists in particular) have long used "cultural traits" as units of analysis for defining what is and is not a specific culture, feature of a particular culture, or otherwise some variant of a specific cultural phenomenon (Moylan et al. 2006; O'Brien et al. 2010; Pocklington 2006). This is because identifying cultural characteristics as "traits" is useful for quantifying the similarities and differences observed between social groups and the diverse expressions of their material culture. Here, the distinction between phenotypic traits and cultural traits becomes blurred. This is because cultural traits are themselves non-biological phenotypic traits. In many cases they can be observed in quite similar ways. Just as we may observe someone possessing brown hair due to their inheritance of genes that code for brown hair, so too we may observe that this same person is wearing their brown hair made up in a French braid—itself a heritable cultural trait, the knowledge of which was culturally transmitted, probably through social learning (e.g., Mace 2005, p. 2).

But, generally speaking, defining any particular cultural trait necessitates an explicitly synchronic perspective that regards the trait in question to be either present or absent in any given group at the moment of observation. This is not to say that variation cannot be taken into account. Indeed, accounting for change is one of the main purposes of the exercise of identifying cultural traits, and this is accomplished by establishing the rate and frequency of trait changes over time within what can be deemed a coherent cultural unit. The set(s) of cultural traits that anthropologists use to define any given cultural group are necessarily subjective. One can easily discern basic culture traits of a given society quite quickly based on extant ethnographic and archaeological literature, and nowadays detailed information can be rendered relatively quickly using digital resources like the Electronic Human Relations Area Files (eHRAF) (http://ehrafworldcultures.yale.edu/ehrafe/), D-PLACE (Kirby et al. 2016), (https://d-place.org/home), and EnvCalc2.1 (Binford and Johnson 2014), (http://ajohnson.sites.truman.edu/data-and-program/) and language databases such as Ethnologue (Grimes 2002; Lewis et al. 2016) (http://www.ethnologue.com/19/) and Glottolog (Hammarström et al. 2017) (http://glottolog.org/).

For instance, ethnographically the nineteenth- to mid-twentieth-century Netsilik Inuit (Balikci 1970, 1984; Rasmussen 1931) of the central Canadian Arctic could be categorized by 14 general cultural traits (e.g., small band-level groups, mixed subsistence, Inuit-Inupiaq language, animistic cosmology, etc.). While arguably more or less accurate, these traits are such gross generalizations that they tell us very little about actual Netsilik culture. As traits, these do not even approach—much less scratch the surface of—what was representative of Netsilik culture at the time of ethnographic encounters (Balikci 1970; Rasmussen 1931). While taking into account basics of cosmology and social structure, the trait list remains purely phenotypic in what it describes of the culture in question, missing entirely the "nonempirical character" of culture (Osgood 1951). Thus, these "cultural traits" no more define the Netsilik culturally than the allele frequency that generates blue eyes defining a blue-eyed individual's biology. Yet, identifying these traits does help us delineate the Netsilik from say the Araweté of Amazonian Brazil (Viveiros de Castro 1992), with whom they have in common only the presence of a generally animistic worldview, a shamanic tradition, and recognition of various taboos, although each of these manifests so remarkably different between the two as to be arguably incongruent at all but the most generic scale. Steward (1955) recognized that the difference lies in "secondary" versus "core" cultural traits, with core traits being the true delimiters of cultural relatedness (a fundamental discussion of the operationalization of a similar concept of prototypical cultural "core" traditions is drafted in Boyd et al. (1997), although this breaks considerably from

Steward's concept of the cultural core being the suite of technological adaptations to the particular ecological niche, how a society adapts to the specific environment in which they live; rather, Boyd et al. imagine "core traditions" as the conservative features of the specific culture in question in a relative sense—the equivalent of a cultural genotype rather than the phenotypical traits that empirically define it and make it discernable from any other culture).

In evolutionary studies in cross-cultural anthropology and archaeology, trait determination is extremely important, because it sets out the units of analysis to be studied. This is imperative for identifying microevolution since it changes in the frequency or sometimes simply the presence or absence of traits themselves that allow us to observe processes of evolution in both biology and culture. In cultural studies, appropriate traits must be determined, collated, and assessed based on the hypothesis being tested. Ideally, it is best that many are considered. This is because the frequency of some traits changes over time at different rates and for different reasons, while other may persist for so long as to show little or no observable change (see Nunn et al. 2010). This should be taken into account when determining any cultural traits as units of analysis (Dunnell 1986; O'Brien et al. 2010). Material culture traits tend to be categorized by explicit details of artifacts or assemblages—presence or absence of morphological features, design elements, probable or known use—functions, materials, etc. (e.g., Andrefsky 2008) but may also encompass manufacturing techniques, stages of curation, and even conceptual-symbolic considerations (e.g., Haidle 2009), all of which are to some degree culturally determined.

Dunnell's early concept of style vs function as dichotomous and incommensurate units of analysis did not take into account that stylistic features and forms can serve symbolic functions that significantly do directly affect the Darwinian fitness of the population in which they occur and that, further, function does not always get reflected as we assume it should. For example, task-specific efficacy of a particular morphology or material (i.e., functional advantages) often does not play as big a role in material culture being passed to the next generation as one might think. In the Final Palaeolithic of northern Europe, for instance, lithic projectile points should be conforming to certain ballistic parameters in relation to the target prey animals (Friis-Hansen 1990). Yet, analyses of the shape variation among different techno-complexes in this period show that such functional considerations were not consistently heeded (Dev and Riede 2012; Riede 2009b), suggesting that functional differences were not discernable or that transmission processes overrode any such concerns. Due to its learning efficiency, the imitative copying of certain practices or materials can and does occur entirely independent of function (Gergely and Csirba 2006). Failing (or refusing) to recognize this, Dunnell (1978, p. 197) ultimately suggested that style could not explain cultural evolution from a rigorous evolutionary framework. However, we clearly see in the archaeological record numerous instances where nonfunctional features of a cultural system evolve through descent with modification and maladaptive traits regularly emerge and persist in human traditions (see Bettinger et al. 1996).

Ultimately, cultural traits *are* analogous to phenotypic traits in that they are observable features of our species expressed through materials, appearances, behaviors, and practices, all resulting from diverse responses to the natural and sociocultural environment experienced by previous generations.

Modes of Transmission: Gene Flow and Diffusion

In biology, gene flow at the microscale takes a simple trajectory: with very few exceptions in the Animal Kingdom, at least parents pass genes on to their offspring at a balanced ratio, half from the biological mother and half from the biological father. Replication errors and mutations may cause significant differences between the genetic makeups of individual offspring as compared to that of parents, but the overall process of genetic inheritance remains quite steady. Recent studies into epigenetics show that developmental stresses and dramatic life changes actually make things a bit more complicated at the level of alleles and in the determination of what genes become switched on and off in an individual as they develop, but at its most basic, the process remains pretty straightforward (Jablonka and Lamb 2005). At the population scale, gene flow gets more complicated and describes the frequencies of traits moving between sample populations, not individuals, though individuals are the vectors of trait movements within the population as a whole. Over time, as individuals reproduce, interbreeding between populations causes the frequency of certain traits to become more or less prevalent, ultimately altering the gene pool of each population. Generally speaking, this leads to variation in the gene pool between the populations in question (but, see the section on fixation below, as genetic diversity does not prevail in all cases of gene migration).

Diffusion is said to occur as introduced variants spread throughout a population, effectively fanning out through the community over generations. Where diffusion is somehow hindered by geophysical isolation, allopatric (or geographic) speciation occurs (Eldredge and Gould 1972; see also, e.g., Mayr 1942, 1963). In different pockets of isolated populations, genetic drift may take place further altering a particular population in unique ways. These same phenomena happen in human culture, as populations can become separated by physical barriers such as mountain ranges, rivers, oceans, and the like. Both gene and information flow can also be stifled by populations simply not interacting for reasons such as differences in language that may hinder communication, conflicting ideologies, or cultural norms—aspects of culture are themselves often barriers to information transmission, and "ecological, psychological, linguistic, and cultural" aspects can all be highly effective *transmission isolating mechanisms*, or "TRIMS" for short (Durham 1982, p. 292; 1992, p. 333). As Boyd and Richerson (1985, p. 9) point out, a cultural mechanism akin to genetic drift can occur when, in small populations, "chance variations in which cultural variants are observed and remembered may cause substantial changes in frequency from time to time . . . rarely performed variants may be lost entirely" simply by not being observed from one generation to the next. Often, the more relatively isolated a group becomes, the more likely processes such as cultural mutation, drift, or inertia will alter the developing culture as it evolves in place (Richerson and Boyd 2005; to be clear, by definition cultural inertia tends to "keep the population the same from one time period to the next," but in the context of isolate populations, it is proposed to affect stasis over the long term even acting to maintain the slightest inevitable changes introduced into the otherwise static system through cultural mutation [e.g., innovation] and drift. In these instances, inertia actually acts to legitimize and perpetuate introduced cultural variants, at least once they have been introduced—see discussion on "fixation" below).

To a certain extent, cultural transmission is much more complex because it need not rely on individual-to-individual modes of contact to initiate or propagate even at the microscale. A single individual can simultaneously communicate ideas to multiple observers at once, thus potentially planting ideas or impressions in the minds of those around them—a process referred to as one-to-many cultural transmission (e.g., Shennan 2002, p. 49). However, at the macroscale, processes of information flow and diffusion empirically appear quite similar to their biological antecedents, if not spreading at a potentially much greater rate and degree. Unlike genes, which require generations across which to spread, ideas (the alleles of culture) often travel fast, change frequently, and can even quite dynamically alter the diffusion of biological information by biasing individuals toward or against interacting with others. While similar in concept, cultural diffusion is thus far more fluid than gene flow, with the potential even to dramatically influence its trajectory.

Modes of Selection: Natural Selection in Nature and on Culture

Conway Zirkle (1941) has traced the concept of natural selection, so intrinsically attributed to Charles Darwin in contemporary reckoning, well beyond Darwin or even Alfred Wallace (1870), and past recognized influences from Thomas Malthus' *An Essay on the Principle of Population* (1798) among others, all the way back to the Greek philosopher Empedocles (c. 400 B.C.). Clearly, concepts synonymous with Darwinian natural selection have been around for a long time. As Zirkle chronicles so well, Darwin was quite open about his influences, although it is generally accepted that he came to his conclusions predominantly on his own. It was often after the fact that others pointed out to Darwin similarities to his explanations that others had earlier developed but not so widely circulated, for example, W.C. Wells' 1813 paper speculating a principle of natural selection at work on human skin pigmentation (see Wade 2010) or Patrick Matthew's 1831 treatise on macroevolutionary processes of natural selection in relation to tree cultivation (see Weale 2015). That there had been numerous earlier observations of natural selection *as such* does not detract from the importance of Darwinian evolutionary theory as we know it. Rather, these observations reinforce our scientific understanding of descent with modification as a result of natural selection as an empirical, testable, and supported theory of change over time in living organisms in relation to the environments in which they develop.

Darwin's (1859, p. 5) own description of natural selection:

> as many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequent recurrent struggle for existence, it follows that any being, if it varies however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be *naturally selected*,

addressed (at least initially) more the ultimate effects of environmental adaptation over time in organisms rather than the mechanisms driving it. Principally, Darwin's concept suggested that natural selection represent the *process* (Darwin's "principle") whereby slight variations accumulate in species over time, adapting them to the environments in which they live. The elegance of this observation is such that—even with the vast expansion of knowledge in regard to evolutionary thinking that has developed out of the last century and a half of research on the subject—contemporary understandings of processes of natural selection do not fundamentally stray far from Darwin's (and Wallace's) original concept. In general, research since has expanded and refined—rather than amended—the theory. It is far beyond the auspices of this chapter to rehash the well-established theory of natural selection as it stands in the biological sciences (see Goodale, this volume). Thus, we take for granted the accepted general definition of natural selection as a process in which organisms that possess variants of (genetic) traits and that facilitate survival and thus reproductive fitness in their host environment tend to pass on those traits to their offspring, imparting an enhanced (at least to some degree) survivability; this in turn over time can be observed as population diversity and distribution at the macroscale. Of particular relevance to anthropology, this same process of course works on humans and influences their behaviors and can therefore be applied to observed diversity and change in cultural traditions such as material culture. In addition to natural selection affecting change over time in cultural phenomena, culture is also subject to cultural selection that significantly influences variability (e.g., Durham 1982, p. 297): a process in which individuals and populations that possess variants of (cultural) traits and that persist and diffuse in their host environment tend to pass on those traits to their descendants and others, imparting an altered (at least to some degree) survivability; this in turn over time can be observed as population diversity and distribution of cultural variants at the macroscale—what Mace and Pagel (2004) so eloquently refer to as "the cultural wealth of nations."

As pointed out widely elsewhere, natural selection and cultural selection are not justly comparable processes (e.g., Ames 1996, p. 115; Durham 1991; Graves-Brown 1996, p. 170; O'Brien and Holland 1990, 1992; Richerson and Boyd 2005; Shennan 2002; among many others). However, it has become clear that each affects the other in dynamic fashion. Laland et al. (2013, p. 68) observe that "natural selection fashions highly specific cultural capabilities in particular species … according to their ecology and life-history." Similarly, cultural selection or more specifically the behavioral variants that emerge by natural selection that are then retained and develop further variation due to cultural constraints, transmission biases, or inertia (such as those leading to the development of agriculture, sensu Rindos [1980]) alter the natural environment and thus have potentially wide-ranging effects on subsequent "natural" selection processes. The feedback loop between natural and cultural selection processes has been of increasing interest in the evolutionary social sciences, particularly under the auspices of niche construction, or triple-inheritance theory of gene-culture-ecology dynamics (sensu Odling-Smee et al. 2003; see Riede, this volume). Up until the last few decades, failing to recognize the symbiosis between these forces has been perhaps the most common failure in evolutionary culture theory and in its relation to contemporary concepts in evolutionary biology (see Lyman and O'Brien 1997 for a review). Natural selection is, of course, a significant force at work on cultural selection. More accurately, natural selection is foundational regarding "the natural selection of behavior" that finds expression in culture (Skinner 1981). As an expression of human behaviors in response to experienced circumstances, cultural selection is a flexible variant of natural selection—a hierarchically dependent variable of much broader natural selection. As Bettinger et al. (1996, p. 150) note, cultural selection, as such, is ultimately the result of "natural selection acting in the long run to produce decision rules that in turn vicariously select cultural variants." Cultural selection is in fact an aspect of natural selection in which culture itself in a broad sense is the fitness-enhancing adaptation.

Fixing Through Chance: Mutation, Drift, Adaptation, and Persistence

Durham (1990, p. 191) proposes that "*coincidence* (i.e. similarity by accident or chance), *analogy* (similarity by convergence or independent invention), *homology* (similarity by descent), and . . . *synology* (similarity by diffusion)" create similarities (or seeming similarities) between cultures. He contends that analogy, homology, and possibly coincidence function in culture more-or-less similarly as they do in biology. However, in culture, all of these processes rely on some form of social transmission of cultural information fundamentally separated from sexual reproductive transfer of genetic information (not taking into account the subsequent parent-offspring relationship that plays a dramatic role in the transmission of cultural information). As information (genetic, cultural, or otherwise) is transmitted between individuals and populations, it is not enough that it emerges and is passed on from a single individual to another—for descent with modification to occur, the unit of information must be transmitted at a broader scale; the products of mutation and drift (i.e., variation) must persist to some degree in a given population; the information has to stick. This occurs through a process known as fixation.

Initially, novel traits must emerge. The issue of true novelty, innovation, and creativity has often been sidestepped by evolutionary archaeologists. The simple solution has been to treat novelty as strictly analogous to mutation and hence to let novel traits emerge by chance only. While fortuitous errors surely do and did occur in the past, this is mostly likely a poor concept for innovation. In a recent attempt to tackle this issue, Riede et al. (2018) suggest that the provisioning of youngsters to play things during childhood—extended in *Homo sapiens* well beyond the duration of other great apes and hominids—primes innovation within the given constraints of a broad cultural evolutionary lineage. The argument is that once reproductive concerns kick in, the costs of experimenting with novel raw materials and combinations of different components are not favored given the risk of failure. During play, however, such constraints are absent, allowing individuals to freely toy with objects and materials and their combinations and uses. As children mature cognitively and physically, they become more likely to be able to hit on genuine innovations making adolescence the sweet spot for creativity. At the same time, the making of scaled toys of functional objects (sleds, carts, bows, etc.) by adults allows them to explore the mechanical affordances and other properties of such objects without incurring the time, energy, and material costs of building a full-scale version. In this approach, the inter-generational niche construction dynamics become critical in seeing innovations not as random but not as the work of some lone genius either (see also Riede, this volume, on further examples of such niche construction processes).

In genetics, fixation occurs when a new allele (variant of a particular gene) appears (i.e., mutation) and it gets passed to the next generation. Conversely, if it doesn't get passed on, it is simply lost. If it does continue to be passed on—inherited from one generation to the next—*and* is passed on in the population *and* eventually replaces the other variant(s) of the same gene, it is said to be "fixed" in the population. Thus, one allele replaces other alleles of the same gene and eventually becomes the only remaining variant of that gene in the population. The fixed variant is then permanent in the population until another mutation occurs, potentially causing this series of events to repeat. Generally, this process is based on random mutation and the subsequent vicissitudes of contextual selection pressures, making the chances of any particular variant becoming lost or fixed quite difficult to predict—seemingly a product of chance (Hartl and Glark 2006; Kimura and Ohta 1969; see also Koerper and Stickel 1980 for an early treatment of drift and fixation processes in cultural phenomena).

In terms of culture, a trait could be said to become fixed through similar processes, but the chances of certain variants being perpetuated are not as subject to change once they have been introduced. In cultural systems, once a new variant shows up (e.g., through the cultural equivalents of mutation, an accidental invention and innovation, or as the result of guided variation; see Walsh et al., Chap. 3, this volume), its fixation potential is subject to both natural selection *and* cultural selection—social-learning, providing an adaptive advantage to local conditions (i.e., imparting enhanced fitness on those choosing to adopt the new variant over those that choose not to), transmission biases, etc. can all contribute to whether a cultural variant is retained and transmitted through the population over time and to what extent. Furthermore, conservative forces such as pedagogy may cause a variant to be selected over others and cultural inertia could effectively "fix" an introduced variant into the existing cultural system (e.g., Neiman 1995).

Neff and Larson (1997) point out that, in evolutionary archaeological theory, adaptation studies focus on deducing how selection processes (e.g., natural selection) lead to diversity. They propose that adaptation "is a key component of a strategy for understanding the living world as the product of natural selection coupled with chance, historical constraints, and developmental constraints" (Neff and Larson 1997, p. 78). In the case of fixation, it is the cultural equivalences of mutation that introduce variability (just as mutation does in biological systems), but individual proclivities, existing cultural norms, the perceived value of the introduced phenomenon within the population in question, and the potential for cultural inertia are significant deciding factors as to what cultural variants become fixed and lost or reach equilibrium (Neiman 1995). In both biological and cultural contexts (Table 2.1), whether or not particular variations persist in a given population—Dunnell's (1980, p. 272) "differential persistence of variability"—is thus the very lens through which we can even begin to observe patterns of descent with modification.

Cultural Selection

Finally, Cloak (1966, p. 10) submitted that "the true biological analogue for cultural diffusion . . . would have to be a sort of *selective* gene flow." "Selective" in this sense is indicative of a flow of information that is purposely directed, assumedly as a result of human intentionality (see Mesoudi et al. 2006, p. 372). This suggests that cultural information can evolve in accordance with the Lamarckian evolutionary process of acquisition of acquired traits or directed variation (e.g., Jablonka and Lamb 1995). In general, biological evolutionary models have not taken such processes very seriously until relatively recently. However, Boyd and Richerson's (1985) dual-inheritance model—which takes into account that biological and cultural systems coevolve in dynamic fashion—has gained significant support in the last few decades across anthropology and archaeology. Added to this, recent research in the fields of epigenetics and niche construction (or triple-inheritance theory) posits inter-dynamics between biological, cultural, and environmental factors in the development of individual organisms.

Table 2.1 Biological processes of evolution and examples of their cultural variants

Biological	Cultural
Mutation "Any heritable change . . . brought about by an alteration in the genetic material. Includes gene conversion, deletion, duplication, insertion and so forth"	Random (but see Riede et al. 2018) change to any aspect of the cultural system as a result of, for example: Invention Innovation Creativity/idiosyncratic variability Accidental variation
Drift (genetic) "Evolutionary change over generations due to random events in small populations . . . operates unless overcome by strong selective forces"	As above, inventions, innovations, idiosyncratic variability, and change as a result of accidents occurring in populations isolated as a result of allopatric separation or resulting from any number of other reproductive isolating mechanism (RIMS) and/or (cultural) transmission isolating mechanisms (TRIMS)
Adaptation "Adjustment to environmental demands through the long-term process of natural selection acting on genotypes"	Adaptation Niche construction (although niche construction theory (NCT) attempts to address the relationships between environments and the organisms that inhabit them, not focused simply on adaptation as such, but rather on the dynamic interplay between organisms and the environment over the long term [see Riede, this volume])
Persistence (The result of fitness/reproductive success) Fitness: "Lifetime reproductive success of an individual... It can be seen as the extent to which an individual successfully passes on its genes to the next generation. It has two components: Survival (viability) and reproductive success (fecundity). Variation in fitness is the major driving force in biological evolution"	Fixation; in cultural this might result from: Cultural inertia Acculturation Conservative transmission biases Pedagogy

Evolutionary biology term definitions taken from M. Tevfik Dorak's online glossary (http://www.dorak.info/evolution/glossary.html)

As a means for evaluating holistic and dynamic selection processes in cultural contexts, such as the acquisition of acquired traits or the horizontal transmission of ideas from one individual to many, cultural selection may have a metaphorical correspondence to epigenetic and constructed environment-induced selection pressures (e.g., niche construction; see Riede, this volume). Understanding selection processes and constraints in general—regardless of whether we designate them as exclusively "natural" or "cultural"—is key to more accurately understand the interplay between humans and their surroundings and vice versa. To distance cultural selection too far from natural selection is to ignore that Darwin's own concept of natural selection was rather plastic and accounted for the "preservation of favourable [*sic*] variations and the rejection of injurious variations" regardless of the overall driving forces involved. Darwin was rather vague as to the specific nature of natural selection forces and certainly did not count out the possibility of human behaviors playing a role in selection pressure. To Darwin, forces at work in producing selection pressures could derive from any number of causes, from natural predator-prey relationships to human proclivities (e.g., domestication), to geophysical constraints such as may be encountered in insular, or otherwise isolated environments, and more (Darwin 1859, p. 81). Thinking about cultural evolution implicitly as variation in the frequency of behaviors from one generation to the next within a society, it is easy to conclude that cultural evolution is driven by natural forces and entirely accountable within the framework of Darwinian evolution by natural selection. One can also remain open-minded to the empirical reality that cultural change in this way appears—and may well be—more dynamic than its biological simile due to the extra-reproductive modes of transmission that are possible thanks to culture.

Cultures evolve in more diverse ways than do biological systems. They can also evolve rapidly in some of their aspects and often along seemingly inexplicable paths. This is why the rate and tempo of cultural evolution is often noted to occur rapidly relative to genetic changes in communities of noncultural biological organisms (although clearly some organisms—such as bacteria and viruses—can and do sometimes evolve very quickly). The combination of purely natural (environmental, circumstantial) and cultural selection pressures is generally much more dynamic, and cultural transmission is of course not limited to the vertical pathway that constrains gene flow. However, not all features of a culture evolve fast and certainly not all the time. Cultural change is not necessarily an inherent property but one that emerges under specific historical conditions (e.g., under conditions favoring enhanced sharing and spread of innovations). Relative to absolute time, the actual and potential speed of evolutionary change depends entirely on "generation length" or the number of replications that a given cultural trait undergoes during a given unit of time (e.g., Fletcher 1996; Jordan and O'Neill 2010). As the expression of human behaviors, themselves, subject to numerous selection and transmission altering forces—from environmental and geophysical to social to idiosyncratic and beyond—cultural traditions clearly change by way of descent with modification over time, founded at the level of single organisms, i.e., human beings interacting with their surroundings. Ultimately, instances of cultural change occur as the result of interactions between individuals (just like changes in allele frequencies passed between or occurring between parents and offspring), and such microscale processes happen constantly in regard to the transmission of cultural variants within and between populations. Yet, it is the *expression* of cultural variants at the population scale that makes any form of descent actually observable. So, while we can theorize about microscale processes in anthropological and archaeological studies, we must operationalize them at the macroscale if we are to say anything relevant about cultural evolution as a process rather than as an isolated incident of change.

In population genetics, it is widely recognized that neutral or nearly neutral mutations—those that have little or no effect on fitness and are therefore weakly or seemingly not at all selected for—predominate at the molecular level (see Wakeley 2010, pp. 123–125). Kimura (1968) calculated that within finite populations of complex organisms, neutral or nearly neutral mutations actually occur at a much higher rate than they do modeled simply as responses to natural selection pressures. Thus, neutral mutations can arise and diffuse within a population relatively rapidly without having any direct impact on the community in question. When fitness is more-or-less equal between differing genotypes (i.e., none of the existing genotypes provides a distinct adaptive advantage under given conditions), there is "weak" or "nearly neutral" selection (Hartl and Clark 2006, pp. 248–251; Ohta 1973). In principle, this same phenomenon is observable in the archaeological record (Kandler and Crema, this volume; Laue and Wright, this volume). In regard to culture, Durham (1982, p. 307) observed that "some cultural variability has little or no impact on the adaptiveness of its carriers." In fact, many attributes of culture have no discernable consequence when it comes to fitness—at least not which can be observed. In cultural evolutionary studies, just as in evolutionary biology, this concept is known as the *neutral* or *nearly neutral model* evolutionary model that accounts for changes in cultural systems that have "little or no impact on human survival and reproduction" (Durham 1982, p. 308). Even in early evolutionary archaeology studies, neutral cultural traits were recognized in the material record, especially when the appearance of new variants of design or morphology appear and disappear rapidly. For example, Dunnell's "stylistic" traits could be seen as neutral in that accordingly their "frequencies in a population are not directly accountable in terms of selection . . . their behavior should be more adequately accommodated by stochastic processes" (Dunnell 1978, p. 199). At the very least, "stylistic" traits as Dunnell conceived them fit the nearly neutral model. As it turns out, in both organisms and cultural phenomena, ephemeral changes resulting from random mutation and drift are more commonly drivers of diversity than have often been theorized (see Laue and Wright, this volume).

In cultural studies, we may be able to more appropriately understand cultural selection as a form of synecdoche with Darwinian natural selection processes—in fact as an intrinsic part of those processes—without dwelling too dogmatically on the constraints imposed by biological imperatives such as the "reductionist argument that focuses solely on human reproductive success" (O'Brien and Holland 1990). Ultimately, culturally selected traits are still subject to natural selection pressures *and* subsequent cultural selection pressures over the long term. The false dichotomy between nature and culture in which culture remained somehow outside of nature has only recently been dismantled. Culture is subject to both Darwinian *and* non-Darwinian selection and evolutionary trajectories (e.g., Lamarckian accumulation of acquired traits [Jablonka and Lamb 2005]). While modes of selection pressure may theoretically appear different between adapting to the natural environment and adapting to, for instance, the social environment, the ultimate broad effects of selection pressures are the same between biological and cultural systems. Changes over time, driven by the natural *and* social environment *and* by chance *and* purposefully directed, still fall within the natural domain, because behaviors themselves are responses to selection pressures (e.g., see Riede, this volume).

Synthesis

The chapters in this section of the handbook illustrate that evolutionary archaeology has developed a significant degree of theoretical and methodological sophistication during recent years. In closing we offer two critical points. First, the archaeological study of cultural microevolution remains as difficult as it remains critical and is providing significant new insights. Scholars are developing increasingly sophisticated models referencing the effects of plasticity, selective context, learning and innovation, transmission bias, and neutral and nearly neutral processes. Walsh et al. (Chap. 3, this volume) argue that the processes by which cultural variations emerge and are transmitted are complex and affected by a variety of factors inclusive of (but not limited to) population density and interaction parameters, cultural constraints on creativity, the nature of cultural entities (e.g., simple artifacts versus more complex cultural configurations), and modes of learning and communication. Goodale (this volume) reflects on the importance of selective context and the impacts of short-term processes on the unfolding of long-term (macroevolutionary) trends. Kandler and Crema illustrate the challenges faced by archaeologists seeking to identify directionally biased cultural transmission and neutral processes in the archaeological record. They offer sophisticated mathematical approaches to initiating the process of testing alternative hypotheses. Second, contributors make it clear that there is no firm boundary between cultural microevolution and macroevolution, at least as measured with archaeological data. Compare, for example, discussions in Kandler and Crema (microevolution section, this volume) versus those of Laue and Wright (macroevolution section, this volume). These two chapters provide a vivid argument as to the necessity that we gain nuanced understanding of both bottom-up and top-down cultural processes. As we do that, we recognize that knowledge derived from studies on different scales is essential to creatively imagine the cultural evolutionary process in general.

Acknowledgments We would like to thank two anonymous reviewers for their constructive comments on this manuscript. Of course, any oversights are the authors' responsibility. Walsh would like to acknowledge prior postdoctoral support from the School of Culture and Society and the Arctic Research Centre at Aarhus University, and the T*ales of Bronze Age Women* project (Carlsberg Foundation grant CF-150878, PI Karin M. Frei) at the National Museum of Denmark, where he is currently a postdoctoral research fellow.

Data Sharing Statement Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

References

Ames, K. M. (1996). Archaeology, style, and the theory of coevolution. In H. D. G. Maschner (Ed.), *Darwinian archaeologies* (pp. 109–131). New York/London: Plenum Press.

Andrefsky Jr., W. (Ed.). (2008). *Lithic technology: Measures of production, use, and curation*. New York: Cambridge University Press.

Assaf, E., Barkai, R., & Gopher, A. (2016). Knowledge transmission and apprentice flint-knappers in the Acheulo-Yabrudian: A case study from Qesem Cave, Israel. *Quaternary International, 398*, 70–85. https://doi.org/10.1016/j.quaint.2015.02.028

Atkinson, Q. D., Meade, A., Venditti, C., Greenhill, S. J., & Pagel, M. (2008). Languages evolve in punctuational bursts. *Science, 319*(5863), 588. https://doi.org/10.1126/science.1149683

Balikci, A. (1970). *The Netsilik Eskimo. Prospect heights*. Long Grove, IL: Waveland Press, Inc..

Balikci, A. (1984). Netsilik. In D. Damas (Ed.), *Handbook of North American Indians, volume 5, arctic* (pp. 415–430). Washington, DC: Smithsonian Institution.

Barton, C. M., & Clark, G. A. (1997). Evolutionary theory in archaeological explanation. In C. M. Barton & G. A. Clark (Eds.), *Rediscovering Darwin: Evolutionary theory and archeological explanation* (pp. 3–15). Arlington, TX: American Anthropological Association.

Bettinger, R. L. (2009). *Hunter-gatherer foraging: Five simple models*. New York: Eliot Werner Publications.

Bettinger, R. L., Boyd, R., & Richerson, P. J. (1996). Style, function, and cultural evolutionary processes. In H. D. G. Maschner (Ed.), *Darwinian archaeologies* (pp. 133–160). New York/London: Plenum.

Binford, L. R. (1962). Archaeology as anthropology. *American Antiquity, 28*(2), 217–225.

Binford, L. R. (1965). Archaeological systematics and the study of culture process. *American Antiquity, 31*(2), 203–210.

Binford, L. R. (1977). General introduction. In L. R. Binford (Ed.), *For theory building in archaeology* (pp. 1–10). New York: Academic.

Binford, L. R. (1981). *Bones: Ancient men and modern myths*. New York: Academic.

Binford, L. R. (2001). *Constructing frames of reference. An analytical method for archaeological theory building using ethnographic and environmental data sets*. Berkeley, CA: University of California Press.

Binford, L. R., & Johnson, A. L. (2014). *Program for calculating environmental and hunter-gatherer frames of reference (ENVCALC2.1)*. Updated Java Version, August, 2014.

Boyd, R., Borgerhoff Mulder, M., Durham, W. H., & Richerson, P. J. (1997). Are cultural phylogenies possible? In P. Weingart, S. D. Mitchel, P. J. Richerson, & S. Maasen (Eds.), *Human by nature: Between biology and the social sciences* (pp. 355–386). Mahwah, NJ: Lawrence Erlbaum Associates.

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago, IL: The University of Chicago Press.

Broughton, J. M., & O'Connell, J. F. (1999). On evolutionary ecology, selectionist archaeology, and behavioral archaeology. *American Antiquity, 64*(1), 153–165.

Bryant, D., Filimon, F., & Gray, R. D. (2005). Untangling our past: Languages, trees, splits and networks. In R. Mace, C. J. Holden, & S. J. Shennan (Eds.), *The evolution of cultural diversity. A phylogenetic approach* (pp. 67–83). London: UCL Press.

Buchanan, B., & Collard, M. (2007). Investigating the peopling of North America through cladistic analysis of early Paleoindian projectile points. *Journal of Anthropological Archaeology, 26*(3), 366–393.

Buckley, C. D. (2012). Investigating cultural evolution using phylogenetic analysis: The origins and descent of the southeast Asian tradition of warp ikat weaving. *PLoS One, 7*(20), 1–20.

Campbell, D. T. (1965). Variation and selective retention in socio-cultural evolution. In H. R. Barringer, G. I. Blanksten, & R. W. Mack (Eds.), *Social change in developing areas* (pp. 19–49). Cambridge: Schenkman Publishing Company.

Cavalli-Sforza, L. L., & Feldman, M. W. (1981). *Cultural transmission and evolution: A quantitative approach*. Princeton, NJ: Princeton University Press.

Claidière, N., & André, J.-B. (2012). The transmission of genes and culture: A questionable analogy. *Evolutionary Biology, 39*, 12–24.

Cloak Jr., F. T. (1966). Cultural microevolution. *Research Previews, 13*, 7–10.

Cochrane, E. E. (2008). Migration and cultural transmission: Investigating human movement as an explanation for Fijian ceramic change. In M. J. O'Brien (Ed.), *Cultural transmission and archaeology: Issues and case studies* (pp. 132–145). Washington, DC: The SAA Press.

Collard, M., & Shennan, S. J. (2000). Ethnogenesis versus phylogenesis in prehistoric culture change: A case-study using European Neolithic pottery and biological phylogenetic techniques. In C. Renfrew & K. Boyle (Eds.), *Archaeogenetics: DNA and the population prehistory of Europe* (pp. 89–97). Cambridge: McDonald Institute for Archaeological Research.

Cronk, L. (1991). Human behavioral ecology. *Annual Review of Anthropology, 20*, 25–53.

Daly, M. (1982). Some caveats about cultural transmission models. *Human Ecology, 10*(3), 401–408.

Darwent, J., & O'Brien, M. J. (2006). Using cladistics to construct lineages of projectile points from northeastern Missouri. In C. P. Lipo, M. J. O'Brien, M. Collard, & S. J. Shennan (Eds.), *Mapping our ancestors: Phylogenetic approaches in anthropology and prehistory* (pp. 185–208). New York: Aldine Transaction.

Darwin, C. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.

Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An introduction to behavioral ecology* (4th ed.). Oxford: Wiley.

Dethlefsen, E., & Deetz, J. (1966). Death's heads, cherubs, and willow trees: Experimental archaeology in colonial cemeteries. *American Antiquity, 31*(4), 502–510.

Dev, S., & Riede, F. (2012). Quantitative functional analysis of late glacial projectile points from northern Europe. *Lithics, 33*, 40–55.

Donahue, R. E., & Fischer, A. (2015). A late glacial family at Trollesgave, Denmark. *Journal of Archaeological Science, 54*, 313–324. https://doi.org/10.1016/j.jas.2014.12.018

Dunnell, R. C. (1978). Style and function: A fundamental dichotomy. *American Antiquity, 43*(2), 192–202.

Dunnell, R. C. (1980). Evolutionary theory and archaeology. In M. B. Schiffer (Ed.), *Advances in archaeological method and theory* (Vol. 3, pp. 35–99). New York: Academic.

Dunnell, R. C. (1986). Methodological issues in Americanist artifact classification. In M. B. Schiffer (Ed.), *Advances in archaeological method and theory* (Vol. 9, pp. 149–207). Orlando, FL: Academic.

Durham, W. H. (1982). Interactions of genetic and cultural evolution: Models and examples. *Human Ecology, 10*(3), 289–323.

Durham, W. H. (1990). Advances in evolutionary culture theory. *Annual Review of Anthropology, 19*, 187–210.

Durham, W. H. (1991). *Coevolution: Genes, culture, and human diversity*. Stanford: Stanford University Press.

Durham, W. H. (1992). Applications of evolutionary culture theory. *Annual Review of Anthropology, 21*, 331–355.

Durham, W. H., Boyd, R., & Richerson, P. J. (1997). Models and forces of cultural evolution. In P. Weingart, S. D. Mitchel, P. J. Richerson, & S. Maasen (Eds.), *Human by nature: Between biology and the social sciences* (pp. 327–354). Mahwah, NJ: Lawrence Erlbaum Associates.

Eldredge, N. (1985). *Unfinished synthesis: Biological hierarchies and modern evolutionary thought*. New York: Oxford University Press.

Eldredge, N., & Gould, S. J. (1972). Punctuated equilibria: An alternative to phyletic gradualism. In T. J. M. Schopf (Ed.), *Models of paleobiology* (pp. 82–115). San Francisco, CA: Freeman, Cooper and Company.

Fletcher, R. (1996). Organizing dissonance: Multiple code structures in the replication of human culture. In H. D. G. Maschner (Ed.), *Darwinian archaeologies* (pp. 61–86). New York/London: Plenum.

Fortunato, L., Holden, C. J., & Mace, R. (2006). From Bridewealth to dowry? A Bayesian estimation of ancestral states of marriage transfers in Indo-European groups. *Human Nature, 17*(4), 355–376.

Friis-Hansen, J. (1990). Mesolithic cutting arrows: Functional analysis of arrows used in the hunting of large game. *Antiquity, 64*(244), 494–504.

Gergely, G., & Csibra, G. (2006). Sylvia's recipe: The role of imitation and pedagogy in the transmission of human culture. In N. J. Enfield & S. C. Levinson (Eds.), *Roots of human sociality: Culture, cognition, and human interaction* (pp. 229–255). Oxford: Berg.

Gould, S. J., & Eldredge, N. (1986). Punctuated equilibrium at the third stage. *Systematic Zoology, 35*, 143–148.

Graves-Brown, P. (1996). In search of the watchmaker: Attribution of Agency in Natural and Cultural Selection. In H. D. G. Maschner (Ed.), *Darwinian archaeologies* (pp. 165–181). New York/London: Plenum.

Gray, R. D., & Atkinson, Q. D. (2003). Language-tree divergence times support the Anatolian theory of Indo-European origin. *Nature, 426*, 435–439.

Gray, R. D., Greenhill, S. J., & Ross, R. M. (2007). The pleasures and perils of Darwinizing culture (with phylogenies). *Biological Theory, 2*(4), 360–375.

Gray, R. D., & Jordan, F. M. (2000). Language trees support the express-train sequence of Austronesian expansion. *Nature, 405*, 1052–1055.

Greenhill, S. J., & Gray, R. D. (2005). Testing population dispersal hypotheses: Pacific settlement, phylogenetic trees and Austronesian languages. In R. Mace, C. J. Holden, & S. J. Shennan (Eds.), *The evolution of cultural diversity: A phylogenetic approach* (pp. 31–52). London: UCL Press.

Grimes, B. F. (2002). *Ethnologue: Languages of the world* (14th ed.). Dallas, TX: Summer Institute of Linguistics.

Haidle, M. N. (2009). How to think a simple spear? In S. A. de Beaune, F. L. Coolidge, & T. Wynn (Eds.), *Cognitive archaeology and human evolution* (pp. 57–73). Cambridge: Cambridge University Press.

Hammarström, H., Forkel, R., & Haspelmath, M. (2017). *Glottolog 3.0.* Jena: Max Planck Institute for the Science of Human History. Accessed November 03, 2017, from http:/\penalty\z@/\penalty\z@glottolog.org

Hartl, D. L., & Clark, A. G. (2006). *Principles of population genetics* (4th ed.). New York: Sinauer Associates/Oxford University Press.

Hodder, I. (Ed.). (2012). *Archaeological theory today* (2nd ed.). Cambridge: Polity.

Högberg, A. (2008). Playing with flint: Tracing a child's imitation of adult work in a lithic assemblage. *Journal of Archaeological Method and Theory, 15*(1), 112–131.

Jablonka, E., & Lamb, M. J. (1995). *Epigenetic inheritance and evolution: The Lamarckian dimension*. Oxford: Oxford University Press.

Jablonka, E., & Lamb, M. J. (2005). *Evolution in four dimensions: Genetic, epigenetic, behavioral, and symbolic variation in the history of life*. Cambridge, MA: The MIT Press.

Johnson, M. (2010). *Archaeological theory; an introduction* (2nd ed.). West Sussex: Wiley.

Jordan, P. (2009). Linking pattern and process in cultural evolution: Investigating material culture diversity among the northern Khanty of Northwest Siberia. In S. Shennan (Ed.), *Pattern and process in cultural evolution* (pp. 61–83). London: Thames and Hudson.

Jordan, P. (2015). *Technology as human social tradition: Cultural transmission among hunter-gatherers*. Oakland, CA: University of California Press.

Jordan, P., & Mace, T. (2006). Tracking culture-historical lineages: "Can descent with modification" be linked to "association by descent"? In C. P. Lipo, M. J. O'Brien, M. Collard, & S. J. Shennan (Eds.), *Mapping our ancestors: Phylogenetic approaches in anthropology and prehistory* (pp. 149–168). New York: Aldine Transaction.

Jordan, P., & Shennan, S. (2005). Cultural transmission in indigenous California. In R. Mace, C. J. Holden, & S. J. Shennan (Eds.), *The evolution of cultural diversity: A phylogenetic approach* (pp. 133–164). London: UCL Press.

Jordan, P., & Shennan, S. (2009). Diversity in hunter-gatherer technological traditions: Mapping trajectories of cultural 'descent with modification' in Northeast California. *Journal of Anthropological Archaeology, 28*(3), 342–365.

Jordan, P. D., & O'Neill, S. (2010). Untangling cultural inheritance: Language diversity and long-house architecture on the Pacific northwest coast. *Philosophical Transactions of the Royal Society B, 365*, 3875–3888. https://doi.org/10.1098/rstb.2010.0092

Kimura, M. (1968). Evolutionary rate at the molecular level. *Nature, 217*, 624–626.

Kimura, M., & Ohta, T. (1969). The average number of generations until fixation of a mutant gene in a finite population. *Genetics, 61*, 763–771.

Kirby, K. R., Gray, R. D., Greenhill, S. J., Jordan, F. M., Gomes-Ng, S., Bibiko, H.-J., et al. (2016). D-PLACE: A global database of cultural, linguistic and environmental diversity. *PLoS One, 11*(7), e0158391. https://doi.org/10.1371/journal.pone.0158391

Koerper, H. C., & Stickel, E. G. (1980). Cultural drift: A primary process of culture change. *Journal of Anthropological Research, 36*(4), 463–469.

Kroeber, A. L. (1948). *Anthropology: Race, language, culture, psychology, pre-history*. New York: Harcourt, Brace.

Laland, K., Cowie, A., & Morgan, T. (2013). What animals other than primates can tell us about human cultural transmission. In R. Ellen, S. Lycett, & S. E. Johns (Eds.), *Understanding cultural transmission in anthropology: A critical synthesis* (pp. 55–79). New York/Oxford: Berghahn.

Lewis, M. P., Simons, G. F., & Fennig, C. D. (Eds.). (2016). *Ethnologue: Languages of the world* (19th ed.). Dallas, TX: SIL International. http:/\penalty\z@/\penalty\z@www.ethnologue.com/\penalty\z@19/\penalty\z@

Lipo, C. P., O'Brien, M. J., Collard, M., & Shennan, S. J. (Eds.). (2006). *Mapping our ancestors: Phylogenetic approaches in anthropology and prehistory*. New York, NY: Aldine Transaction.

Lipo, C. P., & Eerkens, J. W. (2008). Culture history, cultural transmission, and explanation of variation in the southeastern United States. In M. J. O'Brien (Ed.), *Cultural transmission and archaeology: Issues and case studies* (pp. 120–131). Washington, DC: SAA Press.

Lycett, S. J. (2009). Understanding ancient hominin dispersals using artefactual data: A Phylogeographic analysis of Acheulian Handaxes. *PLoS One, 4*(10), 1–6.

Lyman, R. L. (2008). Cultural transmission in north American anthropology and archaeology, ca. 1895-1965. In M. J. O'Brien (Ed.), *Cultural transmission and archaeology: Issues and case studies* (pp. 10–20). Washington, DC: SAA Press.

Lyman, R. L., & O'Brien, M. J. (1997). The concept of evolution in early twentieth-century Americanist archaeology. In C. M. Barton & G. A. Clark (Eds.), *Rediscovering Darwin: Evolutionary theory and archeological explanation* (pp. 21–48). Arlington, TX: American Anthropological Association.

Lyman, R. L., & O'Brien, M. J. (2006). Seriation and cladistics: The difference between Anagenetic and Cladogenetic evolution. In C. P. Lipo, M. J. O'Brien, M. Collard, & S. J. Shennan (Eds.), *Mapping our ancestors: Phylogenetic approaches in anthropology and prehistory* (pp. 65–88). New Brunswick: Aldine Transaction.

Mace, R. (2005). Introduction: A phylogenetic approach to the evolution of cultural diversity. In R. Mace, C. J. Holden, & S. Shennan (Eds.), *The evolution of cultural diversity: A phylogenetic approach* (pp. 1–10). Walnut Creek, CA: Left Coast Press.

Mace, R., & Pagel, M. (1994). The comparative method in anthropology. *Current Anthropology, 35*(5), 549–564.

Mace, R., & Pagel, M. (2004). The cultural wealth of nations. *Nature, 428*, 275–278.

Malthus, T. R. (1798). *Essay on the principle of population*. London: Printed for J. Johnson, in St. Paul's Churchyard.

Marwick, B. (2012). A Cladistic evaluation of ancient Thai bronze Buddha images: Six tests for a phylogenetic signal in the Griswold collection. In D. Bonatz, A. Reinecke, & M. L. Toa-Bonatz (Eds.), *Connecting empires* (pp. 159–176). Singapore: National University of Singapore Press.

Matthews, L. J., Tehrani, J. J., Jordan, F. M., Collard, M., & Nunn, C. L. (2011). Testing for divergent transmission histories among cultural characters: A study using Bayesian phylogenetic methods and Iranian tribal textile data. *PLoS One, 6*(4), 1–10.

Mayr, E. (1942). *Systematics and the origin of species*. New York: Columbia University Press.

Mayr, E. (1963). *Animal species and evolution*. Cambridge, MA: Harvard University Press.

Mesoudi, A., Whiten, A., & Laland, K. N. (2006). Towards a unified science of cultural evolution. *Behavioral and Brain Sciences, 29*, 329–383.

Montelius, G. O. A. (1884). Den förhistoriska fornforskarens metod och material. *Antikvarisk Tidskrift för Sverige, 3*, 1–28.

Montelius, G. O. A. (1899). Typologien eller utvecklingsläran tillämpad på det menskliga arbetet. *Svenska Fornminnesföreningens Tidskrift, 10*, 237–268.

Montelius, G. O. A. (1903). *Die Typologische Methode*. Stockholm: Almqvist & Wicksell.

Moore, J. H. (1994). Putting anthropology Back together again: The Ethnogenetic critique of Cladistic theory. *American Anthropologist, 96*(4), 925–948.

Morgan, L. H. (1877). *Ancient society; or, researcher in the lines of human progress from savagery, through barbarism to civilization*. New York: Henry Holt and Co.

Moylan, J. W., Borgerhoff Mulder, M., Graham, C. M., Nunn, C. L., & Håkansson, N. T. (2006). Cultural traits and linguistic trees: Phylogenetic signal in East Africa. In C. P. Lipo, M. J. O'Brien, M. Collard, & S. J. Shennan (Eds.), *Mapping our ancestors: Phylogenetic approaches in anthropology and prehistory* (pp. 33–52). New Brunswick: Aldine Transaction.

Naroll, R. (1965). Galton's problem: The logic of cross-cultural analysis. *Social Research, 32*(4), 428–451.

Neff, H., & Larson, D. O. (1997). Methodology of comparison in evolutionary archaeology. In C. M. Barton & G. A. Clark (Eds.), *Rediscovering Darwin: Evolutionary theory and archeological explanation* (pp. 75–94). Arlington, TX: American Anthropological Association.

Neiman, F. D. (1995). Stylistic variation in evolutionary perspective: Inferences from decorative diversity and interassemblage distance in Illinois woodland ceramic Assemblages. *American Antiquity, 60*(1), 7–36.

Nettle, D., Gibson, M. A., Lawson, D. W., & Sear, R. (2013). Human behavioral ecology: Current research and future prospects. *Behavioral Ecology, 24*(5), 1031–1040.

Nunn, C. L., Arnold, C., Matthews, L., & Borgerhoff Mulder, M. (2010). Simulating trait evolution for cross-cultural comparison. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1559), 3807–3819.

O'Brien, M. J. (Ed.). (1996). *Evolutionary archaeology: Theory and application*. Salt Lake City, UT: University of Utah Press.

O'Brien, M. J., Boulanger, M. T., Buchanan, B., Collard, M., Lyman, R. L., & Darwent, J. (2014). Innovation and cultural transmission in the American Paleolithic: Phylogenetic analysis of eastern Paleoindian projectile-point classes. *Journal of Anthropological Archaeology, 34*, 100–119.

O'Brien, M. J., Darwent, J., & Lyman, R. L. (2001). Cladistics is useful for reconstructing archaeological phylogenies: Palaeoindian points from the southeastern United States. *Journal of Archaeological Science, 28*, 1115–1136.

O'Brien, M. J., & Holland, T. D. (1990). Variation, selection, and the archaeological record. In M. B. Schiffer (Ed.), *Archaeological method and theory* (Vol. 2, pp. 31–79). Tucson, AZ: University of Arizona Press.

O'Brien, M. J., & Holland, T. D. (1992). The role of adaptation in archaeological explanation. *American Antiquity, 57*(1), 36–59.

O'Brien, M. J., & Lyman, R. L. (1998). Evolutionary archaeology: Reconstructing and explaining historical lineages. In M. B. Schiffer (Ed.), *Social theory in archaeology* (pp. 126–142). Salt Lake City, UT: University of Utah Press.

O'Brien, M. J., & Lyman, R. L. (2000). *Applying evolutionary archaeology: A systematic approach*. New York: Kluwer Academic/Plenum.

O'Brien, M. J., & Lyman, R. L. (2002). *Applying Evolutionary Archaeology: a systematic approach*. New York, NY: Kluwer Academic Publishers.

O'Brien, M. J., Lyman, R. L., Mesoudi, A., & VanPool, T. L. (2010). Cultural traits as units of analysis. *Philosophical Transactions of the Royal Society B, 365*, 3793–3806.

O'Neill, S. (2013). Co-evolution between bentwood box traditions and languages on the Pacific northwest coast. In R. Ellen, S. Lycett, & S. E. Johns (Eds.), *Understanding cultural transmission in anthropology: A critical synthesis* (pp. 165–190). New York/Oxford: Berghahn.

O'Connell, J. F. (1995). Ethnoarchaeology needs a general theory of behavior. *Journal of Archaeological Research, 3*(3), 205–255.

Odling-Smee, J. F., Laland, K. N., & Feldman, M. W. (2003). *Niche construction: The neglected process in evolution*. Princeton, NJ: Princeton University Press.

Ohta, T. (1973). Slightly deleterious mutant substitutions in evolution. *Nature, 246*, 96–98.

Osgood, C. (1951). Culture: Its empirical and non-empirical character. *Southwestern Journal of Anthropology, 7*(2), 202–214.

Pagel, M., Atkinson, Q. D., & Meade, A. (2007). Frequency of word-use predicts rates of lexical evolution throughout Indo-European history. *Nature, 449*, 717–720. https://doi.org/10.1038/nature06176

Pocklington, R. (2006). What is a culturally transmitted unit, and how do we find one? In C. P. Lipo, M. J. O'Brien, M. Collard, & S. J. Shennan (Eds.), *Mapping our ancestors: Phylogenetic approaches in anthropology and prehistory* (pp. 19–31). New Brunswick: Aldine Transaction.

Porčić, M. (2015). Exploring the effects of assemblage accumulation on diversity and innovation rate estimates in neutral, conformist, and anti-conformist models of cultural transmission. *Journal of Archaeological Method and Theory, 22*(4), 1071–1092. https://doi.org/10.1007/s10816-014-9217-8

Premo, L. S. (2014). Cultural transmission and diversity in time-averaged assemblages. *Current Anthropology, 55*(1), 105–114. https://doi.org/10.1086/674873

Prentiss, A. M., Kuijt, I., & Chatters, J. C. (Eds.). (2009). *Macroevolution in human prehistory: Evolutionary theory and processual archaeology*. New York: Springer.

Prentiss, A. M., Skelton, R. R., Eldredge, N., & Quinn, C. P. (2011). Get Rad! The evolution of the skateboard deck. *Evolution: Education and Outreach, 4*, 379–389.

Prentiss, A. M., Walsh, M. J., Foor, T. A., & Barnett, K. D. (2015). Cultural macroevolution among high latitude hunter-gatherers: A phylogenetic study of the Arctic small tool tradition. *Journal of Archaeological Science, 59*, 64–79.

Rasmussen, K. (1931). *The Netsilik Eskimos: social life and spiritual culture. Report of the Fifth Thule Expedition 1921–24, vol. 8, nos. 1–2*. Copenhagen: Glydendals Forlagstrykkeri.

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone. How culture transformed human evolution*. Chicago, IL: The University of Chicago Press.

Richerson, P. J., & Boyd, R. (2010). The Darwinian theory of human cultural evolution and gene-culture coevolution. In M. A. Bell, D. J. Futuyma, W. F. Eanes, & J. S. Levinton (Eds.), *Evolution since Darwin: The first 150 years* (pp. 561–589). Sunderland: Sinauer Associates.

Riede, F. (2006). The Scandinavian connection. The roots of Darwinian thinking in 19th century Scandinavian archaeology. *Bulletin of the History of Archaeology, 16*(1), 4–19.

Riede, F. (2008). Maglemosian memes: Technological ontogeny, craft traditions, and the evolution of northern European barbed points. In M. J. O'Brien (Ed.), *Cultural transmission and archaeology: Issues and case studies* (pp. 178–189). Washington, DC: SAA Press.

Riede, F. (2009a). Tangled trees: Modelling material culture evolution as host-associate co-speciation. In S. Shennan (Ed.), *Pattern and process in cultural evolution* (pp. 85–98). Berkeley, CA: University of California Press.

Riede, F. (2009b). The loss and re-introduction of bow-and-arrow technology: A case study from the southern Scandinavian late Palaeolithic. *Lithic Technology, 34*(1), 27–45.

Riede, F. (2010). Why Isn't archaeology (more) Darwinian? A historical perspective. *Journal of Evolutionary Psychology, 8*(2), 183–204.

Riede, F. (2011). Steps towards operationalising an evolutionary archaeological definition of culture. In B. W. Roberts & M. Vander Linden (Eds.), *Investigating archaeological cultures. Material culture, variability, and transmission* (pp. 245–270). New York: Springer.

Riede, F., Johannsen, N. N., Högberg, A., Nowell, A., & Lombard, M. (2018). The role of play objects and object play in human cognitive evolution and innovation. *Evolutionary Anthropology: Issues, News, and Reviews, 27*(1), 46–59. https://doi.org/10.1002/evan.21555

Rindos, D. (1980). Symbiosis, instability, and the origins and spread of agriculture: A new model. *Current Anthropology, 21*, 751–772.

Sahlins, M. D., & Service, E. R. (Eds.). (1960). *Evolution and culture*. Ann Arbor, MI: University of Michigan Press.

Shennan, S. (2002). *Genes, memes, and human history: Darwinian archaeology and cultural evolution*. London: Thames and Hudson.

Shennan, S. (2008). Evolution in archaeology. *Annual Review of Anthropology, 37*, 75–91.

Shennan, S. (2009). *Quantifying archaeology*. Edinburgh: Edinburgh University Press.

Skinner, B. F. (1981). Selection by consequences. *Science, 213*(4507), 501–504.

Steward, J. H. (1955). *Theory of culture change: The methodology of multilinear evolution*. Chicago, IL: University of Illinois Press.

Tehrani, J. J. (2010). The past and future of the evolutionary taxonomy of cultures. *Journal of Evolutionary Psychology, 8*(2), 169–182.

Tehrani, J., & Collard, M. (2013). Do Transmission Isolating Mechanisms (TRIMS) influence cultural evolution? Evidence from patterns of textile diversity within and between Iranian tribal groups. In R. Ellen, S. Lycett, & S. Johns (Eds.), *Understanding cultural transmission in anthropology: A critical synthesis* (pp. 148–164). New York, NY: Berghahn.

Tehrani, J. J., & Collard, M. (2009). On the relationship between inter-individual cultural transmission and population-level cultural diversity: A case study of weaving in Iranian tribal populations. *Evolution and Human Behavior, 30*(4), 286–300.

Tehrani, J. J., & Reide, F. (2008). Towards an archaeology of pedagogy: Learning, teaching and the generation of material culture traditions. *World Archaeology, 40*(3), 316–331.

Trigger, B. G. (2006). *A history of archaeological thought* (2nd ed.). Cambridge: Cambridge University Press.

Tylor, E. B. (1881). *Anthropology: An introduction to the study of man and civilization*. London: MacMillan and Co.

Viveiros de Castro, E. (1992). *From the enemy's point of view: Humanity and divinity in an Amazonian society* (C. V. Howard, Trans.). Chicago, IL: The University of Chicago Press.

Wade, N. J. (2010). The Darwins and Wells: From revolution to evolution. *Journal of the History of the Neurosciences, 19*(2), 85–104.

Wakeley, J. (2010). Natural selection and coalescent theory. In M. A. Bell, D. J. Futuyma, W. F. Eanes, & J. S. Levinton (Eds.), *Evolution since Darwin: The first 150 years* (pp. 120–149). Sunderland: Sinauer Associates, Inc.

Wallace, A. R. (1870). *Contributions to the theory of natural selection*. London/New York: Macmillan and Co.

Weale, M. E. (2015). Patrick Mathew's law of natural selection. *Biological Journal of the Linnean Society, 115*(4), 785–791.

Weingart, P., Mitchel, S. D., Richerson, P. J., & Maasen, S. (Eds.). (1997). *Human by nature: Between biology and the social sciences*. Mahwah, NJ: Lawrence Erlbaum Associates.

White, L. A. (1949). *The science of culture: A study of man and civilization*. New York: Grove Press, Inc.

White, L. A. (1959). *The evolution of culture: The development of civilization to the fall of Rome*. New York: McGraw-Hill.

Winterhalder, B. (1981). Optimal foraging strategies and hunter gatherer research in anthropology: Theory and models. In B. Winterhalder & E. A. Smith (Eds.), *Hunter-gatherer foraging strategies: Ethnographic and archaeological analyses* (pp. 13–35). Chicago, IL: University of Chicago Press.

Winterhalder, B., & Smith, E. A. (Eds.). (1981). *Hunter-gatherer foraging strategies: Ethnographic and archaeological analyses*. Chicago, IL: University of Chicago Press.

Zirkle, C. (1941). Natural selection before the "origin of species". *Proceedings of the American Philosophical Society, 84*(1), 71–123.