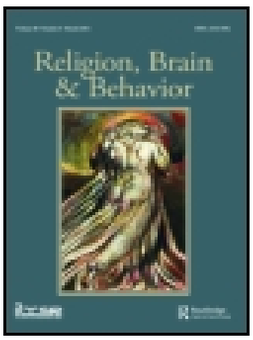

Religion, Brain & Behavior

ISSN: 2153-599X (Print) 2153-5981 (Online) Journal homepage: http://www.tandfonline.com/loi/rrbb20

The promise and limits of eco-evolutionary studies of human culture

Carlos A. Botero, Luke J. Harmon & Quentin Atkinson

To cite this article: Carlos A. Botero, Luke J. Harmon & Quentin Atkinson (2016): The promise and limits of eco-evolutionary studies of human culture, Religion, Brain & Behavior, DOI: 10.1080/2153599X.2015.1132249

To link to this article: http://dx.doi.org/10.1080/2153599X.2015.1132249

RELIGION, BRAIN & BEHAVIOR, 2016
http://dx.doi.org/10.1080/2153599X.2015.1132243

Routledge
Taylor & Francis Group

TARGET ARTICLE

The nature of religious diversity: a cultural ecosystem approach

David Sloan Wilson[a], Yasha Hartberg[b], Ian MacDonald[b], Jonathan A. Lanman[c], and Harvey Whitehouse[d]

[a]Departments of Biological Sciences and Anthropology, Binghamton University, State University of New York, Binghamton, NY, USA; [b]Department of Biological Sciences, Binghamton University, State University of New York, Binghamton, NY, USA; [c]School of History and Anthropology, Institute of Cognition and Culture, Queens University, Belfast, Ireland; [d]Institute of Social and Cultural Anthropology, University of Oxford, Oxford, UK

ABSTRACT

Studies of religious and other cultural groups tend to be particularistic or focus on one or more axes of variation. In this article we develop a more comprehensive approach to studying cultural diversity that emulates the study of biological diversity. We compare our cultural ecosystem approach with the axis approach, using the distinction between "tight" and "loose" cultures as an example. We show that while the axis approach is useful, the cultural ecosystem approach adds considerable value to the axis approach. We end by advocating the establishment of field sites for the study of religious and cultural diversity, comparable to biological field sites.

ARTICLE HISTORY
Received 2 May 2014
Accepted 5 June 2015

KEYWORDS
biocultural evolution; cultural diversity; ecosystems; evolution; religious diversity

Religions and other cultural forms exist in almost endless variety, with old forms disappearing and new forms arising all the time. It is easy to use the word "evolution" to describe these changes, but past efforts to develop a comprehensive theory of cultural evolution did not become widely accepted and in retrospect can be seen to suffer from misconceptions that do not follow from evolutionary theory (such as cultural evolution as a linear progression from "savagery" to "civilization"; see Carniero, 2003 for a review). More recent research on human cultural evolution promises to succeed where past efforts have failed and enable a more rigorous comparison between religious diversity, cultural diversity, and biological diversity. A useful overview based on a recent conference is provided by Richerson and Christiensen (2013) in addition to other references cited below.

Studies of religious and cultural diversity that are not based on evolution tend to be particularistic, reflecting detailed scholarship on single systems but lacking a common methodology or broader theoretical framework. When attempts at integration are made, they often take the form of identifying axes of variation, such as between strict vs. lax churches (Iannaccone, 1994; Kelley, 1972; Thomas & Olson, 2010), tight vs. loose cultures (Gelfand, Nish, & Raver, 2006; Gelfand et al., 2011; Pelto, 1968), individualistic vs. collectivist cultures (Triandis, 1989; Triandis & Gelfand, 2012), and even gradients in the incidence of diseases and parasites (Fincher & Thornhill, 2012). Statistical methods such as factor analysis are sometimes employed to identify multiple axes of variation (Hofstede, 1980). These attempts at integration are more synthetic than particularistic approaches but the choice of axes (other than by factor analysis) tends to be haphazard, isolated literatures grow around the study of each axis, and different axes are seldom systematically related to each other.

In this article, we will first summarize the current status of cultural evolutionary theory and evolutionary religious studies, both of which have become centered on group-level functional

CONTACT David Sloan Wilson dwilson@binghamton.edu

organization. Second, we will outline the cultural ecosystem approach to the study of religious and cultural diversity, modeled on the study of biological diversity. Third, we will discuss the axis-of-variation approach (hereafter called the axis approach), focusing on the distinction between "tight" and "loose" cultures as an extended example. We have chosen the tight/loose axis as an exemplar because it has been used mostly to study variation in traditional cultures and modern nations but not religions, even though it is highly relevant to religions, thereby illustrating the problem of isolated literatures. Fourth, after discussing the merits of the axis approach and the relevance of the tight/loose distinction for the study of religious diversity, we will show how the cultural ecosystem approach goes beyond the axis approach for the study of tightness and looseness and by extension other axes of variation.

A fifth and final contribution of this article is to argue for the establishment of field sites for the study of cultural variation that are comparable to biological field sites – sizeable geographical areas where different functionally organized groups (the analog of biological species) can be studied in relation to each other and their physical environment. Federal grant agencies such as the National Science Foundation devote considerable resources to long-term field research on biological ecosystems. We think that a similar approach is required for the study of cultural ecosystems.

Before proceeding, it is important to clarify the audience for which this article is intended. We hope to reach scholars and scientists who employ all three approaches mentioned above – "thick descriptions" of single cultural groups, axes of variation, and what we are calling the cultural ecosystem approach. Our purpose is not to replace the first two with the third. On the contrary, the cultural ecosystem approach requires detailed descriptions of single cultural groups in relation to other groups and their physical environments. Axes of variation can be useful as a broad-brush approach to studying cultural diversity, but they don't substitute for the study of large-scale cultural systems comprised of many functionally organized groups that are actively co-evolving with each other and their biological and physical environments. The study of biological diversity provides a well-established model for how "thick descriptions" of single species, axes of variation, and multi-species ecosystems can be integrated with each other from a unified theoretical perspective. Our objective is to integrate the same three approaches for the study of cultural diversity.

1. The maturation of cultural evolutionary theory

The rapidly expanding study of human biocultural evolution can be briefly summarized with the following statements (see Boehm, 2011; Cashdan, 2001; Collard & Foley, 2002; Deacon, 1998; Haidt, 2012; Henrich, Boyd, & Richerson, 2008; Henrich & Henrich, 2007; Jablonka & Lamb, 2006; Nettle, 1998; Pagel, 2012; Richerson & Boyd, 2005; Richerson & Christiensen, 2013; Tomasello, 2009; Turchin, 2005, 2010; D.S. Wilson, 2002, 2012; E.O. Wilson, 2012 for extended discussions).

1) Humans have an exceptional ability to cooperate in groups of genetically unrelated individuals (this point is stressed by all of the above cited references).
2) Cooperation includes the ability to transmit learned information across generations and to encode information in the form of symbolic mental relations, which are communicated in part through language. These abilities amount to an inheritance system that enables human groups to adapt rapidly to their current environments, as opposed to the much slower process of genetic evolution (Deacon, 1998; Haidt, 2012; Jablonka & Lamb, 2006; Pagel, 2012).
3) The capacity for rapid adaptation enabled humans to expand their geographical range to include the entire planet, occupying all climatic zones and myriad different ecological niches. This cultural adaptive radiation is comparable to the genetic adaptive radiations of major taxonomic groups such as the dinosaurs, birds, and mammals (Cashdan, 2001; Collard & Foley, 2002; Nettle, 1998; Pagel, 2012; Richerson & Boyd, 2005; E.O. Wilson, 2012).
4) Cultural and genetic evolution mutually influence each other. Culturally derived practices shape genetic selection pressures just as genetic selection pressures shape cultural practices. Gene-culture co-evolution has been taking place for a very long time, so it is incorrect to regard culture as a

means to increase genetic fitness, as if the latter can be defined without reference to the former (Jablonka & Lamb, 2006; Pagel, 2012; Richerson & Boyd, 2005).

5) Gene-culture co-evolution took place within relatively small social groups for most of our evolutionary history, although this includes a tribal scale of social organization comprising thousands of individuals, in addition to the small face-to-face groups of approximately 30–150 individuals who lived and worked together at any particular time (all of the above cited references make this point).
6) The advent of agriculture enabled the scale of human society to increase by many orders of magnitude, but this required a process of cultural evolution whereby practices that caused a society to function as a cooperative unit at a larger scale replaced other practices. Between-group competition could take the form of warfare, economic competition, or some groups imitating the practices of other groups. Practices that contributed to functional organization at a larger scale were often opposed by other practices that benefitted individuals and factions within the society at the expense of society-level functional organization. Recorded history provides a fossil record of multilevel cultural evolution, which continues to operate among contemporary societies (see especially Turchin, 2005, 2010; Turchin, Whitehouse, Francois, Slingerland, & Collard, 2012).

In short, *human groups are functionally organized units (for the most part) that adapt to their environments by a process of cultural evolution.* The capacity for cultural evolution evolved by genetic evolution but also comprises an inheritance system and evolutionary process in its own right. Our qualifying phrase "for the most part" acknowledges that not everything that evolves requires an adaptive explanation (Gould & Lewontin, 1979). Adaptations are often accompanied by byproducts, correlated traits, and so on. These qualifiers apply to cultural evolution no less than genetic evolution.

Our summary of modern cultural evolutionary theory is framed in terms of multilevel selection, which has its own controversial history (Borrello, 2010; Okasha, 2006; Sober & Wilson, 1998; Wilson, 2015). Nevertheless, there is widespread agreement on the points that we have summarized above for two reasons. First, multilevel selection has become the theoretical framework of choice for many authors studying human cultural evolution (e.g., Boehm, 2011; Henrich, 2003; Johnson, Price, & Van Vugt, 2013; Richerson & Boyd, 2005; Turchin, 2010; D.S. Wilson, 2002, 2015; E.O. Wilson, 2012; Yaworsky, Horowitz, & Kickham, 2015). Second, authors who do not frame their argument in terms of multilevel selection employ frameworks that are equivalent for all intents and purposes, such as the concept of vehicles in selfish gene theory (e.g., Pagel, 2012; see Kurzban, Burton-Chellew, & West, 2014; Marshall, 2011; Wilson, 2015; Wilson & Wilson, 2007 for more on the concept of equivalent theoretical frameworks). Thus, the degree of consensus for the points outlined above is wider than the so-called controversy over multilevel selection would seem to suggest.

1.1. The secular utility of religion

Returning to our summary statement that *human groups are functionally organized units (for the most part)*, it is possible for this statement to hold for aspects of culture that are classified as secular, such as language and technology, but not for aspects that are classified as religious, such as belief in gods and costly rituals. After all, religion puzzles the scientific imagination in part because it seems so non-utilitarian. How can belief in supra-empirical agents and the costly practices associated with religion be adaptive, in the same way as the ability of an Inuit to make an igloo or a kayak?

Utilitarian and non-utilitarian theories of religion have been debated ever since religion became the subject of scholarly inquiry. Emile Durkheim (1912) regarded religious belief and practice to have great "secular utility," as he put it, which is reflected in his well-known definition of religion as "a unified system of beliefs and practices relative to sacred things … which unite into one single moral community called a Church, all those who adhere to them" (p. 44).

Durkheim initiated the tradition of functionalism, which became popular during the first half of the twentieth century for studying cultural systems in general, in addition to religion. Functionalists interpreted the properties of cultures as adaptive for the whole culture, somewhat axiomatically and without much thought to how such group-level functionality might have arisen. For these and other reasons, functionalism was largely abandoned during the second half of the twentieth century (Carniero, 2003), including the study of religion (e.g., Iannaccone, 1995; Stark, 1999; discussed in Wilson, 2002, ch. 2).

Nevertheless, the modern consensus on cultural evolution described above amounts to a revival of group-level functionalism and places it on a stronger theoretical foundation than it ever had before. Previous objections to functionalism, such as its inattention to history and individual agency, do not apply to the modern formulation. History, for instance, plays a critical role in the phylogenetic aspect of the cultural ecosystem approach. Moreover, the agency of individuals is not denied in such an approach, as evolutionary accounts seek to explain why some products of human agency manage to be successful and endure.

Most important, the functionalist account applies as strongly for aspects of culture associated with religion as for aspects that are obviously utilitarian (Atran & Henrich, 2010; Bulbulia, 2012; Henrich, 2009; Norenzayan & Shariff, 2008; Richerson & Christiensen, 2013; Sosis, 2009; Wilson, 2002, 2005a, 2015). In other words, no matter how otherworldly the belief or costly the practice, when the elements of religion are evaluated on the basis of what they cause people to do, they often (although by no means always) play an important role in the functional organization of groups. This does not mean that religions lack non-adaptive byproducts. All evolutionary processes result in non-adaptive byproducts. To employ Gould and Lewontin's (1979) architectural metaphor, functional aspects of a building such as an arch frequently result in nonfunctional aspects such as a spandrel. This is different than positing that religious beliefs and practices are primarily byproducts of traits whose functional basis is not religious.

2. The cultural ecosystem approach

Against this background, we can outline the cultural ecosystem approach for explaining patterns of cultural diversity in the same way that biologists explain patterns of biological diversity. Biological ecosystems consist of myriad species that interact with each other and their physical environments. Each species possesses a suite of adaptations that enables it to survive and reproduce in the ecosystem; otherwise it would quickly disappear. Many species coexist because ecosystems afford many different ways to survive and reproduce.

Ecosystems are full of historical contingencies; becoming common might be a consequence of being first to arrive, for example. Ecosystems are frequently out of equilibrium. The process of succession, for example, involves species changing their environments in ways that cause them to be replaced by other species. Unless ecosystems are selected as whole units (Panke-Buisse, Poole, Goodrich, Ley, & Kao-Kniffin, 2014; Swenson, Wilson, & Elias, 2000; Wilson, 1980, 1997), they are typically not functionally organized in the same way as single species. The idea of a balance of nature that works best when undisturbed is largely erroneous (Bodkin, 1990; Kricher, 2009). When beavers move into an area, for example, they transform the landscape, influencing ecosystem processes and the distributions and abundances of many other species – but the beaver-influenced ecosystem is no more balanced, efficient, or resilient than the pre-beaver ecosystem. The best way to understand beaver-influenced ecosystems is by understanding how beavers behave to enhance their own fitness (e.g., by selectively eating palatable trees and flooding areas for their own protection) and the consequences of these actions for other species, which are mediated through their own fitness-enhancing actions (Bailey et al., 2004; Whitham et al., 2008).

The species that exist in a given locality are drawn from a larger pool of species that exist close enough to colonize the locality. Geographical barriers therefore add a layer of diversity on top of the diversity that is afforded by multiple niches within a given location. Over longer time scales,

species give rise to other species through a complex interaction between disruption of gene flow and ecological diversification (Coyne & Orr, 2004). The outcomes of these interactions cause some geographical regions to be much more diverse than others. One large-scale pattern is a latitudinal gradient, with the tropics much more diverse than the polar regions, but substantial variation exists within any given latitude based on other factors.

To say that species are the units that make up ecosystems is a simplification. A single species can itself be diverse, consisting of populations that become locally adapted to their environments and individuals within any given population that pursue different adaptive strategies. For example, individuals of a single tree species can differ 100-fold in levels of protective toxins. When beavers move into an area, their impact on the genetic composition of a single tree species is at least as important as their impact on the species composition of trees. Ultimately, the functionally organized entities that interact in ecosystems are the individuals and groups (in social species) at any particular locality.

If human groups are functionally organized units adapted to their environments, as argued above, then they can be regarded as like the functionally organized entities that interact in biological ecosystems. Before continuing, it is important to be aware of inappropriate connotations of this analogy that humans are all too prone to make (Gil-White, 2001). Comparing different cultural groups to different species is a statement about their histories and functional organization in relation to their environments and other cultural groups. The differences between cultural "species" are primarily cultural, although genetic differences are also a possibility that is inherent in the concept of gene-culture co-evolution (Cochran & Harpending, 2009; Mrazek, Chiao, Blizinsky, Lun, & Gelfand, 2013). All human cultural groups are part of a common humanity and it is never legitimate to dehumanize a given culture by calling it a different species, in the way that the Nazis called the Jews rats and the Tutsis called the Hutus parasites (Smith, 2012). At the same time, these inappropriate connotations cannot stand in the way of exploring the various ways in which human cultural groups may legitimately be viewed as functionally equivalent to biological species.

The most important legitimate connotation is that *understanding the properties of an ecosystem requires knowledge of the fitness-enhancing properties of the functionally organized units that comprise the ecosystem*. To understand beaver-influenced ecosystems, look to the fitness-enhancing properties of beavers (and the other species). To understand human cultural ecosystems, look to the fitness-enhancing properties of the functionally organized groupings that comprise the ecosystem – the religious congregations and secular organizations that interact with each other at particular locations. Higher-level cultural nomenclatures such as denominations and major religious traditions are roughly comparable to higher-level biological nomenclatures such as species, genera, and families. It can be challenging to identify the salient cultural groupings (as it can for biological species), but in many cases the relevant social identities are clear-cut precisely because they provide the basis for organizing interactions within and among the groups, as we will illustrate with an example provided below. It is important to stress that individuals can participate in more than one functional grouping and groups can remain very different in their identities and functional organization despite a high rate of flow of individuals between groups. This kind of differentiation is accomplished by individuals recognizing which group they are in and adopting the appropriate norms and practices.

Each grouping has a history that is comparable to the phylogeny of a species, which influences its current structure and how it adapts to environmental change. The fact that cultural evolution is more reticulate than genetic evolution (which is itself more reticulate than previously thought) does not alter the importance of history. Each grouping must have a set of proximate mechanisms that cause its members to behave in functionally appropriate ways. Groupings must also have a replication machinery and developmental process that cause them to persist across generations and to give rise to other groups (see Matthews, Edmonds, Wildman, & Nunn, 2013 for a detailed study of the cultural transmission of religious traits). Geographical isolation will give rise to groups in separate locations that are functionally roughly equivalent but achieve their functionality in different ways, like the reproductive physiologies of placental mammals and marsupials. Complex interactions

will cause some geographical regions to be much more culturally diverse than others (Cashdan, 2001; Collard & Foley, 2002; Nettle, 1998; Pagel, 2012; Pagel & Mace, 2004).

This approach fits well with particularistic studies, such as detailed historical scholarship on past groups and detailed sociological and cultural anthropological study of current groups. However, the cultural ecosystem approach adds value by providing a general theoretical framework for organizing detailed information on past and present groups that current historical, sociological, and cultural anthropological scholarship often lacks. Some comparative religion scholars have begun to appreciate the importance of evolutionary theory for providing a conceptual framework for their discipline (e.g., Paden, 2008).

2.1. An example of the cultural ecosystem approach

Economist Janet Landa's (2008) analysis of middleman merchant groups nicely illustrates these theoretical points. A middleman merchant serves as an intermediate link between the producers and consumers of goods, for example by purchasing food from farmers and conveying it to a market. This economic niche requires a high degree of coordination and cooperation, often dispersed over long distances. Another problem is the volatility of many markets, which requires striking deals on short notice. The middleman merchant niche therefore requires a high degree of cooperation and is especially vulnerable to cheating, such as stealing merchandise or failing to honor contracts.

Around the world, the middleman merchant niche tends to be occupied by minority groups such as the Jains in India, the Chinese in Southeast Asia, and the Jews in Western Europe. Another feature of these groups is that they are often highly religious or bound by other ethical codes such as Confucianism. At first these facts seem paradoxical. How can minority groups, which are typically at a social disadvantage within a larger culture, capture a lucrative economic niche? What does religion have to do with economics? The answer is that highly religious and ethnically homogenous minority groups have a competitive advantage, based on their ability to cooperate within their own ranks. The factors that contribute to their competitive edge include genetic relatedness, strong social ties among non-relatives within the ethnic group, and the moral dictates of their ethical systems.

Middleman merchant groups have an intriguing blend of similarities and differences, as expected for convergent evolution. The similarities are based on the functional demands of occupying the same niche. Thus, both Jains and Jews live in diaspora communities where they dominate in certain markets, such as the gem trade, and become agents of the upper classes to collect taxes from the lower classes. Both religions include food restrictions, distinctive manners of dress, and many other features that make it difficult to socialize (apart from formal trade relations) outside the group. Other aspects of both religions can be interpreted as design features that protect against cheating and insure that the most powerful members act on behalf of the group (see Wilson, 2005a for a description of Jainism distilled from Laidlaw, 1995).

The differences are based on the fact that middleman merchant groups come from very different cultural traditions, due in large part to their geographical isolation. Each tradition includes elements that can be adapted to the middleman niche without causing the traditions to converge with each other. Thus, Judaism is a monotheistic religion, Jainism is polytheistic, and Confucianism is an ethical system that only marginally qualifies as theistic, but all of them are capable of adapting their members to the same economic niche in different ways. By analogy, kangaroos in Australia and whitetail deer in North America occupy the same herbivorous niche, but in very different ways based on their separate phylogenies and geographical locations. All examples of convergent evolution, whether genetic or cultural, are expected to result in a mix of functional similarities and differences based on historical isolation and proximate mechanisms that fulfill the same functions in different ways.

The fact that middleman merchant groups function as highly cooperative units does not mean they necessarily benefit the larger multi-group ecosystem. Just as the impact of beavers on their ecosystem needs to be understood in terms of the fitness-enhancing properties of beavers, the impact of

middleman merchant groups on their cultural ecosystems need to be understood in terms of the fitness-enhancing properties of middleman merchant groups – and the same goes for all of the other functionally organized groups in a multi-group cultural ecosystem. For biological and cultural ecosystems alike, we can expect the entire spectrum of positive and negative interactions among the functionally organized units, including competition, predation, and mutualism. One of the most important insights of the cultural ecosystem approach is that ecosystems are typically not functionally organized in the same way as the agents that make up the ecosystems. There is a difference between a complex system that is adaptive *as a system* and a complex system composed of agents pursuing separate adaptive strategies (Wilson, 2015). We hope that the example of middleman merchant groups clarifies what it means to study human cultural diversity in the same way as biological diversity and how it adds value to other approaches in the humanities and social sciences. A separate particularistic literature exists for every culture included by Landa in her study. Landa is an economist by training and originally used club theory from economics (which seeks to explain groups whose members share a resource and exclude non-members; Buchanan, 1965) as her theoretical framework. But the point of her article is to argue that the particularistic literatures and a middle-range theory such as club theory need to be incorporated into a broader framework provided by cultural evolutionary theory. The cultural ecosystem approach can clarify what it means for a culturally defined group to coexist with other groups in a given geographical location, how the elements of religion are entwined with the secular elements of the groups, and the similarities and differences of cultural ecosystems in different geographical regions.

Notice that the salient groups are easy to identify in this example, at least to a crude approximation. This is because functionally organized human groups need to create identities for themselves and the other salient groups with which they interact. Identifying the salient groups in cultural ecosystems need not be more difficult than identifying the salient functional units in biological ecosystems, although there can be challenges in both cases.

To summarize, the study of biological diversity draws upon both evolutionary and ecological theory. Both are required because evolution takes place in multi-species ecosystems. The maturation of cultural evolutionary theory requires a similar approach to the study of cultural diversity.

3. The axis approach

How do scholars and social scientists study cultural diversity, if not from an ecological and evolutionary perspective? As we have seen, one common approach is to eschew theory and be content with descriptions of particular cultures. In this fashion, extensive literatures have accumulated on myriad cultures and religions, largely ignoring each other's observations or fabricating connections at a level of interpretive abstraction remote from behavior "on the ground" (Bloch, 2005).

Another more synthetic approach is to compare cultures along axes of variation. Sometimes the axes are determined by a statistical method such as factor analysis. In what has become known as cultural dimensions theory, Hofstede (1980) identified five axes of variation based on a large cross-cultural database: Power distance, Individualism, Uncertainty avoidance, Masculinity, and Long-term orientation. This method is similar to the use of factor analysis to study individual differences in personality, leading to the "big five" factors of Openness, Conscientiousness, Extraversion, Agreeableness, and Neuroticism (Goldberg, 1990). Sometimes an axis of cultural variation is identified, not by a statistical method, but based on the interest and insight of a particular investigator. A partial list of axes identified in this manner includes the following.

3.1. Strict/lax axis

Kelley (1972) made a distinction between strict and lax churches to explain the growth of conservative and evangelical churches and decline of mainline churches in America during the 1960s, a process that continues to the present. Strict churches maintain a separate and distinctive lifestyle in areas

such as dress, diet, drinking, and entertainment, whereas lax churches affirm the lifestyle of the surrounding culture (this is similar to the distinction between sects and churches; Finke & Stark, 2001; Niebuhr, 1929). Protestant denominations can be ranked very reliably along this axis of variation (Hoge & Roozen, 1979; Iannaccone, 1994). According to Iannaccone (1994), strict churches are strong because they prevent free-riding and therefore function better as cooperative units. See Thomas and Olson (2010) for a recent review of this axis of variation.

3.2. Tight/loose axis

Traditional cultures have long been known to vary in their expression of and adherence to social norms and Pelto (1968) made an important contribution by developing objective criteria for placing cultures along a continuum from "tight" to "loose." Tight cultures have strong norms of expected behavior that are enforced by punishment. Loose cultures are more permissive of individual differences. Michele Gelfand and her associates have used the tight/loose distinction to study differences among modern nations (Gelfand et al., 2006, 2011; see also Chan, 1996) and states within the United States (Harrington & Gelfand, 2014). It has not been systematically applied to differences among religions or related to the literature on strictness and laxness, again illustrating the problem of isolated literatures that we are stressing in this article.

3.3. Individualism/collectivism axis

Members of collectivist cultures view themselves primarily as part of their groups, whereas members of individualistic cultures view themselves primarily as self-interested agents. This axis of variation was identified by Hofstede's factor analysis and has been studied extensively by Triandis (1989) and others (reviewed by Triandis & Gelfand, 2012).

3.4. Doctrinal/imagistic axis

Whitehouse and his associates (Atkinson & Whitehouse, 2011; Whitehouse, 2004; Whitehouse & Lanman, 2014) distinguished between two modes of religiosity, doctrinal and imagistic. The doctrinal mode involves highly routinized rituals repeated at frequent intervals (e.g., a Catholic Mass). The imagistic mode makes use of high-intensity (usually dysphoric) rituals that are repeated at infrequent intervals (such as a fire-walking ritual; Konvalinka et al., 2011). Unlike the other axes listed above, which are envisioned as unimodal continua, Whitehouse regards these two modes as distinct "attractor positions" with a rarity of intermediate forms.

The axis approach is insightful and is used for comparative research in biology in addition to cultural and religious studies. We want to be clear that the cultural ecosystem approach does not *exclude* the detailed study of single cultural groups or axes of variation, but rather *situates them within a broader theoretical framework*. Biologists study single species in great detail and often identify major axes of variation that reflect variation in critical environmental factors or basic tradeoffs in the allocation of resources. A sample of axes identified by biologists that are relevant to the study of human cultures include the following.

3.5. Latitudinal gradients in species diversity

The fact that species diversity increases from the polar regions to the tropics is a pattern that has long fascinated biologists and begs for an explanation (Pianka, 1966; Willig, Kaufman, & Stevens, 2003). Intriguingly, human linguistic and cultural diversity exhibit the same pattern (Cashdan, 2001; Collard & Foley, 2002; Nettle, 1998; Pagel, 2012; Pagel & Mace, 2004; Van de Vliert, 2013), suggesting that biological and cultural diversity do have a common set of explanations.

3.6. Slow vs. fast life histories in response to mortality

The life history of an organism includes the timing of its growth, reproduction, and senescence (Flatt & Heyland, 2011). A continuum exists between "fast" and "slow" life history strategies that is explained largely by the degree of mortality (e.g., species with high mortality rates grow fast, reproduce early, and die young; see Promislow & Harvey, 1990 for a comparative study of mammals). This distinction is increasingly being applied to human phenotypic plasticity and cross-cultural variation (e.g., Hackman & Hruschka, 2013; Van Leeuwen, Koenig, Graham, & Park, 2014).

3.7. Parasite stress

Parasites (broadly defined to include infectious diseases) can be a major source of mortality, resulting in specific adaptations in addition to fast life history strategies that evolve in response to any form of mortality. Just as the presence of disease triggers a physiological immune response, it might also trigger a psychological response that includes restricting interactions to members of one's own group and becoming xenophobic toward outsiders (Schaller & Park, 2011; but see Hackman & Hruschka, 2013; Hruschka & Hackman, 2014). A number of authors have started to interpret human cross-cultural variation, including religiosity, as a response to parasite prevalence (Fincher & Thornhill, 2008a, 2008b, 2012; Fincher, Thornhill, Murray, & Schaller, 2008; Murray, 2014; Murray, Trudeau, & Schaller, 2011; Schaller & Park, 2011).

These axes of variation allow for a degree of generalization without studying each species as a special case. Nevertheless, they provide only a coarse-grained look at biological diversity and do not substitute for a more fine-grained approach that examines functional units as products of natural selection interacting with each other in ecosystems – the biological counterpart to the cultural ecosystem approach. The best way to make this point for cultural diversity is to focus on one axis of variation in detail to understand both its merits and limitations compared to the cultural ecosystem approach. We have chosen the tight/loose axis in part because its focus on norms enforced by punishment makes it easy to relate to the modern literature on cultural evolution. In addition, it affords an opportunity to relate the tight/loose axis to religions in addition to traditional cultures and modern nations. There are similarities between the tight/loose axis and strict–lax axis, but since they are defined somewhat differently and the literatures have developed in nearly total isolation from each other, there are also important differences. A detailed comparison is beyond the scope of this article but we will highlight some key similarities and differences.

3.8. More on the tight/loose axis

Perrti J. Pelto was an Italian anthropologist who called attention to variation among traditional societies in their expression of and adherence to social norms (Pelto, 1968). He described societies such as the Pueblo Indians and Hutterites as "tight," in which norms are expressed very clearly and enforced with severe sanctions. In contrast, societies such as the Skolt Lapps of northern Finland and the Thais (the main ethnic group of Thailand) were described as "loose," with informally expressed norms and a high tolerance of deviant behavior. Interest in the tight/loose distinction waned over the decades but has been revived and used to describe variation among modern nations and states within the United States by Michele J. Gelfand and her associates (see above cited references). Just as the Pueblo Indians differ from the Skolt Lapps, "tight" countries such as Japan and Germany differ from "loose" countries such as New Zealand and Brazil in the strength of their norms and strictness of enforcement.

In an important conceptual review, Gelfand et al. (2006) stress that the tight/loose distinction describes only one axis of cultural variation, based on the strength and sanctioning of social norms. It is different from the distinction between individualism and collectivism, which concerns the degree of individual autonomy in a society and constitutes another axis of cultural variation

(Triandis, 1989; Triandis & Gelfand, 2012). All four combinations are possible, such as Germany (tight/individualist), Japan (tight/collectivist), New Zealand (loose/individualist), and Brazil (loose/collectivist).

Gelfand et al. (2006, 2011) do not explicitly employ an evolutionary perspective, but they do appreciate that tightness and looseness have different costs and benefits, making each well adapted for different circumstances. This is in contrast to the literature on strict and lax churches, which portrays the former as always stronger than the latter. Tightness promotes solidarity, coordination, and the perpetuation of tradition. Looseness provides elbow room for individuals to pursue their own goals, which need not be bad for the group. Looseness also might promote innovation, which enables a society to adapt to new environments and to itself become an agent of change (e.g., the autocatalytic changes brought about by the Industrial Revolution documented by Acemoglu & Robinson, 2012).

Empirical research has shown that a number of environmental factors appear to favor strong norms enforced by sanctions. Agricultural societies are typically tighter than hunter-gatherer societies, because norms are required to coordinate and police the activities required to produce crops (Boldt, 1978; Pelto, 1968). Another major environmental factor appears to be existential security, since societies must often respond to threats in a collective fashion. According to McKelvey (1982, p. 186), "Environmental threat more than anything else seems to be accompanied by organizations having tight and extensive control systems" (see Norris & Inglehart, 2004 and Barber, 2011, 2012 for more on existential security, which can include parasite stress, as an important axis of environmental variation for religiosity). Notice that these two environmental factors are different from each other: a society can be tight in an existentially secure environment because of the coordination required to regulate food production, or it can be tight in an existentially threatening environment because of the coordination needed to surmount the threat. These two forms of tightness might well differ from each other at a finer level of resolution. For example, in a secure environment that nevertheless presents group members with diverse and pressing collective action problems, normative tightness might emphasize a strict division of labor, adherence to gender roles, and obedience to authority. By contrast, in an existentially insecure environment, normative tightness might emphasize norms of charity, generosity, and loyalty.

Gelfand et al. (2006) derive a number of propositions from their conceptual analysis that are highly relevant to the study of religion. One (Proposition 2A) states that societal institutions in tight societies generally favor narrow socialization practices such as unquestioning obedience to specific rules enforced by strict punishment. In contrast, children in loose societies are encouraged to be their own judge of their actions based on general ethical principles, with more lenient punishment for deviant behavior. This contrast describes strict and lax churches as well as other kinds of societies (Kelley, 1972). As an example, Storm and Wilson (2009) used a national database of American high school students to compare Protestant denominations that are strict and lax according to Iannaccone's (1994) classification. For members of lax churches, there was a strong positive correlation between agreement with the question "Do you regard yourself as a religious person?" and the statement "In my family, we express opinions even when they differ." For members of strict churches, the correlation was strongly negative.

One strength of Gelfand et al.'s (2006) conceptual analysis is that it emphasizes the interplay between societal-level variables, such as the strictness of norms, and individual-level psychological variables (see also Carpenter, 2000). According to two of their propositions (2B and 3A), individuals in tight societies have a higher degree of felt accountability (the subjective experience that one's actions are subject to evaluation), tend to solve problems using established procedures rather than innovating, are less open to experience, and have a greater desire for stability. All of these psychological variables are likely to describe members of strict congregations. As an example, the aforementioned database of American teenagers (Storm & Wilson, 2009) included experience sampling method data in addition to one-time questionnaire items. In the experience sampling method, individuals are signaled at random times during the day, which prompts them to record their immediate psychological experience (Hektner, Schmidt, & Csikszentmihalyi, 2006). Teenage members of strict

and lax churches differed dramatically in their psychological experience on a moment-by-moment basis. Members of strict churches were highly sensitive to the presence of others and tended to go slack when alone (e.g., to feel lonely, bored, and wishing to do something else). Members of lax churches maintained the same psychological profile in the presence and absence of others.

We hope that this brief introduction will encourage scholars of religion to learn more about the tight/loose distinction as an important axis of variation that does not entirely map onto the strict/lax distinction. One of the most important differences is that the strict/lax distinction does not explain how variation is maintained over time and space because strict churches are portrayed as invariably stronger than lax churches. However, thinking about tightness and looseness as a single axis of variation misses insights that can be revealed by the cultural ecosystem approach, which focuses on functionally organized groups that co-evolve with each other and their biological and physical environments. In the next section we will attempt to demonstrate the "added value" of the cultural ecosystem approach for the concept of tightness and looseness.

4. Added value of the cultural ecosystem approach

Non-human organisms are highly context-sensitive in their behavior, which is necessary to survive and reproduce in their challenging environments. If human groups are functionally organized units, then they too must behave in a highly context-sensitive fashion. Insofar as human behaviors are orchestrated by norms, then functionally organized units will have myriad norms to insure that their members do the right thing at the right time in the right way. The tight/loose distinction will need to be applied within functionally organized units in addition to across them.

Particularistic approaches to cultural and religious diversity, including social constructivist and postmodern traditions, take context sensitivity for granted. Their shortcoming is that they fail to provide a general theoretical framework for studying context sensitivity within and across cultures. Social constructivism needs to become *evolutionary social constructivism* (Wilson, 2005b). Axis of variation approaches do not deny context sensitivity within cultural groups but they are not well equipped for the study of it, since their main goal is to explain differences among them. As an example, Gelfand et al. (2006, 2011) concentrate almost entirely on differences between cultures and have little to say about context-dependent variation within cultures, other than to acknowledge its possibility (but see Realo, Linnamägi, & Gelfand, 2014 for a more context-sensitive study of Greece and Estonia). The cultural ecosystem approach can therefore help to address the shortcomings of both the axis approach and particularistic approaches.

Two examples of tight and loose norms within cultural groups, one drawn from anthropology and the other from religious studies, will illustrate this basic point. The Chewong are a cultural group inhabiting the rainforest of the Malay Peninsula, where they combine hunting and gathering with shifting agriculture. The sharing of food and other scarce resources is a strong norm governed by a system of superstitions known as *punen*, which roughly means "a calamity or misfortune, owing to not having satisfied an urgent desire" (Howell, 1984, p. 184). The Chewong go to elaborate efforts to avoid *punen* by sharing – in other words, they are a tight culture, but only when resources are in short supply. When resources can be easily obtained, such as bamboo growing close by or water during the rainy season, the norm is relaxed. The appropriate context is signaled by linguistic distinctions such as "bamboo far away (lao tyotn)" vs. "bamboo nearby (lao duah)." This flexible system makes clear functional sense, although more research would be required to show that it actually evolved for the purpose of adapting the culture to variation in resource availability.

Our second example involves norms of acceptable behavior and punishment of deviance for pastors and secular rulers prescribed by John Calvin in the Catechism and Ecclesiastical Ordinances that he wrote for the city of Geneva (see Wilson, 2002, ch. 3 for an extended discussion). Both were expected to be on their best behavior, but deviant pastors were severely punished while deviant secular rulers were interpreted as God's way of punishing one's own transgressions ("For as a good prince is proof of divine beneficence for the preservation of human welfare, so a bad and wicked ruler is his whip to chastise the peoples' transgressions" (quoted in Wilson, 2002, p. 95)). The reason for this variation in

the strength of enforcement (one of the two components of tightness) is easy to understand with a little knowledge of the political situation in Geneva at the time. Calvin's church had the authority to punish its own pastors but no authority to punish secular rulers. Calvin tailored the religious rules to his political environment, which is reflected not just superficially but in the core documents of the Catechism and Ecclesiastical Ordinances.

If all well-adapted cultures have myriad norms such as these, tailored to their particular environments, then a norm-by-norm analysis is required for each culture in addition to cross-cultural comparisons. The strength of each norm and the degree to which it is enforced (the two components of the concept of tightness) will be highly contingent on the situation, the phylogeny of the culture, and so on. Cultures might vary in their average degree of tightness, but this would be better regarded as an aggregate of many factors rather than a single axis of variation.

Researchers who focus on a single axis or employ factor analysis as a multi-dimensional method are likely to acknowledge the usefulness of fine-grained examples such as these, but might also stress the need for a coarser grain of analysis that does not require such a detailed understanding of single cultures in relation to their environments. We agree – but only to a degree (see also Levin, 1999). The history of thinking in ecosystem ecology began by trying to derive generalities at the systemic level without requiring detailed understanding of species as the strategic agents that comprise ecosystems. That approach yielded a few generalities but ultimately became limiting. Ecosystem ecologists are increasingly employing a species-based approach that even pays attention to genetic change within each species, since genetic evolution often takes place on ecological time scales (Bailey et al., 2004; Whitham et al., 2008). Those who study human cultural variation are well advised to take the same path. In the following sections, we identify a number of topic areas for future development of the tight/loose distinction suggested by the cultural ecosystem approach.

4.1. On the relationship between the strength of social norms and the strength of sanctioning

In one of their propositions (1A), Gelfand et al. (2006, p. 1227) state that "tightness–looseness consists of the strength of social norms (number and clarity) and the strength of sanctioning (tolerance for deviance from norms)." Having stressed two components, however, they do not elaborate on the relationship between them. One possibility is that they strongly correlate with each other, such that whenever a norm is strongly clarified, it is strongly enforced by punishment. Another possibility is that strongly clarified norms might or might not be strongly enforced by punishment, depending upon the context. The latter possibility makes most sense from an evolutionary perspective. It is important to distinguish between the need for coordination to achieve group goals and the temptation to defect to achieve more self-serving goals. A strong need to coordinate without a temptation to defect is likely to result in a strong clarifying norm with little punishment for deviance. As an example, a martial arts dojo includes dozens of norms that define the rules of sparring, transitioning between exercises, and awarding more advanced belts to its members (James & Jones, 1982). These norms are clearly articulated with no tolerance for deviance (e.g., you must bow to your opponent before and after each sparring exercise), but friendly reminders are sufficient to correct individuals who forget the rules because there is no incentive to cheat. In contrast, the rules of sparring in martial arts competitions (and other sports competitions) are closely monitored by referees and enforced by punishment because there is an incentive to cheat. To summarize, the study of tightness and looseness should distinguish between the need for coordination and the temptation to cheat, which can create a complex relationship between the two components defining tightness and looseness.

4.2. On the diverse selection pressures that favor tightness and looseness

Insect species vary in the brightness of their coloration, but does it make sense to identify a "bright–drab" axis of phenotypic variation? Most entomologists would say no, because bright colors can

evolve for so many different reasons. Some species evolve brightness as a mating display, others as a way to warn predators that they are toxic, and others to conceal themselves against a background that also happens to be bright. Better to focus on the different selection pressures than to lump them under the category of "bright."

The tight/loose distinction runs the risk of being a poorly chosen axis of cultural variation, like the bright/drab axis in insects. Consider two of the major environmental correlates of tight societies identified by Gelfand et al. (2006): agricultural societies and environmental threat. These are very different from each other and can exist in all four combinations. An agricultural society can be unthreatened but still require strong norms to orchestrate the subsistence economy. Any society can become threatened in ways that require a collective response, which might be different depending upon the nature of the threat (e.g., warfare vs. a natural disaster). Lumping together cultures that become tight for such different reasons might be useful for some purposes, but additional progress will require distinguishing types of tightness and looseness based on different selection pressures.

In this spirit, we propose a third major context (in addition to labor-intensive agriculture and environmental threat) for the biocultural evolution of tightness, based on a distinction between extractive and inclusive societies made by Acemoglu and Robinson (2012) in their book *Why Nations Fail*. Inclusive societies are relatively egalitarian and allow the average member to profit from his or her labor and ingenuity. Extractive societies are organized for the benefit of a small group of elites at the expense of the rest of the society. Extractive societies must have strong laws enforced by punishment to suppress rebellion. This is a different selection pressure than the need to coordinate a complex subsistence economy or the need to respond collectively to a threat, which can apply to both inclusive and extractive societies. It also provides an example of how a loose social structure can be highly adaptive at the group level, insofar as innovative societies adapt to changing environments and especially when they do so in an autocatalytic fashion. To summarize, the tight/loose axis of cultural variation reflects diverse selection pressures, like the bright/drab axis of coloration in insects. Progress requires studying each selection pressure in its own right.

4.3. Are norms separately optimized or are cultures systemically tight or loose?

Biologists often study evolution on a trait-by-trait basis, as if the traits can evolve independently of each other. However, biologists also realize that traits are interconnected through shared genes, developmental programs, and physiological systems (Gould & Lewontin, 1979; Oyama, Griffiths, & Gray, 2003). For example, is boldness a single personality trait that is expressed in all contexts, or can it be optimized separately for different contexts such as predator defense, competition for mates, and exploration of the physical environment? This is an active area of research in animal behavior under the heading of "behavioral syndromes" (Garamszegi, Markó, & Herczeg, 2012; Sih, Bell, & Johnson, 2004).

A similar question can be asked for the cultural evolution of norms. Some of the examples provided earlier illustrate an impressive degree of context sensitivity, such as norms of sharing that only apply when resources are scarce, or punishment norms that apply to pastors but not secular rulers. If all norms can be optimized separately, then differences between cultures would be nothing more than the sums of their respective norms. We think that this is an exaggeration for cultural evolution, as it is for biological evolution. In reality, there are probably cultural equivalents of shared genes, developmental programs, and physiological systems that cause norms to become interconnected and limit context sensitivity. Child socialization practices provide a likely example. It might be difficult for a culture to insist upon unquestioning adherence to specific rules (or conversely, for children to be their own judge) in some contexts but not others. If so, then cultures will become systemically tight or loose and will have limited abilities to tailor tightness and looseness to different contexts (e.g., for a tight culture such as Singapore to become highly innovative in business and industry, much as its leaders might want it to). This is an empirical question that can only be decided

by future research. We think that this research will be most productive if framed explicitly in terms of cultural evolutionary theory.

4.4. On the importance of studying temporal change

The most comprehensive studies of genetic evolution track changes in the frequencies of traits over time, such as the morphology of finch beaks on a Galapagos Island following a drought (Weiner, 1994), the evolution of multiple traits in guppies in the presence and absence of predators (Endler, 1995), or the evolution of enzymatic adaptations in bacteria over thousands of generations (Lenski, 2011). Most studies framed in terms of tightness and looseness are static, not longitudinal, but longitudinal studies are feasible, based on historical data or changes in contemporary societies in response to environmental change for example (see McCann, 1999; Norris & Inglehart, 2004 for longitudinal studies of religiosity in relation to existential security). It might even be possible to conduct the cultural analog of experimental evolution studies in biology, whereby groups are allowed to establish norms under conditions that are varied for parameters such as the need for coordination or the temptation to defect.

Numerous predictions about changes in tightness and looseness over time can be derived from an evolutionary perspective. For example, when there is a strong temptation to defect on a norm, ways to circumvent the norm will tend to evolve within a culture over time. Either the norm will become looser (to the detriment of the culture), or new means to enforce the norm will evolve in a co-evolutionary race. Cultures that become too loose in this detrimental sense can succumb to tighter cultures in between-group competition. Turchin (2005, 2010) has described this process of multilevel biocultural evolution for the rise and fall of empires and other macrohistorical trends.

Another prediction concerns variation within and between religious denominations. A new variety of religion starts out somewhere on the tight/loose continuum. As it grows, some individuals might come to prefer a tighter or looser style of religion. Although they could convert to another denomination, they might often feel more comfortable creating a different version of their own worship tradition. In this fashion, the tight/loose continuum recreates itself within every major denomination (Finke & Stark, 2001; Wilson, 2002, pp. 182–186).

To summarize, identifying axes of variation is a useful analytic method for the study of both biological and cultural diversity, but at best it is a broad-brush approach that does not substitute for the detailed study of functionally organized units in relation to each other and their environment. Microevolution is the engine that generates pattern at larger scales. It needs to be studied directly for cultural evolution no less than for genetic evolution.

5. The need for field sites for the study of cultural ecosystems

The cultural ecosystem approach is first and foremost a conceptual framework that organizes the study of cultural diversity, which includes religious diversity. It does not require novel empirical or statistical methods. Its novelty lies in the questions that it poses, based on the recognition that functionally organized human groups are complex adaptive units that possess myriad adaptations for surviving and reproducing in their physical and social environments. This framework can be used to guide social science research and scholarship at all scales, from single investigators studying single cultures to teams of investigators studying whole cultural ecosystems.

In the example of middleman merchant groups that we used to illustrate the cultural ecosystem approach (Landa, 2008), a single investigator conducted research on a single culture (Chinese middleman merchant groups operating in Southeast Asia) and synthesized the literature on other middleman merchant groups. Her contribution is distinctive, not for her empirical methods or the scale of her research, but for the multilevel cultural evolutionary framework that she employed.

While anyone can adopt the cultural ecosystem approach for their individual research programs, there is also a need to study whole cultural ecosystems – sizeable areas where many functionally

organized human groups interact with each other and their environment. This is inherently a large-scale research effort. Federal granting agencies invest considerable resources in the study of whole biological ecosystems, such as the National Science Foundation's Ecosystem Science Cluster (http://www.nsf.gov/funding/pgm_summ.jsp?pims_id = 503663&org = E). The fact that comparable funding programs do not exist for the study of cultural ecosystems indicates the novelty of the approach.

We are pioneering this approach for Binghamton, New York as a model for other locations and end this article with a brief description of our efforts, with the goal of encouraging similar efforts at other locations rather than the presentation of specific results, which will be presented elsewhere. Binghamton is a small city in upstate New York that experienced economic growth during the nineteenth and most of the twentieth century but economically declined during the last few decades, similar to many American "rust belt" cities. It was chosen as a field site for studying a whole cultural ecosystem because a campus-wide evolutionary studies program at Binghamton University called EvoS provided the infrastructure for a team effort (Wilson, 2011). The religious component of the cultural ecosystem includes nearly 100 congregations within the city limits and approximately 100 additional congregations in the surrounding county. While this component is easiest to identify, it exists within a larger milieu of religious believers who are not churchgoers, as well as secular individuals and cultural organizations. An advantage of creating a field site is that the religious congregations can be studied against the background of the rest of the cultural ecosystem in detail.

The comprehensive study of any ecosystem requires a historical dimension, because so much depends upon historical factors and priority effects (e.g., which species or cultural group arrived first). Historical information is often difficult to obtain for biological ecosystems but it exists in abundance for the Binghamton area and most other locations. Not only is the local history well known, dating back to the colonization of the region shortly after the Revolutionary War, but the church histories are often exceptionally well preserved. In addition to individual church histories, a treasure trove of record keeping takes place at the district level for single denominations such as the United Methodist Church. We have found that local historians, single congregations, and district offices are happy to share their information and take a keen interest in our analyses and results, helping them understand the factors that result in growth and decline. The historical dimension of our research provides a "thick description" of cultural ecosystem dynamics over time. Methodologically, it is little different than other kinds of historical research – the crucial difference is that the information is gathered and analyzed from a unified theoretical perspective. In addition, our theoretical perspective provides a guide for quantifying historical information for statistical analysis (see Turchin et al., 2012 for the need for history to become a quantitative science).

The historical dimension of our research is complemented by the study of current religious congregations in relation to each other and the secular elements of the cultural ecosystem. While particularistic sociological studies sometimes take place at this scale (e.g., McRoberts, 2003), most studies that employ the axis-of-variation approach focus on much larger scales, such as nations, states, and major religious denominations, if only because of the availability of data at those scales. The creation of field sites enables factors such as existential insecurity and the strictness of norms to be studied in the context of everyday life. As an example, every American city has churches that proclaim their faith as the invariant truth and other churches that proclaim their tolerance of diverse views. The differences between these religious forms are so great that "tight" pastors have more in common across Christian denominations than with "loose" pastors within their own denomination. Some people who join "loose" congregations are casualties of intolerance that they experienced as members of "tight" congregations, while some people who join "tight" congregations are casualties of a lack of meaning and structure that they experienced in "loose" congregations. All congregations lose members to and draw members from the heterogeneous ranks of non-churchgoers. These complex dynamics need to be studied at the local scale where they actually occur, in addition to national and denominational scales, which are mostly aggregates of local trends (see Wilson, 2002, ch. 6 for a discussion of "the fog of aggregation").

Starting a field site for the study of whole cultural ecosystems might seem daunting, but it can be accomplished incrementally and can accommodate the interests of individual researchers rather than being excessively top-down in its organization of projects. This is also true for biological field sites, where every study contributes to a database for the whole ecosystem in a cumulative fashion.

The need for *multiple* field sites is as important for the study of cultural ecosystems as for the study of biological ecosystems. All ecosystems are complex and therefore diverse in their properties, based on differences that can seem trivial (illustrating the principle of sensitive dependence on initial conditions; Gleick, 1987). Even biological ecosystems of a single type, such as lake ecosystems or stream ecosystems, can be very different from each other in their dynamics. The only way for generalities to emerge is to establish many field sites. Biological ecosystem ecologists have had decades to implement this approach with major funding from federal granting agencies. We look forward to the day when cultural ecosystems are investigated in the same way with a comparable investment of resources.

6. Conclusion

The goals of this article are: (1) to summarize the current status of cultural evolutionary theory and evolutionary religious studies, both of which have become centered on group-level functional organization; (2) to outline the cultural ecosystem approach, which studies cultural diversity in the same way that biologists study biological diversity; (3) to compare the cultural ecosystem approach with the most common method of cross-cultural research, which is to identify axes of variation; (4) to illustrate the comparison with a detailed case study of one axis of variation (the distinction between "tight" and "loose" cultures), showing how the cultural ecosystem approach adds value to the axis approach; and (5) to call for the establishment of field sites for the study of cultural ecosystems.

The biological sciences offer a proven example of how a highly complex subject – the diversity of life – can be organized by a single theoretical framework. We hope we have convinced the reader that the study of cultural evolution has advanced to the point where another complex subject – the diversity of human cultures – can be organized in the same way.

Acknowledgements

We thank Michele Gelfand for extended conversations about the tight/loose axis of cultural variation.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This research was supported by a grant from the John Templeton Foundation [grant number 37624] titled "Religion's Impact on Human Life: Integrating Proximate and Ultimate Perspectives."

References

Acemoglu, D., & Robinson, J. (2012). *Why nations fail: The origins of power, prosperity, and poverty*. New York: Crown.

Atkinson, Q. D., & Whitehouse, H. (2011). The cultural morphospace of ritual form. *Evolution and Human Behavior*, *32*(1), 50–62. doi:10.1016/j.evolhumbehav.2010.09.002

Atran, S., & Henrich, J. (2010). The evolution of religion: How cognitive by-products, adaptive learning heuristics, ritual displays, and group competition generate deep commitments to prosocial religions. *Biological Theory: Integrating Development, Evolution, and Cognition*, *5*, 18–30.

Bailey, J. K., Schweitzer, J. A., Rehill, B. J., Lindroth, R. L., Martinsen, G. D., & Whitham, T. G. (2004). Beavers as molecular geneticists: A genetic basis to the foraging of an ecosystem engineer. *Ecology*, *85*, 603–608. doi:10.1890/03-3049

Barber, N. (2011). A cross-national test of the uncertainty hypothesis of religious belief. *Cross-Cultural Research*, *45*(3), 318–333. doi:10.1177/1069397111402465

Barber, N. (2012). Country religiosity declines as material security increases. *Cross-Cultural Research*, *47*(1), 42–50. doi:10.1177/1069397112463328
Bloch, M. (2005). Where did anthropology go? Or the need for "human nature". In M. Bloch (Ed.), *Essays on cultural transmission* (pp. 1–20). Oxford: Oxford University Press.
Bodkin, B. B. (1990). *Discordant harmonies: A new ecology for the twenty-first century*. New York, USA: Oxford University Press USA.
Boehm, C. (2011). *Moral origins: The evolution of virtue, altruism, and shame*. New York: Basic Books.
Boldt, E. D. (1978). Structural tightness and cross-cultural research. *Journal of Cross-Cultural Psychology*, *9*, 151–165.
Borrello, M. (2010). *Evolutionary restraints: The contentious history of group selection*. Chicago: University of Chicago Press.
Buchanan, J. M. (1965). An economic theory of clubs. *Economica*, *32*, 1–14.
Bulbulia, J. (2012). Spreading order: Religion, cooperative niche construction, and risky coordination problems. *Biology & Philosophy*, *27*(1), 1–27. doi:10.1007/s10539-011-9295-x
Carniero, R. (2003). *Evolution in cultural anthropology: A critical history*. New York: Westview Press.
Carpenter, S. (2000). Effects of cultural tightness and collectivism on self-concept and causal attributions. *Cross-Cultural Research*, *34*(1), 38–56. doi:10.1177/106939710003400103
Cashdan, E. (2001). Ethnic diversity and its environmental determinants: Effects of climate, pathogens, and habitat diversity. *American Anthropologist*, *103*(4), 968–991. doi:10.1525/aa.2001.103.4.968
Chan, D. K.-S. (1996). Tightness-looseness revisited: Some preliminary analyses in Japan and the United States. *International Journal of Psychology*, *31*(1), 1–12. doi:10.1080/002075996401179
Cochran, G., & Harpending, H. (2009). *The 10,000 year explosion: How civilization accelerated human evolution*. New York: Basic Books.
Collard, I. F., & Foley, R. A. (2002). Latitudinal patterns and environmental determinants of recent human cultural diversity: Do humans follow biogeographical rules? *Evolutionary Ecology Research*, *4*(3), 371–383.
Coyne, J. A., & Orr, H. A. (2004). *Speciation*. Sunderland, MA: Sinauer.
Deacon, T. W. (1998). *The symbolic species*. New York: Norton.
Durkheim, E. (1912). *The elementary forms of religious life*. New York: The Free Press.
Endler, J. A. (1995). Multiple-trait coevolution and environmental gradients in guppies. *Trends in Ecology and Evolution*, *10*, 22–29.
Fincher, C. L., & Thornhill, R. (2008a). A parasite-driven wedge: Infectious diseases may explain language and other biodiversity. *Oikos*, *117*(9), 1289–1297. doi:10.1111/j.0030-1299.2008.16684.x
Fincher, C. L., & Thornhill, R. (2008b). Assortative sociality, limited dispersal, infectious disease and the genesis of the global pattern of religion diversity. *Proceedings. Biological Sciences / The Royal Society*, *275*(1651), 2587–2594. doi:10.1098/rspb.2008.0688
Fincher, C. L., & Thornhill, R. (2012). Parasite-stress promotes in-group assortative sociality: The cases of strong family ties and heightened religiosity. *The Behavioral and Brain Sciences*, *35*(2), 61–79. doi:10.1017/S0140525X11000021
Fincher, C. L., Thornhill, R., Murray, D. R., & Schaller, M. (2008). Pathogen prevalence predicts human cross-cultural variability in individualism/collectivism. *Proceedings. Biological Sciences / The Royal Society*, *275*(1640), 1279–1285. doi:10.1098/rspb.2008.0094
Finke, R., & Stark, R. (2001). The new holy clubs: Testing church-to-sect propositions. *Sociology of Religion*, *62*(2), 175. doi:10.2307/3712454
Flatt, T., & Heyland, A. (2011). *Mechanisms of life history evolution: The genetics and physiology of life history traits and trade-offs* (p. 512). New York, USA: Oxford University Press.
Garamszegi, L. Z., Markó, G., & Herczeg, G. (2012). A meta-analysis of correlated behaviours with implications for behavioural syndromes: Mean effect size, publication bias, phylogenetic effects and the role of mediator variables. *Evolutionary Ecology*, *26*(5), 1213–1235. doi:10.1007/s10682-012-9589-8
Gelfand, M. J., Nishii, L. H., & Raver, J. L. (2006). On the nature and importance of cultural tightness-looseness.. *Journal of Applied Psychology*, *91*, 1225–1244.
Gelfand, M. J, Raver, J. L., Nishii, L., Leslie, L. M., Lun, J., Lim, B. C., … Yamaguchi, S. (2011). Differences between tight and loose cultures: A 33-nation study. *Science*, *332*(6033), 1100–1104. doi:10.1126/science.1197754
Gil-White, F. J. (2001). Are ethnic groups biological "species" to the human brain? Essentialism in our cognition of some social categories. *Current Anthropology*, *42*, 515–553. doi:10.1086/321802
Gleick, J. (1987). *Chaos: Making a new science*. New York: Penguin Books.
Goldberg, L. R. (1990). An alternative "description of personality": The Big-Five factor structure. *Journal of Personality and Social Psychology*, *59*, 1216–1229.
Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the panglossian paradigm: A critique of the adaptationist program. *Proceedings of the Royal Society of London*, *B205*, 581–598.
Hackman, J., & Hruschka, D. (2013). Fast life histories, not pathogens, account for state-level variation in homicide, child maltreatment, and family ties in the U.S. *Evolution and Human Behavior*, *34*(2), 118–124. doi:10.1016/j.evolhumbehav.2012.11.002
Haidt, J. (2012). *The righteous mind: Why good people are divided by politics and religion*. New York: Pantheon.

Harrington, J. R., & Gelfand, M. J. (2014). Tightness-looseness across the 50 united states. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(22), 7990–7995. doi:10.1073/pnas.1317937111
Hektner, J. M., Schmidt, J. A., & Csikszentmihalyi, M. (2006). *Experience sampling method: Measuring the quality of everyday life*. SAGE Publications, Inc. Retrieved from http://www.amazon.com/Experience-Sampling-Method-Measuring-ebook/dp/B004B8UXW2
Henrich, J. (2003). Cultural group selection, coevolutionary processes and large-scale cooperation. *Journal of Economic Behavior and Organization*, *53*, 3–35.
Henrich, J. (2009). The evolution of costly displays, cooperation and religion. *Evolution and Human Behavior*, *30*(4), 244–260.
Henrich, J., Boyd, R., & Richerson, P. J. (2008). Five misunderstandings about cultural evolution. *Human Nature*, *19*, 119–137.
Henrich, J., & Henrich, N. (2007). *Why humans cooperate: A cultural and evolutionary explanation*. Oxford, UK: Oxford University Press.
Hofstede, G. (1980). *Culture's consequences*. Beverly Hills, CA: Sage.
Hoge, D. R., & Roozen, D. A. (1979). *Technical appendix to understanding church growth and decline, 1950–1978*. Hartford, CN: Hartford Seminary Foundation.
Howell, S. (1984). *Society and cosmos: Chewong of peninsular Malaya*. Singapore: Oxford University Press.
Hruschka, D. J., & Hackman, J. (2014). When are cross-group differences a product of a human behavioral immune system? *Evolutionary Behavioral Sciences*, *8*(4), 265–273.
Iannaccone, L. R. (1994). Why strict churches are strong. *American Journal of Sociology*, *99*, 1180–1211.
Iannaccone, L. R. (1995). Voodoo economics? Reviewing the rational choice approach to religion. *Journal for the Scientific Study of Religion*, *34*, 76–89.
Jablonka, E., & Lamb, M. J. (2006). *Evolution in four dimension: Genetic, epigenetic, behavioral, and symbolic variation in the history of life*. Cambridge, MA: MIT Press.
James, A., & Jones, R. (1982). The social world of karate-do. *Leisure Studies*, *1*(3), 337–354. doi:10.1080/02614368200390271
Johnson, D. D. P., Price, M. E., & Van Vugt, M. (2013). Darwin's invisible hand: Market competition, evolution and the firm. *Journal of Economic Behavior & Organization*, *90*, S128–S140.
Kelley, D. M. (1972). *Why conservative churches are growing: A study in sociology of religion*. New York: Harper & Row.
Konvalinka, I., Xygalatas, D., Bulbulia, J., Schjødt, U., Jegindø, E.-M., Wallot, S., Van Orden, G., et al. (2011). Synchronized arousal between performers and related spectators in a fire-walking ritual. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(20), 8514–8519. doi:10.1073/pnas.1016955108
Kricher, J. (2009). *The balance of nature: Ecology's enduring myth*. Princeton: Princeton University Press.
Kurzban, R., Burton-Chellew, M. N., & West, S. A. (2014). The evolution of altruism in humans. *Annual Review of Psychology*, *66*, 575–599.
Laidlaw, J. (1995). *Riches and renunciation: Religion, economy and society among the Jains*. Oxford: Oxford University Press.
Landa, J. T. (2008). The bioeconomics of homogenous middleman groups as adaptive units: Theory and empirical evidence viewed from a group selection framework. *Journal of Bioeconomics*, *10*, 259–278.
Lenski, R. E. (2011). Evolution in action: A 50,000-generation salute to Charles Darwin. *Microbe*, *6*, 30–33.
Levin, S. A. (1999). *Fragile dominion: Complexity and the commons*. Cambridge, MA: Perseus.
Marshall, J. A. R. (2011). Group selection and kin selection: Formally equivalent approaches. *Trends in Ecology & Evolution*, *26*(7), 325–332. doi:10.1016/j.tree.2011.04.008
Matthews, L. J., Edmonds, J., Wildman, W. J., & Nunn, C. L. (2013). Cultural inheritance or cultural diffusion of religious violence? A quantitative case study of the Radical Reformation. *Religion, Brain & Behavior*, *3*(1), 3–15. doi:10.1080/2153599X.2012.707388
McCann, S. (1999). Threatening times and fluctuations in American church memberships. *Personality and Social Psychology Bulletin*, *25*, 325–336.
McKelvey, B. (1982). *Organizational systematics: Taxonomy, classification, and evolution*. Los Angeles: University of California Press.
McRoberts, O. M. N. (2003). *Streets of glory: Church and community in a black urban neighborhood*. Chicago: University of Chicago Press.
Mrazek, A. J., Chiao, J. Y., Blizinsky, K. D., Lun, J., & Gelfand, M. J. (2013). The role of culture-gene coevolution in morality judgment: Examining the interplay between tightness-looseness and allelic variation of the serotonin transporter gene. *Culture and Brain*, *1*, 100–117. doi:10.1007/s40167-013-0009-x
Murray, D. R. (2014). Direct and indirect implications of pathogen prevalence for scientific and technological innovation. *Journal of Cross-Cultural Psychology*, *45*(6), 971–985. doi:10.1177/0022022114532356
Murray, D. R., Trudeau, R., & Schaller, M. (2011). On the origins of cultural differences in conformity: Four tests of the pathogen prevalence hypothesis. *Personality & Social Psychology Bulletin*, *37*(3), 318–329. doi:10.1177/0146167210394451

Nettle, D. (1998). Explaining global patterns of language diversity. *Journal of Anthropological Archaeology*, *17*, 354–374.
Niebuhr, H. (1929). *The social sources of denominationalism*. New York: Holt. Retrieved from http://scholar.google.com/scholar?hl = n&q = iebuhr + ocial + ources + f+denominationalism&btnG=&as_sdt = 1%2C33&as_sdtp=#1
Norenzayan, A., & Shariff, A. F. (2008). The origin and evolution of religious prosociality. *Science*, *322*, 58–62.
Norris, P., & Inglehart, R. (2004). *Sacred and secular: Religion and politics worldwide*. Cambridge, UK: Cambridge University Press.
Okasha, S. (2006). *Evolution and the levels of selection*. Oxford, UK: Oxford University Press.
Oyama, S., Griffiths, P. E., & Gray, R. (2003). *Cycles of contingency: Developmental systems and evolution*. Cambridge, MA: MIT Press.
Paden, W. (2008). Connecting with evolutionary models: New patterns in comparative religion? In *Introducing religion: Essays in honour of Jonathan Z. Smith* (pp. 4006–4417). Sheffield, UK: Equinox.
Pagel, M. (2012). *Wired for culture: The natural history of human cooperation*. New York: Allen Lane.
Pagel, M., & Mace, R. (2004). The cultural wealth of nations. *Nature*, *428*, 275–278.
Panke-Buisse, K., Poole, A. C., Goodrich, J. K., Ley, R. E., & Kao-Kniffin, J. (2014). Selection on soil microbiomes reveals reproducible impacts on plant function. *The ISME Journal*, *9*, 980–989.
Pelto, P. (1968). The difference between "tight" and "loose" societies. *Transaction*, *5*, 37–40.
Pianka, E. (1966). Latitudinal gradients in species diversity: A review of concepts. *American Naturalist*, *100*, 33–46.
Promislow, D. E. L., & Harvey, P. H. (1990). Living fast and dying young: A comparative analysis of life-history variation among mammals. *Journal of Zoology*, *220*(3), 417–437. doi:10.1111/j.1469-7998.1990.tb04316.x
Realo, A., Linnamägi, K., & Gelfand, M. J. (2014). The cultural dimension of tightness-looseness: An analysis of situational constraint in Estonia and Greece. *International Journal of Psychology: Journal International de Psychologie*, (4423), 1–12. doi:10.1002/ijop.12097
Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.
Richerson, P. J., & Christiensen, M. H. (2013). *Cultural evolution*. Cambridge, MA: The MIT Press.
Schaller, M., & Park, J. H. (2011). The behavioral immune system (and why it matters). *Current Directions in Psychological Science*, *20*(2), 99–103. doi:10.1177/0963721411402596
Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, *19*(7), 372–378. doi:10.1016/j.tree.2004.04.009
Smith, D. L. (2012). *Less than human: Why we demean, enslave, and exterminate others*. New York: St. Martin's Griffin.
Sober, E., & Wilson, D. S. (1998). *Unto others: The evolution and psychology of unselfish behavior*. Cambridge, MA: Harvard University Press.
Sosis, R. (2009). The adaptationist-byproduct debate on the evolution of religion: Five misunderstandings of the adaptation program. *Journal of Cognition and Culture*, *9*, 315–332.
Stark, R. (1999). Micro foundations of religion: A revised theory. *Sociological Theory*, *17*, 264–289.
Storm, I., & Wilson, D. S. (2009). Liberal and conservative protestant denominations as different socio-ecological strategies. *Human Nature*, *20*, 1–24.
Swenson, W., Wilson, D. S., & Elias, R. (2000). Artificial ecosystem selection. *Proceedings of the National Academy of Sciences*, *97*, 9110–9114.
Thomas, J. N., & Olson, D. V. A. (2010). Testing the strictness thesis and competing theories of congregational growth. *Journal for the Scientific Study of Religion*, *49*(4), 619–639. doi:10.1111/j.1468-5906.2010.01534.x
Tomasello, M. (2009). *Why we cooperate*. Boston: MIT Press.
Triandis, H. C. (1989). The self and social behavior in differing cultural contexts. *Psychological Review*, *96*, 506–520.
Triandis, H. C., & Gelfand, M. J. A. (2012). A theory of individualism and collectivism. In V. Van Lange, A. Kruglanski, & E. T. Higgins (Eds.), *Handbook of theories of social psychology* (pp. 498–520). New York: Sage.
Turchin, P. (2005). *War and peace and war*. Upper Saddle River, NJ: Pi Press.
Turchin, P. (2010). Warfare and the evolution of social complexity: A multilevel selection approach. *Structure and Dynamics*, *4*(3). Retrieved from http://escholarship.org/uc/item/7j11945r
Turchin, P., Whitehouse, H., Francois, P., Slingerland, E., & Collard, M. (2012). A historical database of sociocultural evolution. *Cliodynamics: The Journal of Theoretical and Mathematical History*, *3*(2), 271–293.
Van Leeuwen, F., Koenig, B. L., Graham, J., & Park, J. H. (2014). Moral concerns across the United States: Associations with life-history variables, pathogen prevalence, urbanization, cognitive ability, and social class. *Evolution and Human Behavior*, *35*(6), 464–471. doi:10.1016/j.evolhumbehav.2014.06.005
Van de Vliert, E. (2013). Climato-economic habitats support patterns of human needs, stresses, and freedoms. *Behavioral and Brain Sciences*, *36*(5), 465–480. Retrieved from http://journals.cambridge.org/abstract_S0140525X12002828
Weiner, J. (1994). *The beak of the finch: A story of evolution in our time*. New York: Knopf.
Whitehouse, H. (2004). *Modes of religiosity: A cognitive theory of religious transmission*. Lanham, MD: AltaMira Press.
Whitehouse, H., & Lanman, J. A. (2014). The ties that bind us. *Current Anthropology*, *55*(6), 674–695. doi:10.1086/678698

Whitham, T. G., DiFazio, S. P., Schweitzer, J. A., Shuster, S. M., Allan, G. J., Bailey, J. K., & Woolbright, S. A. (2008). Extending genomics to natural communities and ecosystems. *Science*, *320*, 492–495.
Willig, M. R., Kaufman, D. M., & Stevens, R. D. (2003). Latitudinal gradients of biodiversity: Pattern, process, scale and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 273–309.
Wilson, D. S. (1980). *The natural selection of populations and communities* (p. 186). Menlo Park, CA: Benjamin/Cummings.
Wilson, D. S. (1997). Biological communities as functionally organized units. *Ecology*, *78*(7), 2018–2024.
Wilson, D. S. (2002). *Darwin's cathedral: Evolution, religion and the nature of society*. Chicago: University of Chicago Press.
Wilson, D. S. (2005a). Testing major evolutionary hypotheses about religion with a random sample. *Human Nature*, *16*, 382–409.
Wilson, D. S. (2005b). Evolutionary social constructivism. In J. Gottshcall & D. S. Wilson (Eds.), *The literary animal: Evolution and the nature of narrative* (pp. 20–37). Evanston, IL: Northwestern University Press.
Wilson, D. S. (2011). *The neighborhood project: Using evolution to improve my city, one block at a time*. New York: Little, Brown.
Wilson, D. S. (2012). Human cultures are primarily adaptive at the group level. Social Evolution Forum. Retrieved from https://evolution-institute.org/focus-article/david-sloan-wilson-human-cultures-are-primarily-adaptive-at-the-group-level/
Wilson, D. S. (2015). *Does altruism exist?* New Haven: Yale University Press.
Wilson, D. S., & Wilson, E. O. (2007). Rethinking the theoretical foundation of sociobiology. *Quarterly Review of Biology*, *82*, 327–348.
Wilson, E. O. (2012). *The social conquest of earth*. New York: Norton.
Yaworsky, W., Horowitz, M., & Kickham, K. (2015). Gender and politics among anthropologists in the units of selection debate. *Biological Theory*, *10*(2), 145–155. doi:10.1007/s13752-014-0196-5

COMMENTARIES

The promise and limits of eco-evolutionary studies of human culture

Carlos A. Botero[a], Luke J. Harmon[b], and Quentin Atkinson[c,d]

[a]Department of Biology, Washington University, Saint Louis, MO, USA; [b]Department of Biological Sciences, University of Idaho, Moscow, ID, USA; [c]School of Psychology, University of Auckland, Auckland, New Zealand; [d]Max Planck Institute for the Science of Human History, Jena, Germany

Wilson et al. review past efforts to infuse evolutionary thinking into cultural studies and suggest that an ecosystems approach may be a fruitful way to move forward. We strongly endorse the notion that a thoughtful synthesis of the social and biological sciences can lead to robust and exciting discoveries about human nature. Here we elaborate on this premise and identify some of the opportunities and challenges of this exciting intellectual partnership.

As Wilson et al. point out, the use of evolutionary theory as a tool for generating and testing hypotheses in cultural research has been around for a long time. What then is the novelty of the proposed approach? Two things stand out in our opinion: context and scope. In terms of context, recent developments in evolutionary theory and cultural research have greatly facilitated the synthesis between fields. For example, the use of cognate sets to infer genealogical relationships between languages and the cultures who speak them (Bouckaert et al., 2012; Gray & Atkinson, 2003) has prompted the application of a wide array of modern evolutionary tools, collectively known as phylogenetic comparative methods (hereafter PCM), to cross-cultural research. One benefit of PCM is that they provide historical reconstructions of relationships among groups, thereby enabling tests of

CONTACT Carlos A. Botero cbotero@wustl.edu

explicit models of cultural evolution even in the absence of time-series data. Current applications of PCM in cross-cultural research include ancestral state reconstruction (Jordan, Gray, Greenhill, & Mace, 2009), estimation of rates of change between alternative trait states (Currie, Greenhill, Gray, Hasegawa, & Mace, 2010), estimation of the influence of drivers of diversification rates (Atkinson, Meade, Venditti, Greenhill, & Pagel, 2008), and assessment of evolutionary correlation (Currie et al., 2010). In moving forward, we caution that assumptions of PCM are typically grounded in organismal biology and therefore may not necessarily translate easily to the study of cultural traits. At the most basic level, researchers should consider the extent to which memes and cultural groups behave as their presumed biological counterparts – i.e., genes and species (Boyd, Richerson, Borgerhoff-Mulder, & Durham, 1997; Gray, Greenhill, & Ross, 2007; Mesoudi & Whiten, 2004). Overall, though, the application of PCM to cultural research has the potential to enrich both the social and biological sciences by fostering collaboration and cross-fertilization between scholars with sometimes different views of the processes through which traits can change over time. Grassroots efforts and discussion forums like R-sig-phylo (https://stat.ethz.ch/mailman/listinfo/r-sig-phylo) and phylobabble (http://phylobabble.org/) are already facilitating this dialogue.

In terms of scope, we believe that a cultural ecosystems approach can productively draw from a broad set of promising biological tools that have not typically been combined in cultural studies. Axes of variation studies help us gain general insight into the landscape of human cultural diversity by quantifying variation and testing hypotheses regarding its proximate drivers. A novel contribution of Wilson et al.'s proposal is the explicit recognition that we stand to learn more about human nature when considering simultaneously the history (evolution) of cultural groups, and the way in which these groups interact with each other and their natural settings (ecology). Incidentally, cultural ecosystem studies may benefit as much from the tools of ecology (e.g., niche modeling, landscape genetics, or population dynamics) as from those of evolutionary biology.

Wilson et al. use multilevel selection theory to justify their emphasis in group-level functional organization. Nevertheless, we note that within the framework of this theory, selection on individuals is often expected to outweigh selection on groups (Wilson & Sober, 1994). Thus, it will be important to keep in mind that cultural groups are aggregates of individuals (Richerson & Boyd, 2005) – i.e., Darwinian populations (Godfrey-Smith, 2011) – and that group-level functions may not always drive cultural change. Some interesting unanswered questions that emerge from this realization include: what is the relative importance of group-level selection versus individual-level processes – such as copying biases (Richerson & Boyd, 2005) or the action of group leaders (Matthews, Edmonds, Wildman, & Nunn, 2013) – in shaping the design of cultural traits? How does individual variation within populations give rise to group-level dynamics? Addressing these questions will require more clarity regarding the currency of cultural evolution (Henrich et al., 2005; Richerson & Boyd, 2005). Specifically, biology tends to focus on the principle that selection maximizes the weighted sum of direct and indirect contributions to the next generation (inclusive fitness) but the cultural analog of this metric is currently unclear.

A final point we wish to make relates to Wilson et al.'s call for the establishment of long-term field sites for the study of culture. The value of long-term data sets is unquestionable, particularly for understanding the temporal dynamics of communities. However, we note that such efforts are not entirely new (anthropologists and human behavioral ecologists have maintained sites of this kind for decades). In our opinion, what is perhaps most needed to advance the eco-evolutionary study of human culture is the collection of standardized and open access data. Only through such collaborative efforts will we be able to properly test predictions via systematic comparisons across sites (see Henrich et al., 2005).

To summarize, we welcome the prospect of continued synthesis between the social and biological sciences and wish to convey our excitement about the promise and opportunities that this emerging field is beginning to provide. Overcoming the challenges described above will not be easy, but we are confident that they are not insurmountable and that these efforts will ultimately benefit all of the fields involved. We look forward to a positive and exciting exchange of ideas, and to the many interesting directions that this research program can potentially take.

References

Atkinson, Q. D., Meade, A., Venditti, C., Greenhill, S. J., & Pagel, M. (2008). Languages evolve in punctuational bursts. *Science*, *319*(5863), 588–588.

Bouckaert, R., Lemey, P., Dunn, M., Greenhill, S. J., Alekseyenko, A. V., Drummond, A. J., & Atkinson, Q. D. (2012). Mapping the origins and expansion of the Indo-European language family. *Science*, *337*(6097), 957–960.

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

Currie, T. E., Greenhill, S. J., Gray, R. D., Hasegawa, T., & Mace, R. (2010). Rise and fall of political complexity in island South-East Asia and the Pacific. *Nature*, *467*, 801–804.

Godfrey-Smith, P. (2011). *Darwinian populations and natural selection*. Oxford, UK: Oxford University Press.

Gray, R. D., & Atkinson, Q. D. (2003). Language-tree divergence times support the Anatolian theory of Indo-European origin. *Nature*, *426*(6965), 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.

Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., & Tracer, D. (2005). "Economic man" in cross-cultural perspective: Behavioral experiments in 15 small-scale societies. *Behavioral and Brain Sciences*, *28*(6), 795–855.

Jordan, F. M., Gray, R. D., Greenhill, S. J., & Mace, R. (2009). Matrilocal residence is ancestral in Austronesian societies. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1664), 1957–1964.

Matthews, L. J., Edmonds, J., Wildman, W. J., & Nunn, C. L. (2013). Cultural inheritance or cultural diffusion of religious violence? A quantitative case study of the Radical Reformation. *Religion, Brain & Behavior*, *3*(1), 3–15.

Mesoudi, A., & Whiten, A. (2004). Is human cultural evolution Darwinian? Evidence reviewed from the perspective of the origin of species. *Evolution*, *51*(1), 1–11.

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

Wilson, D. S., & Sober, E. (1994). Reintroducing group selection to the human behavioral sciences. *Behavioral and Brain Sciences*, *17*(4), 585–654.

On the evolution of tightness-looseness in cultural ecosystems

Joshua Conrad Jackson and Michele J. Gelfand

University of Maryland, College Park, MD, USA

In their thought-provoking article, *The Nature of Religious Diversity: A Cultural Ecosystem Approach*, Wilson and co-authors propose a new framework for studying the evolution of culture, termed the "cultural ecosystem approach" and juxtapose it with tightness–looseness theory (Gelfand et al., 2011; Harrington & Gelfand, 2014; Pelto, 1968; Triandis, 1989) to understand how diverse religious cultures evolve. While cultural scientists have increasingly studied the differences between religious systems (see Cohen & Varnum, 2016, for a review), they have seldom considered ecological factors in the evolution of religious groups. Therefore, Wilson and colleagues' integration of tightness–looseness with the ecosystems perspective is an important step in the study of religious as well as secular culture. We use this commentary to discuss similarities and differences between the cultural ecosystem approach and tightness–looseness theory, and how a marriage of the two frameworks further informs the study of cultural evolution.

Similarities between tightness–looseness theory and the cultural ecosystem approach

Wilson and colleagues' analysis suggests a number of similarities between tightness–looseness and the cultural ecosystem approach. Both theories expand upon cross-cultural psychology's focus on

CONTACT Joshua Conrad Jackson jjackso1@umd.edu

value taxonomies and static cultural differences, instead viewing culture as a system of group-level adaptations to environmental demands (see Gelfand & Jackson, 2016; Gelfand et al., 2011; Harrington & Gelfand, 2014). In a recent agent-based model, for example, Roos, Gelfand, Nau, and Lun (2015) were able to capture the emergence of group cooperation as a response to ecological threat.

But even where Wilson and colleagues contrast tightness–looseness and the ecosystem approach, we see similarities. For example, we believe that tightness–looseness theory, like the ecosystem approach, is well suited to study contextual variation within cultures. Indeed, Harrington and Gelfand (2014) were able to predict state-level variation in tightness–looseness by gathering data on rates of ecological threat across the United States. Other studies have shown that within any cultural group, "priming" situational threat affects psychological affordances of tightness. For example, Mu, Gelfand, and Han (in preparation) found that Chinese participants primed with a Japanese territorial threat showed greater behavioral and neural synchrony compared to those in a control condition (see also Roos et al., 2015 on situational activation of tightness). Just as we might find shifting levels of tightness based on resource availability among the Chewong (Wilson et al.), we can see dynamic shifts in tightness-looseness within any cultural group depending on environmental changes.

Furthermore, while the authors debate the convergent validity of tightness–looseness due to its multiple determinates (e.g., societal complexity, ecological threat), we believe that the diverse *multifinal* predictors of tightness–looseness add to the construct's richness while preserving its parsimony. While different ecological challenges may lead to a strengthening of norms, the multilevel signature of tightness–looseness remains largely the same around the world. Regardless of whether it is driven by ecological threat or agricultural complexity, tightness–looseness is experienced as a shift of power from the individual to the culture, which results in changes to individuals' decision-making and belief structures. Across different levels of analysis, tightness is related to more coordination and order, more self-control, yet more ethnocentrism and lower creativity, while looseness is related to more openness and creativity, yet less coordination, order, and self-control (Gelfand et al., 2011; Harrington & Gelfand, 2014; Mu, Kitayama, Han, & Gelfand, 2015). This suggests that while cultures may need to coordinate for different reasons, the result of this coordination is a strengthening of norms that has distinct and predictable psychological and social correlates. In light of this evidence, we believe the diverse predictors of tightness make the construct stronger, showing that a range of ecological circumstances can converge on the same psychological phenomenon.

Complementary views on cultural diversity

Despite the similarities between tightness–looseness and the ecosystem approach, the two frameworks are also complementary, and in combination they can address questions that have not yet been examined by either approach. One exciting frontier is to examine the factors that lead to a selection advantage for tight versus loose groups that co-exist in a community. Tightness–looseness theory would predict that ecological pressures produce fluctuations in the evolutionary fitness of competing tight or loose cultural groups. In the wake of a major virus or a terrorist threat, for instance, tighter communities may grow to dominate the larger culture, resulting in a more centralized power structure and hostility toward religious and ethnic minorities. In contrast, low threat and high mobility and prosperity likely facilitate the growth of loose cultural groups. Environments of moderate threat might even facilitate the simultaneous thriving of both tight and loose cultures, as each fills a respective cultural niche (i.e., loose groups thrive through innovation while tight groups thrive through regulation). Within cultural field sites (Wilson, 2013), researchers are well equipped to address these issues by studying the strength of cultural norms with respect to both changing ecological conditions and the rise and fall of competing communities through various methods including self-report, behavioral observation, and measurement of fluctuating ecological factors (e.g., warfare, climate, prevalence of infectious disease, and mobility).

We also encourage future research to model catastrophic, non-linear cultural shifts that occur between cultures of extreme tightness and looseness within an ecosystem. Recent work (Harrington, Boski, & Gelfand, 2015) has shown that both extremely tight and extremely loose groups are politically unstable and have high rates of depression and suicide. We might find that these extremes produce a pattern of dynamic oscillating shifts, wherein contexts that are either radically tight or loose will be succeeded by their polar opposite. One familiar example of such a swing is America's transition from the 1950s (known to many as the decade of conformity) to the swinging 1960s. This dynamic can also be used to understand the recent Arab Spring movement, wherein progressive movements toppled a number of North African autocracies, only to be supplanted by similarly despotic governments. In this case, selection pressures took the form of public opinion, which at first favored progressive reform in the wake of oppression, but then favored tight control, as newly formed democratic governments were unable to establish order (see Nowak, Gelfand, Borkowski, & Kruglanski, forthcoming). Both examples demonstrate that an emerging culture's niche is significantly influenced by the preceding generation's tightness–looseness alongside environmental pressures.

Tightness–looseness could even be studied within a single cultural system by analyzing norm strength across different domains (religious norms, sexual norms, table manners, etc.). In their article, Wilson and colleagues point out that, while biologists study evolution on a trait-by-trait basis, they also recognize that genes are connected through interdependent systems. We similarly propose that norm strength is largely systemic, and tends to covary across domains. The longitudinal study of this covariance, however, is a topic worthy of study. Norms may initially strengthen in domains that are critical for cultural coordination. Fidelity norms in Bedouin cultures, for example, may have helped prevent domestic disputes within strongly bonded communities, while sanitation norms in Singapore likely helped the country manage intense population density. Over time, however, normative tightness tends to "spill over" into less functional domains as people bestow symbolic importance on following normative behavior. We may be confused by Singapore's prohibition of flying kites on many public beaches, but this "non-adaptive byproduct" (Wilson et al.) has likely derived from more functional norms relating to public cleanliness and public safety.

Each of these future directions challenges our field to move beyond typical one-shot cross-cultural experiments and linear theoretical models. We propose that combining tightness–looseness theory with the cultural ecosystem approach is an ideal intellectual marriage for helping the study of culture "evolve" as a discipline. In this sense, the future is bright (and certainly not drab) for those who wish to understand the nature of religious diversity, and cultural evolution in general.

References

Cohen, M., & Varnum, M. E. (2016). Beyond east vs. west: Social class, region, and religion as forms of culture. *Current Opinions in Psychology, 8*, 5–9.

Gelfand, M. J., & Jackson, J. C. (2016). From one mind to many: The emerging science of cultural norms. *Current Opinions in Psychology, 8*, 175–181.

Gelfand, M. J., Raver, J. L., Nishii, L., Leslie, L. M., Lun, J., Lim, B. C., … Yamaguchi, S. (2011). Differences between tight and loose cultures: A 33-nation study. *Science*, *332*(6033), 1100–1104.

Harrington, J. R., Boski, P., & Gelfand, M. J. (2015). Culture and national well-being: Should societies emphasize freedom or constraint? *PloS One*, *10*(6), e0127173. doi:10.1371/journal.pone.0127173.

Harrington, J. R., & Gelfand, M. J. (2014). Tightness–looseness across the 50 united states. *Proceedings of the National Academy of Sciences*, *111*(22), 7990–7995.

Mu, Y., Han, S., & Gelfand, M. J. (2015). Threat, brain synchrony, and coordination in human groups. *Manuscript in Preparation*.

Mu, Y., Kitayama, S., Han, S., & Gelfand, M. J. (2015). How culture gets embrained: Cultural differences in event-related potentials of social norm violations. *Proceedings of the National Academy of Sciences*, *112*(50), 15348–15353.

Nowak, A., Gelfand, M. J., Borkowski, W., & Kruglanski, A. W. (forthcoming). When autocracy fails. In M. Moaddel & M. J. Gelfand (Eds.), *The Arab spring and changes in values and political actions in the middle east and north Africa: Exploration of visions and perspectives*. New York, NY: Oxford University Press.

Pelto, P. J. (1968). The differences between "tight" and "loose" societies. *Society, 5*(5), 37–40.

Roos, P., Gelfand, M., Nau, D., & Lun, J. (2015). Societal threat and cultural variation in the strength of social norms: An evolutionary basis. *Organizational Behavior and Human Decision Processes*, *129*, 14–23.
Triandis, H. C. (1989). The self and social behavior in differing cultural contexts. *Psychological Review*, *96*(3), 506–520.
Wilson, D. S. (2013). Human cultures are primarily adaptive at the group level. *Cliodynamics: The Journal of Theoretical and Mathematical History*, *4*(1), 103–138.

Selecting field sites for the cultural ecosystems approach

Kathryn A. Johnson

Department of Psychology, Arizona State University, Tempe, AZ, USA

The religious landscape is constantly changing, and Wilson and his colleagues challenge social scientists to take a more expansive and comprehensive approach to understanding the evolution of religious culture. Rather than focusing on change within a single religious group or in regard to a single variable across cultures, the authors suggest that social scientists ought to study the interaction of multiple groups, across a number of axes of variation, as a dynamic system located in a particular environment. Investigating how multiple groups interact and, in turn, shape each group's beliefs, social norms, rituals, values, and/or community structures in certain environments seems to be a promising research strategy.

One can quickly think of several religious cultural ecosystems that would be interesting candidates for field sites. Sedona is a city of approximately 10,000 people situated among the Red Rocks and pine forests of Oak Creek Canyon in northern Arizona. With its rich history of American Indian, Mexican, and pioneer influences, Sedona stands out today as an important site for New Age pilgrimages. National surveys suggest that religion in the US is becoming increasingly syncretic (Pew Forum on Religion & Public Life, 2009), and Sedona would be an excellent field site to gain a better understanding of how the interaction of various cultural groups may have facilitated the development of this relatively new face of mystical spirituality. Many other interesting field sites come to mind.

Much progress could be made by gathering teams of anthropologists, historians, sociologists, biologists, psychologists, linguists, theologians, and philosophers together at each site to create a cumulative resource, as the authors suggest, for understanding why humans in that locale think, feel, and behave the way they do. However, the biggest challenge, in my view, to the cultural ecosystems approach will be to create and manage the multi-disciplinary teams whose members will, no doubt, have different and sometimes conflicting questions, methodologies, data, and research agendas.

Just as biological ecosystems have parallels with religious ecosystems, religious ecosystems have parallels with academic ecosystems. Thus, Binghamton University itself (or any university) may also be a fascinating field site for the cultural ecosystems approach. Here we have scholars from all disciplines located in a particular locale, sharing a commitment to educate a common student body; governed by the same president, provost, and board; with access to the same library, arts, and sport facilities; and all sharing (at least to some degree) a passion for understanding how the world works. Yet, for the most part, the members of the individual disciplines that comprise the research team will certainly also have disparate literatures, utilize different research databases, publish in separate journals, employ diverse methodologies, and have unique intellectual histories and core theoretical perspectives. There may even be epistemological differences about what can be known.

Hopefully, the authors will not overlook the opportunity to examine their *own* cultural ecosystem as a field site and eventually publish their recommended best practices for multi-disciplinary research. It will be especially helpful for future research teams if the authors will convey: (1) how

CONTACT Kathryn A. Johnson kathryn.a.johnson@asu.edu

the project team was organized and the degree to which it was structured (tight vs. loose); (2) how project resources were distributed; (3) whether all academic disciplines were equally represented or whether there was a dominant discipline; (4) how the authors handled the merger of ethnographic data and quantitative analyses; (5) whether novel or unexpected research questions arose through interactions between members of the various disciplines; (6) whether new social norms emerged; (7) how strategies for conflict resolution were developed; and (8) to what extent change occurred at the individual vs. the group (e.g., departmental) level.

Nearly all researchers see very clearly the benefits of multi-disciplinary research, but are also aware of the challenges. Thus, it may be most interesting to learn how the EvoS program and the cultural ecosystem of Binghamton University evolved during the course of this research. Ideally, the authors will share not only what was learned in Binghamton but also look introspectively and eventually share what was learned at Binghamton *University*: how the interactions of the researchers transformed their own group(s) and, more broadly, how what they learned can be used to impact the cultural ecosystem of the academy.

Reference

Pew Forum on Religion & Public Life. (2009). Many Americans mix multiple faiths: Eastern, New Age beliefs widespread. Retrieved October 18, 2010, from http://pewforum.org/Other-Beliefs-and-Practices/Many-Americans-Mix-Multiple-Faiths.aspx#1

Don't worry, be funded!

Craig T. Palmer

Department of Anthropology, University of Missouri, Columbia, MO, USA

Wilson et al. provide great news: "the current status of cultural evolutionary theory and evolutionary religious studies, both of which have become centered on group-level functional organization," has become so popular that projects using this approach may obtain funding from no less of a source than the National Science Foundation! Further, this "group-level functional organization" model is based on two very simple assertions. First, both secular and religious human groups are functionally organized "units." Second, these functionally organized units, or "entities" are the analog of biological species and form part of a cultural ecosystem. An approach that is both so simple, and asserted to be so similar to the concepts used in the better funded biological sciences, is indeed great news to researchers searching for funding. However, these benefits can be reaped *if and only if* researchers knowingly or unknowingly overlook some troubling discrepancies between the "illusory conceptual abstractions" (Murdock, 1971, p. 19) of the group-level functional organization model, and "the very real phenomena of individuals interacting with one another and with their natural environment" (Murdock, 1971).

The first indication of discrepancies between the model and identifiable human behavior are the qualifiers added to the assertions that form the basis of the model. For example, the addition of the qualifier "*(for the most part)*," added to the claim that "human groups are functionally organized units," is necessary because without it the claim is clearly false. A "functionally organized unit" describes a category of people with clear boundaries that establish exactly who is and is not a member of the unit, and within which all members of the unit interact together toward a common goal. In stark contrast, even in the categories of humans where *some* of the members interact in a way

CONTACT Craig T. Palmer palmerct@missouri.edu

that qualifies as functionally organized, many people may never interact in any way with many of the other members of that category, much less in a way that could be described as functionally organized. This is true of even the example used in the article: the members of ethnic minorities who have migrated to new areas and become middleman merchants. Some of the members of such a category may interact in a way that can be described as functionally organized, but even these members may never interact with all of the members of the same category living in the same city, and will certainly never have any interaction with many members of the same category living in different nations. Adding the qualifier "for the most part" serves to give the false impression that this discrepancy between the model and identifiable human behavior is nothing to worry about.

Qualifiers are also used to assuage concern over the admission that "[i]t can be challenging to identify the salient cultural groupings … .". The authors provide the reassurance that this challenge is not really a problem because it can be overcome "in many cases" where "the relevant social identities are clear-cut." This diverts attention from the untold number of cases where the challenge cannot be overcome, as well as from the fact that even in the example of middleman merchants, where supposedly "the salient groups are easy to identify," the authors have to add "at least to a crude approximation."

The necessity of including qualifiers is also found in the further claim that human groups are "the analog of biological species," and thereby multiple human groups in an area form an ecosystem. An obvious problem with this analogy is that members of a biological species cannot become members of other species, while individual humans "can participate in more than one functional grouping" and there can even be "a high rate of flow of individuals between groups." Another problem with this argument is that it assumes that species necessarily form functionally organized units. In reality the members of most species are not functionally organized into a unit, and this may be true even of the members of a species living in the same location. Attention is deftly drawn away from the failure of both human groups and biological species to form the functionally organized entities required by the model, by packaging this fact as if it was evidence that supported the model by demonstrating the similarity between human groups and species: "It can be challenging to identify the salient cultural groupings (as it can for biological species), … ."

One final discrepancy between the model and what can actually be identified is the claim that "belief in supra-empirical agents" can be used to distinguish a religious group from a secular group. The problem concerns how to identify such a belief. It clearly is not a matter of just asking people if they believe in God, as non-believers can answer this question "yes" and believers can answer it by saying "no." Church attendance also fails to separate the believers from the non-believers, as the article acknowledges. To convince me that someone has found a solution to the problem of how to identify belief in supra-empirical agents, all the authors have to do is tell me whether or not I believe in God, and the basis of that determination. Until then, those researchers wishing to avoid explaining human behavior with variables that cannot be identified might consider defining religion, not by unverifiable beliefs, but by an identifiable form of talk (i.e., the communicated acceptance of a supernatural claim; see Steadman & Palmer, 2008).

In light of both the current popularity of the "group-level functional organization" model, and the discrepancies between the model and identifiable human behavior, researchers studying religious behavior from an evolutionary perspective are faced with a choice. They can reject the model in favor of less popular models that better coincide with human behavior (Steadman & Palmer, 2008), or they can choose to not worry about such discrepancies in order to be funded.

References

Murdock, G. (1971). Anthropology's mythology. *Journal of the Royal Anthropological Society, 1971* (Huxley Memorial Lecture), 17–21.

Steadman, L. B., & Palmer, C. T. (2008). *The supernatural and natural selection: The evolution of religion*. Boulder, CO: Paradigm.

An evolutionary study of culture that is actually evolutionary

Robert A. Paul

Department of Anthropology, Emory University, Atlanta, GA, USA

For most of its history, the attempt to subject culture to evolutionary principles has been based on a Spencerian rather than a Darwinian framework. Herbert Spencer had argued that societies (consistent with the trend in the rest of the universe) changed in the direction of growing more populous and more internally complex over time. While it is possible to claim that this is empirically the case, as human groups have indeed changed from the small unsegmented groups that were presumably the primordial societies into the vast nation-states of today, there is no system of selection among variants in this model. The successors of Morgan and Tylor, such as Steward (1955), Sahlins and Service (1960), and Johnson and Earle (2000), refined the idea of a series of stages through which human societies develop in an overall unilineal direction, implying a trend of the sort Spencer envisaged; but they did so largely without proposing and defending a mechanism of selection that would produce this historical trajectory.

Only in the 1970s did a more Darwinian approach to the study of sociocultural groups emerge, after many decades during which the anti-evolutionism of Franz Boas's followers prevailed in anthropology. When it did so, with the appearance of sociobiology, evolutionary psychology, and behavioral ecology, it borrowed the models of population genetics in studying the rates of rise and declines of numbers of constituent individuals over time, but using the transmission across generations of cultural ideas and techniques rather than genes. The assumption upon which this approach is based is that of methodological individualism, which holds that just as species are best seen as populations of individual phenotypes that interbreed, so too "societies" and "cultures" do not really exist as entities in themselves, but are abstractions based on the summed behavior of the similarly enculturated individuals that constitute them. The results have therefore been limited, since this assumption is only partial at best.

David Sloan Wilson, a lone voice in the biological wilderness, has argued for the proposition that groups should be interpreted not just as collections of individuals but as entities in themselves. Groups are systems with their own internal organization, not reducible to the level of individual members. Like individual organisms, groups are subject to selection factors at their own level. This idea is now beginning to take hold, and, as this present article suggests, might make possible a truly Darwinian evolutionary approach to the study of cultures – one that, for the reasons I have sketched above, has hardly existed until now.

A close examination of supposedly evolutionary accounts of cultural factors usually reveals that there is nothing specifically evolutionary about them. Thus, Landa's analysis (2008) of merchant middlemen cited by Wilson et al. in the present article, while probably valid, could just as easily have been written by a social theorist who had never heard of evolution: that there is a social niche that encourages tight cohesion does not propose any mechanism of selection. A great classic in the ecological study of religion such as Rappaport's *Pigs for the Ancestors* (1968) presents a convincing case that the Tsembaga ritual cycle is a homeostatic system balancing factors of war or peace with neighbors, the carrying capacity of the land, the rise of unsustainable pig populations, and so on; but the only way this is "evolutionary" is by the tautological reasoning that it exists so it must be adaptive, and if it is adaptive, it must have been selected. No actual demonstration that selection has occurred, or how or when, is proposed, much less supported.

For an analysis of selection at the level of sociocultural systems, including religions, to qualify as evolutionary, the statistical analysis it uses must not be of individuals comprising the groups, as has been the long-standing practice, but rather of populations of groups competing in a Darwinian

CONTACT Robert A. Paul rpaul@emory.edu

process among themselves. Such an analysis would have to test hypotheses about why and how groups as such survive or do not survive. The question of what it would even mean for groups to "reproduce" themselves would have to be addressed: of course they can reproduce themselves over the generational time of constituent members, but does this mean that the groups themselves reproduce, or merely sustain themselves? And if Darwinian processes depend on differential rates of reproduction, then what is the operant selection mechanism if there is no "reproduction?"

The difficulties confronting such an analysis continue with the fact that while individuals are numerous, and comparable insofar as they reproduce, and can be counted, the same cannot be said so easily of groups. Does it make any sense to compare the Tsembaga ritual system with that of the Catholic Church, or of any particular Catholic church?

This is where I think the great value of Wilson et al.'s project lies, though of course it is only conceptual so far and has not been realized. If there are 200 well-documented individual churches in and around Binghamton, each with a well-documented history, and each belonging for the most part to just a few closely related Christian denominational "lineages," then one does in fact have a sufficient "n," sufficient longitudinal data, and sufficient comparability of units to make a controlled comparison possible. This comparison is one in which the rise and decline of individual groups can be correlated with both external "ecological" factors (not so much in the natural realm as in the realms of political, demographic, economic, technological, and similar factors) as well as with internal characteristics such as the tightness/ looseness axis discussed by Wilson et al. Under such circumstances, selection processes can in principle be hypothesized and tested.

It remains to be seen whether this project will actually materialize; if it does, it may actually come close to applying Darwinian evolutionary ideas to culture. As for whether the National Science Foundation will fund several ambitious projects like this, however – I wouldn't hold my breath.

References

Johnson, A., & Earle, T. (2000). *The evolution of human societies: From foraging group to agrarian state*. (2nd ed.). Stanford: Stanford University Press.

Landa, J.T. (2008). The bioeconomics of homogenous middleman groups as adaptive units: theory and empirical evidence viewed from a group selection framework. *Journal of Bioeconomics*, *10*, 259–278.

Rappaport, R.A. (1968). *Pigs for the ancestors: Ritua; in the ecology of a new Guinea people*. New Haven: Yale University Press.

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

Steward, J. (1955). *Theory of cultural change*. Urbana: University of Illinois Press.

Archaeology and the study of cultural ecosystems

Peter Peregrine

Lawrence University, Appleton, WI, USA; Santa Fe Institute, Santa Fe, NM, USA

Wilson and colleagues have provided an important and thought-provoking discussion of how the cultural ecosystem approach might inform the study of religious diversity. In doing so they also critically examine the "axis" approach to cross-cultural research and make a case for developing field sites for implementing studies of cultural ecosystems. They discuss the work of not only cultural anthropologists, but evolutionary biologists, psychologists, sociologists, and macrohistorians. A surprising oversight is their failure to discuss the work of archaeologists, who have long employed a cultural ecosystem framework, who have implemented and critically assessed "axis" approaches to

CONTACT Peter Peregrine Peter.N.Peregrine@Lawrence.edu

cross-cultural research, and who have developed a number of important field sites that continue to be the locus of research on the evolution and ongoing processes of cultural ecosystems.

Archaeology has long been a discipline rooted in evolution, although that root was not completely accepted by the field until the 1960s. Before then archaeologists primarily concerned themselves with culture-history; that is, establishing the sequence (or history) of cultures that had inhabited a given region over time (e.g., Phillips & Willey, 1953). The focus on culture-history rather than cultural evolution before the 1960s was a product of several factors, including a rudimentary ecosystem concept, a paucity of evolutionary theory focused on behavior and groups (as opposed to the physical characteristics of individuals), and the lack of dating techniques that could readily establish cultural chronologies. Once these had developed, archaeology quickly turned to examining evolutionary processes, and particularly the evolution of agriculture and centralized political systems.

Even the earliest research on the evolution of agriculture can be viewed as an application of the cultural ecosystem approach. Agriculture, both in the Levant and Mesoamerica (the loci of the first research on agricultural evolution), was understood to have evolved in a complex ecosystem in which human exploitation of the environment led to environmental changes that fostered the emergence of agriculture (which we would today call environmental engineering or niche construction). The environment included neighboring social groups with whom competition over resources provided a context for innovation that led to sedentarism and agricultural intensification. The long history of interactions between plants, people, and neighbors was seen as crucial to understanding the evolution of agriculture (e.g., Braidwood, 1960; Flannery, 1973). While some of this work seems rudimentary today, within the context of evolutionary theory as it existed at the time this early work on the evolution of agriculture fit well within what Wilson and colleagues argue should be a central focus on cultural ecosystems. And that work has only become more sophisticated over time.

Similarly, early work on the evolution of centralized polities examined complex ecosystemic relationships between people, places, and resources. It was the balancing of intensive resource extraction surrounding sedentary communities regularly interacting with one another to access non-local resources that was seen to be the processes underlying political centralization (e.g. Hole, Flannery, & Neely, 1969). Viewed from today, these early efforts at implementing a cultural ecosystem approach were again rudimentary, but they were effective, and developed into ongoing research crossing the lines between evolutionary biology, genetics, anthropology, psychology, and complex systems theory – precisely the broad interdisciplinary approach that Wilson and colleagues present in their article. Yet they unfortunately overlook this work.

More recently the "axis" approach to cross-cultural research has found traction as a useful analytical and perhaps explanatory device in archaeological research. As a developer of this approach, I will limit my discussion to one aspect in order to avoid the perception of self-promotion. Wilson and colleagues recognize the value of the "axis" approach, but identify important problems with it and urge caution in its implementation. This has been the case in archaeology from the beginning, and important work within the comparative school of archaeology has been aimed at addressing the potential pitfalls of the "axis" approach (e.g., Peregrine, 2012).

Finally, Wilson and colleagues make an appeal for the development of long-term research sites for the study of cultural ecosystems. It is their most significant oversight to have not discussed the seminal archaeological projects that over decades of sustained work have developed precisely these types of field sites – sites where research is ongoing and where the greatest theoretical innovations are being made. For example, the Four Corners area of the southwestern United States has been the focus of sustained and (mostly) coordinated research for at least a half-century. Large "salvage" projects undertaken to recover archaeological materials before construction of dams, highways, and communities have been incorporated into ongoing scholarly research, large-scale yet detailed environmental reconstruction, and theoretically focused analysis and modeling to create impressive explorations of cultural ecosystems (e.g., Varien, Ortman, Kohler, Glowacki, & Johnson, 2007). While none of these (to my knowledge) has focused explicitly on the nature of religious diversity, they do illustrate the fact that archaeology has long engaged in efforts that parallel those promoted

by Wilson and colleagues. Indeed, I suggest that archaeology provides a model that empirically demonstrates the importance of the approach they promote, and it is an unfortunate oversight that archaeology was not discussed in this important article.

References

Braidwood, R. J. (1960). The agricultural revolution. *Scientific American 203* (September), 130–148.
Flannery, K. V. (1973). The origins of agriculture. *Annual Review of Anthropology*, *2*, 271–310.
Hole, F., Flannery, K. V., & Neely, J. A. (1969). *Prehistory and human ecology of the Deh Luran plain. Memoirs of the Museum of Anthropology, No. 1*. Ann Arbor: University of Michigan.
Peregrine, P. N. (2012). Power and legitimation: Political strategies, typology, and cultural evolution. In M. E. Smith (Ed.), *Comparative archaeology of complex societies* (pp. 165–191). New York: Cambridge University Press.
Phillips, P., & Willey, G. R. (1953). Method and theory in American archaeology. *American Anthropologist*, *55*, 615–633.
Varien, M. D., Ortman, S., Kohler, T., Glowacki, D., & Johnson, C. D. (2007). Historical ecology in the Mesa Verde region: Results from the village ecodynamics project. *American Antiquity*, *72*, 273–299.

Cultural and religious diversity

Harry C. Triandis

Psychology Department, University of Illinois, Urbana, IL, USA

This is an excellent contribution that integrates a diverse literature and suggests many avenues for further research. It makes a convincing case for the cultural ecosystem approach. The article might have been even more convincing if the authors had listed explicitly half a dozen testable hypotheses derived from the cultural ecosystem approach. The authors make a very good case for parallelisms among religious, cultural, and biological diversity. Consequently this shows the desirability of establishing field sites that focus on the cultural ecosystem.

In the section that presents various axes, the authors might add two more axes: cultural simplicity–complexity and the vertical–horizontal axis. In simple cultures, such as among hunters and gatherers, the theology (e.g., Shamanism) tends to be simple. In complex cultures the theology is often complex (e.g., discussions of whether or not the Holy Spirit is of the same or different substance as other deities). The development of writing probably increased the complexity of cognitive systems, including religious beliefs. An important factor, when writing is available, is that theological debates can occur over generations, thus increasing the complexity of theologies. Cultural and cognitive complexity tend to be correlated. Cognitive simplicity is associated with fundamentalism, while cognitive complexity is associated with tolerance (Hall & Crisp, 2005). An excellent example of the link between cognitive simplicity and intolerance is provided by the Documentation Center of the Nazi Period in Nürenberg, Germany. The Nazi ideology reflected cognitive simplicity. In this Center one can read widely used statements of the Nazi period, such as "Mein Führer, you are Germany," "We are ready to carry Germany to new glories," "One people, one Führer, one Reich – Germany." The Nazis provided perhaps the most extreme example of intolerance in world history.

A related hypothesis is that polytheism is more cognitively complex than monotheism, and hence the observation that the most peaceful period in history, from the point of view of religious wars, was during the Roman Empire (Gibbon, 1963).

CONTACT Harry C. Triandis triandis@illinois.edu

The vertical–horizontal axis also appears useful. For example, the Catholic Church is more vertical (hierarchical) than many Protestant Churches. The Shiah are more vertical than the Sunnis. In vertical cultures the authorities are often coercive, thus the deities are often very active, in support of the authorities. In horizontal cultures the deities are seen as being of almost similar nature (substance) as humans.

The utility of each axis might be estimated by the number of hypotheses that are readily generated when using the axis. The simplicity–complexity axis generates relatively few hypotheses. The vertical–horizontal axis does a little bit better. But the tightness–looseness axis suggests many hypotheses:

(1) In tight cultures the gods will be more punishing for deviations from established norms.
(2) In tight cultures there will be more rules, and more punishment for deviations from rules. For example, the Taliban has an enormous number of rules (one is not allowed to fly kites, listen to music, watch television, and women are not allowed to walk in the street without a male relative, etc.). Punishment is often in the form of execution.
(3) The tighter the culture the more elaborate the rituals of the religion. For example, the ritual associated with the hajj is elaborate: believers must be clean, should have cut their hair and nails, should not have had sex, and should put on their white robes no less than 10 miles before they reach Mecca. Women should be totally covered. The ritual requires circling the Ka'ba seven times. Ideally the pilgrims should kiss or at least touch the stone. At a given moment they are supposed to say, speaking to God, "I am present and awaiting orders." After that, they are supposed to run seven times between the hills of Safâ and Marva. They are then supposed to walk to Arafa, which is a few hours' walk from Mecca, where they wait until sunset, "before the eyes of God." Upon returning from Arafa they must collect 49 stones which they must throw at a monument in the city of Minã, recalling the stoning of the devil by Ismael. (Incidentally, it is at this point where several hundred pilgrims died in February 2004, when they were trampled to death.) Finally, on the tenth day of the twelfth month they are supposed to sacrifice an animal remembering the sacrifice of Abraham (Jannoulatos, 1975, pp. 184–185).
(4) The tighter the culture the more likely it is that the sacred books of its religion will be seen as literally correct.
(5) The tighter the culture the more likely it is that its sacred books are pronouncements of a supernatural entity.
(6) The tighter the culture the more likely it is that the deities will severely punish non-conformity.
(7) The tighter the culture the more likely it will be that the deities observe every move of individuals.
(8) The tighter the culture the more likely it is that the religious authorities will control every action of individuals.
(9) The tighter the culture the more likely it is that the deities will pay attention to what people do rather than to what people believe.
(10) Tightness is related to religiosity according to Gelfand et al. (2011).

Thus the authors are correct in identifying the tightness–looseness axis as especially relevant to religion. There are many kinds of tightness and one of them is the homogeneity of beliefs, attitudes, and values. Uz (2015) developed three indices of homogeneity from data from 68 societies. She found the most homogeneity in Bangladesh, Egypt, Indonesia, Jordan, Morocco, and Pakistan. In non-Muslim countries homogeneity was lower.

In short, this is a valuable contribution showing the utility of the cultural ecosystem approach, the parallelism of religious, biological, and cultural diversity, and the need to establish field sites that explore cultural and religious diversity.

References

Gelfand, M. J., Raver, J. L., Nishii, L., Leslie, L. M., Lun, J., Lim, B. C., … Yamaguchi, S. (2011). Differences between tight and loose cultures: A 33-nation study. *Science*, *332*, 1100–1104.

Gibbon, E. (1963). *The decline and fall of the Roman empire*. New York: Dell Publishing.

Hall, N. R., & Crisp, R. J. (2005). Considering multiple criteria for social categorization can reduce intergroup bias. *Personality and Social Psychology Bulletin*, *31*, 1345–1444.

Jannoulatos, A. (1975, 11th printing in 2001) *Islam*. Athens: Porefthendes.

Uz, I. (2015). The index of cultural tightness and looseness among 68 countries. *Journal of Cross-Cultural Psychology*, *46*, 319–335.

An ecosystem approach to explaining religious diversity: why, how, and what?

Bram Tucker

Department of Anthropology, University of Georgia, Athens, GA, USA

In the target article Wilson and colleagues offer a general theoretical framework meant to advance our understanding of the adaptive nature of religion beyond specific cases, functional adaptations, synchronic snapshots, and unidimensional axes. Their framework extends focus to an ecosystem scale, where religious communities are "functionally organized units" that cooperate, compete, and colonize niches just as species do, resulting in regional and global diachronic fabrics of belief and practice. The authors' agenda is a classic one within anthropology, to explain cultural diversity, and the central problem their framework addresses is equally classic, to investigate to what degree cultural diversity and similarity result from common behavioral solutions to ecological challenges versus shared traditions of meaning and belief. Their ecological approach is a logical extension of evolutionary theories of religion based on multi-level selection.

I appreciate the authors' courage to think large, their caution to acknowledge cultural history and context-sensitivity, and their enthusiasm to connect evolutionary and socio-cultural theories and practitioners. The result is a fascinating theoretical synthesis. I can imagine the framework leading to fruitful inquiry. Yet I am left with three rather basic questions about the approach they offer.

Why?

It is unclear what research questions the framework is meant to address. Is the framework intended to explain the origin and spread of religious traditions, or perhaps the forms and functions of different norms? Or more specific hypotheses inspired by these broad inquiries? What is gained intellectually by labeling religions loose or tight, or individualist versus collectivist? It is also not clear what questions motivate the Binghamton, NY study.

Systems explanations are inherently complex, and thus costly to conduct due to high data requirements, and challenging to analyze (Smith, 1984; Starfield & Bleloch, 1986). Complex models also tend to sacrifice generality in favor of realism or precision (Levins, 1966). It is difficult to judge whether a complex framework is justified over a simpler and cheaper framework without knowing the questions the researchers are trying to answer.

How?

It is not clear how one embarks on the cultural ecosystem trajectory they propose. The authors identify many tricky issues, including identifying the fitness-enhancing properties of functionally

CONTACT Bram Tucker bramtuck@uga.edu

organized units and the proper scale at which to study them, the diverse selection pressures that may produce similar norms, whether norms are optimized separately versus as larger chunks of culture, and dynamic historical interactions. There is also the problem of sorting function from phylogeny, an issue complicated by the fact that cultural traits persist that are neutral and maladaptive. These are all problems that have faced cultural evolutionary theory since its inception, and there is not wide consensus on how to handle many of these issues. It would be useful to know how the authors envision overcoming them.

What?

It is unclear to me both (a) whether the proposed framework is about religion or culture more generally, and (b) whether the framework forces "religions" into greater commensurability than they actually share by focusing on functional social units and norms rather than the ontological aspects of religion. Another way of saying this is that there are non-religious aspects of culture that involve functionally organized social units and social norms, most obviously kinship; and there are aspects of religion that do not involve functionally organized units and social norms, most obviously causality and meaning.

To follow the example of kinship, it is easy to imagine a group of people occupying Landa's (2008) middleman niche who solve coordination and trust issues through familial norms rather than religious ones; organized crime families come to mind. Belief in supernatural forces is part of what unifies families, including unity with ancestors and social continuity beyond death, but mob families are hardly a "religious" phenomenon. It seems that a religious ecosystem must include a similar number of functionally equivalent non-religious organized social units.

Bloch (2008) has argued that religion is "nothing special," by which he means that it is embedded within cultural cognition more generally, part of the human ability to imagine "other worlds" which forms the basis of most social institutions, including kinship. He argues that supernatural beliefs become "religion" when they are institutionalized by states to fulfill state goals; religions spread as state influence spreads and religions may linger after state influence wanes. Thus it may be misleading to contrast Catholicism to Chewong "cosmo-rules" (to borrow Howell's phrase; Howell, 2012), as both are slightly different domains within these two cultures.

Norms are a convenient research tool because they seem to offer a vocabulary of discrete social rules with clear phenotypic effects that lend themselves to cross-cultural comparison. One religion may taboo pork while another taboos beef, and we can test how these norms reinforce cooperation or reduce the spread of zoonotic disease. But it is a mistake to say that religions or cultures *are* collections of norms. Culture and religion are also patterns of mental representations that people carry in their heads and apply to understand the world around them. Meanings such as the symbolic uncleanness of pork or purity of cattle are more than just "non-adaptive byproducts," more than excuses for behavioral rules. Because they influence how people perceive basic categories of matter and relationships and cause-and-effect interactions, the content of cultural knowledge is likely to have a huge effect on people's judgment of the value of options and thus on their behavior, also with phenotypic outcomes. If norms offer a vocabulary of rules, meaning (the ontological stuff of cultural knowledge) is the grammar that determines whether the vocabulary is even important. "Tightness" or "collectivism" may mean something qualitatively different for different peoples, or they may have no relevance all.

References

Bloch, M. (2008). Why religion is nothing special but is central. *Philosophical Transaction of the Royal Society B*, *363*, 2055–2061. doi:10.1098/rstb.2008.0007

Howell, S. (2012). Knowledge, morality, and causality in a 'luckless' society: The case of the Chewong in the Malaysian rain forest. *Social Analysis*, *56*, 133–147.

Landa, J.T. (2008). The bioeconomics of homogenous middleman groups as adaptive units: Theory and empirical evidence viewed from a group selection framework. *Journal of Bioeconomics*, *10*, 259–278.

Levins, R. (1966). The strategy of model building in population biology. *American Scientist*, *54*, 421–431.
Smith, E.A. (1984). Anthropology, evolutionary ecology, and the explanatory limitations of the ecosystem concept. In E. Moran (Ed.), *The ecosystem concept in anthropology* (pp. 51–95). Boulder, CO: Westview Press.
Starfield, A.M., & Bleloch, A.L. (1986). *Building models for conservation and wildlife management*. New York: MacMillan Publishing Company.

Limits of analogy: are religions metaphoric species, individuals, or organs?

David Zeitlyn

School of Anthropology and Museum Ethnography, Institute of Social and Cultural Anthropology, Oxford, UK

I am deeply sympathetic to the ambitions of the authors (and hugely supportive of the idea of collaborative field sites). The domain in which they are working is fraught with contention and with linguistic traps, many of which they have evaded but, I fear, not all.

Let me attempt to unpick one set of confusions which I think needs further consideration since it has implications for the explanatory style being used. It may well be that the authors have thought through the following points but the article leaves this unclear.

The core parallel they take as their starting point is between biological and cultural evolution. In biology an ecological system contains many different species each struggling to survive. Cultural evolution takes place as different human groups coexist, possibly compete, but certainly change across time.

The summary statement about biological evolution contains a metaphor since species do not struggle; the individual members that comprise them do. Evolution takes place across generations and with hindsight we can identify that phenomena such as extinction and speciation have occurred. Constituent features of the organisms change over time and this is how things like organs can been said to have evolved.

When we turn to establishing parallels between biological and cultural evolution, we need to be hyper-alert to the terms of the parallel and to any traps that may be contained. So I think it is fairly clear that Wilson et al. see a parallel between biological species and "cultural groups." I am using scare quotes because there is a crucial difference (in my opinion) between a cultural group in the sense of a national or ethnic group (a single society) and a cultural group as a constituent grouping of one or more of these: think of football supporters or the members of a religious confession. We could talk of these latter sub-groups as cultural groups within Cultural Groups. Another metaphor which goes back to Durkheim is to think of them as analogous to the organs of a body, hence the idea of organic solidarity and so forth.

My concern is that Wilson et al. move between the different meanings of "cultural group" without fully considering the implications. Just as Jonathan Z. Smith reminds us that there is no such thing as religion, only different forms of religiosity (1982, p. xi), we have to be ever conscious that there is no exclusively religious social grouping. As some form of bottom line, consider that the members have to eat and shelter from the elements so there will always be economic aspects of their social grouping.

Some examples in the text:

> To understand human cultural ecosystems, look to the fitness-enhancing properties of the functionally organized groupings that comprise the ecosystem – the religious congregations and secular organizations that interact with each other at particular locations.

CONTACT David Zeitlyn david.zeitlyn@anthro.ox.ac.uk

This contains a move from cultures as wholes/entities (parallel to species) to groups within cultures (e.g., religious congregations, etc.). However, groups within cultures are not the same sort of thing as the beavers in their biological parallel.

As a consequence I am unsure what level they are talking about when they say "identifying the salient groups in cultural ecosystems need not be more difficult than identifying the salient functional units in biological ecosystems." I think they mean sub-groups such as the different churches in Binghamton but these are *not* like beavers in an ecological system; they are like organs in a body or the beavers' teeth. Later this becomes clearer when they argue for

> the detailed study of functionally organized units in relation to each other and their environment. Microevolution is the engine that generates pattern at larger scales. It needs to be studied directly for cultural evolution no less than for genetic evolution.

This may or may not be a helpful metaphor. My point is that they set up their parallel between biological species and large-scale social groups (e.g., nations, tribes, etc.) but then when they deploy it they move to discussing what in the terms of the biological metaphor should be organs, not species.

Having been critical I will end on two positive notes. First is to endorse the need for long-term field sites to enable connected collaborative research on religious behavior and many other connected phenomena in ways that will allow evolutionary questions, and many others, to be addressed. Second is to point to an intriguing parallel where evolutionary questions are beginning to be asked in far more sophisticated ways than has been done in the past: I am thinking of some developments in sociolinguistics and conversation analysis where in collections such as *The Morality of Knowledge in Conversation* (Stivers, Mondada, & Steensig, 2011) sociolinguists are dealing not only with epistemics but with the social loadedness of how, for example, assertion is managed. This provides a way of examining the microevolutionary engine that Wilson et al. are concerned with. I look forward to seeing the results.

References

Smith, J. Z. (1982). *Imagining religion: From Babylon to Jonestown*. Chicago: University of Chicago Press.

Stivers, T., Mondada, L., & Steensig, J. (Eds.). (2011). *The morality of knowledge in conversation*. Cambridge: Cambridge University Press.

RESPONSE

Cultural diversity really is like biological diversity: reply to comments on *The Nature of Religious Diversity: A Cultural Ecosystem Approach*

David Sloan Wilson[a,b], Yasha Hartberg[b], Ian MacDonald[b], Jonathan A. Lanman[c], and Harvey Whitehouse[d]

[a]Department of Biological Sciences, Binghamton University, State University of New York, Binghamton, NY, USA; [b]Department of Anthropology, Binghamton University, State University of New York, Binghamton, NY, USA; [c]Institute of Cognition and Culture, School of History and Anthropology, Queens University, Belfast, Ireland; [d]Institute of Social and Cultural Anthropology, University of Oxford, Oxford, UK

We are grateful to the commentators for their stimulating reflections on our target article. Most, but not all, are supportive of the cultural ecosystem approach and many of the supportive comments go beyond our own contribution in developing the approach. A number of major themes emerged in the commentaries that we will attempt to address by organizing our reply into the following

CONTACT David Sloan Wilson dwilson@binghamton.edu

categories: (1) biological units and units of selection; (2) field sites for the study of cultural evolution; (3) forming testable hypotheses; (4) more on tightness and looseness; and (5) cultural diversity vs. religious diversity.

Biological units and units of selection. The biological sciences abound with units: organs, organisms, single-species groups, multi-species ecosystems, and higher-level taxonomic units such as genera, families, and phyla. Some of these units are discrete and easy to identify (e.g., an organism or a termite colony), others have fuzzy boundaries (e.g., most ecosystems), some are notoriously hard to define (e.g., species), and some are more salient to the biologist than to the interacting organisms (e.g., higher-level taxonomic categories). This might seem dauntingly complex (Zeitlyn, Tucker), but biologists manage to turn all of these units into productive research programs. The cultural ecosystem approach strives to do the same for the study of cultural diversity, without requiring point-for-point correspondences. Cultural inheritance mechanisms do not require "memes" that correspond to genes, for example (Henrich, Boyd, & Richerson, 2008).

For both biological and cultural ecosystems, it is crucial to identify the units of functional organization, which arise by a process of selection at the unit level (as discussed in section 1 of the target article). This could even be said to be the anchor concept that makes the two approaches similar. In biological ecosystems, these are most often individual organisms (not species, as emphasized by Zeitlyn and as we also emphasize in section 3 of the target article). A single-species social group and even a multi-species ecosystem can be a unit of functional organization, but only if it has been a unit of selection. Eusocial insect societies are famous examples. If you were to study single honeybees as if they were similar to solitary insect species, you would be making a profound error, equivalent to the error of assuming that an organ such as the heart is an autonomous organism.

In human cultural ecosystems, the units of functional organization can be individuals or groups, but they are groups more often than in biological ecosystems because group selection is a more potent force in cultural evolution than in genetic evolution (Richerson & Boyd, 2006; Wilson, 2013). This is a major development in evolutionary thought that challenges previous dogma in both evolutionary biology and anthropology. In the former case, individual-level selection was thought to almost always prevail over group-level selection. In the latter case, individuals were axiomatically made the unit of analysis by a philosophical stance called methodological individualism, which Paul defines as the assumption that "'societies' and 'cultures' do not really exist as entities in themselves, but are abstractions based on the summed behavior of the similarly enculturated individuals that constitute them."

Palmer's commentary is in the tradition of methodological individualism. For him, individuals *must* be the unit of analysis and groups are "illusory conceptual abstractions." He regards qualifiers such as "for the most part" and "in many cases" as weaknesses in our conceptual framework, as if a more individualistic account would not need such qualifiers. We disagree. Methodological individualism must account for the same complexities of cultural diversity, in all their fuzziness, as a multilevel selection account.

We are very pleased to have Paul's commentary to juxtapose with Palmer's. Paul is one of the first socio-cultural anthropologists to take dual-inheritance theory seriously and his recent book, *Mixed Messages*, is filled with examples of human groups that function as corporate units, thanks to cultural mechanisms that hold disruptive within-group competition in check (Paul, 2015). Viewing such cultures through the lens of methodological individualism is almost as misleading as studying honeybees as if they are solitary insects.

Deciding what is *not* functionally organized goes hand in hand with deciding what *is* functionally organized. Some early schools of thought in ecosystem ecology axiomatically assumed that whole ecosystems are functionally organized (e.g., Margalef, 1963), much as the tradition of functionalism in anthropology axiomatically assumed that human cultures are functionally organized. Today it is more common to study ecosystems as collections of functionally organized units whose interactions do not necessarily result in functional organization at the ecosystem level (e.g., Bodkin, 1990). The ability to determine the *presence or absence* of functional organization at any level of a multi-tier

hierarchy is what makes the framework that we propose for the study of cultural diversity so distinctive and useful in the biological sciences (Wilson, 2015).

Field sites for the study of cultural evolution. Peregrine is right that we ignored archaeology in our target article and that archaeologists exemplify the field site approach that we call for. In addition, archaeologists are likely to study human cultural ecosystems in relation to biological ecosystems, making them even more exemplary from our perspective. Cultural anthropology and sociology are also field-oriented disciplines that are applied to industrial, in addition to traditional, societies. Nevertheless, our call for more field sites for the study of cultural evolution resonated with most of the commentators (e.g., Botero, Harmon, and Atkinson; Johnson; Zeitlyn; Tucker). Several empirical methodologies were discussed, such as phylogenetic comparative methods (Botero, Harmon, and Atkinson), standardized and open-access data for comparisons across field sites (Botero, Harmon, and Atkinson), and sociolinguistic methods to delineate meaning systems that, along with norms and institutions, constitute the proximate mechanisms of functionally organized groups (Zeitlyn).

What distinguishes the approach that we call for from other approaches that take place in field settings? First and foremost is the conceptual framework, which informs the questions that are asked. If one were to construct a Venn diagram of human-related research conducted from an ecological and evolutionary perspective and human-related research conducted in everyday settings, the overlap would be very small. Second, when a geographical location is chosen as a field site for an extended period of time, then successive studies can build upon each other. This is what distinguishes long-term field sites from single field studies in biological research.

It is easy to regard the creation of a field site as such a large project that it can only be undertaken with a large team and with the help of major funding (Johnson, Tucker). We tried to forestall this impression in our target article and will try again here. The cultural ecosystem approach is first and foremost a conceptual framework that can be employed by individual researchers in addition to teams. A field site can begin as a single study and grow incrementally. This is how the Binghamton Neighborhood project developed (Wilson, 2011a). The first project was an unfunded collaboration with the Binghamton City School District that enabled us to study the dynamics of prosociality at a citywide scale (Wilson, O'Brien, & Sesma, 2009). That led to several additional studies to validate and extend the results of the first study (e.g., O'Brien, Gallup, & Wilson, 2012; O'Brien & Wilson, 2011). Applied research oriented toward improving the quality of life went hand in hand with basic scientific research (e.g. Wilson, Kauffman, & Purdy, 2011; Wilson, 2011b).

The communities surrounding colleges and universities are especially amenable to this incremental approach because of the abundant supply of faculty and students who can become involved in the research. In addition, Johnson makes the fascinating suggestion that colleges and universities can themselves be studied from a cultural ecosystem perspective as a collection of lower-level units that are functionally organized but interact in ways that do not result in functional organization at the university level. This might provide a novel perspective on why it is difficult to be interdisciplinary and how a campus-wide program such as EvoS can help a university function as a single intellectual community (Wilson, Geher, Waldo, & Chang, 2011). While EvoS at Binghamton is far from achieving this goal, its mission is indeed to create a "United Ivory Archipelago" (Wilson, 2007) and it is a good example of a program that started small and is growing incrementally.

We are amused by Palmer's misreading of our target article to say that major funding is already available for the creation of field sites and that readers should climb aboard the gravy train. Paul has the more accurate assessment: "I wouldn't hold my breath." It is possible to take matters into our own hands, however. The Evolution Institute has created a new Society for the Study of Cultural Evolution (SSCE) that has attracted over 1000 founding members from over 50 nations. The creation of field sites is likely to be one of the "grand challenges" that forms the agenda of the SSCE (for more, please visit https://evolution-institute.org/project/society-for-the-study-of-cultural-evolution/).

Forming testable hypotheses. For some commentators, our target article gave the impression that the cultural ecosystem approach is hard to use (Tucker) and does not lead to the formation of crisp

testable hypotheses (Triandis), compared to the axis approach. We are delighted that Triandis provided a commentary, because he is so well known for the axis approach. We were careful to acknowledge the utility of the axis approach in our target article and to describe the cultural ecosystem approach as complementary. We are glad that Triandis's commentary is written in the same spirit. We did present some testable hypotheses in section 4 of our target article but perhaps we did not make them explicit enough. They include the following:

(1) Cultures should be context-specific in their tightness and looseness, depending upon the need for regulation of behavior in any given context.
(2) Strong norms (one component of tightness) should vary in their degree of enforcement (the other component of tightness) based on the incentives to violate norms.
(3) Strong norms enforced by punishment should be characteristic of extractive societies (sensu Acemoglu & Robinson, 2012), in addition to agricultural societies and societies in which everyone is existentially insecure, providing a new environmental context for the study of tightness.
(4) The degree to which tightness and looseness can be optimized for each context within a given culture, as opposed to tight and loose syndromes analogous to behavioral syndromes in animal behavior research, is an important research topic, although it is impossible to predict the outcome beforehand.
(5) The tight–loose continuum should recreate itself within every new religious tradition. In other words, no matter where a new tradition (such as Methodism or Mormonism) starts out on the tight–loose continuum, congregations will start differing along the continuum as the tradition grows in popularity.

Multilevel selection theory provides additional crisp testable hypotheses, especially concerning the core design principles required for groups to function as corporate units (Wilson, Ostrom, & Cox, 2013). In general, we think that the cultural ecosystem approach will compare favorably to the axis approach in its ability to formulate testable hypotheses.

More on tightness and looseness. We are also delighted that Jackson and Gelfand provided a commentary, given that the research of Gelfand and her associates on the tight–loose axis of cultural variation features so prominently in our target article. One reason that this axis complements the cultural ecosystem approach so well is because both rely centrally on the concept of norms, or expectations of appropriate behaviors that are often enforced by punishment. Norms define the tight–loose axis and they also play a major (although not exclusive) role in structuring behavioral variation within and among cultures. Jackson and Gelfand endorse a behavioral syndrome view, whereby tightness and looseness have the same "signatures" around the world, regardless of environmental determinants (e.g., societal complexity vs. ecological threat), and the selection of tightness (or looseness) in one context "spills over" to other contexts. Thus, they conjecture that Singapore evolved tight norms to manage intense population density and that the prohibition against flying kites on public beaches is a spillover, or non-adaptive byproduct. More generally, the presumption is that Singapore's tightness cannot be relaxed at will, much as its leaders may wish to do so for special purposes, for instance to promote innovation in targeted areas of the economy. The more the behavioral syndrome perspective turns out to be the case, the more appropriate it is to think about tightness and looseness as a single axis of cultural variation. Jackson and Gelfand stress, as we do, that these questions can only be answered by more empirical research.

We would like to offer a counter-example to Jackson and Gelfand's example of Singapore, in which extreme tightness and extreme looseness can be combined in a single culture. Two of us (Wilson and MacDonald) are beginning to study a movement called Interspirituality (Johnson & Ord, 2013) and also the burgeoning number of intentional communities that are forming in America and around the world (Lockyer & Veteto, 2015). One ecovillage called Dancing Rabbit (http://www.dancingrabbit.org) shows how extreme tightness and extreme looseness can be combined in a single functionally organized group. Dancing Rabbit is extremely tight in its ecological norms. Members

must sign a covenant abiding by the village rules and serious infractions would result in exclusion. For members that uphold the ecological norms, however, any spiritual belief (including atheism), sexual orientation, or other lifestyle (as long as it does not harm others) is tolerated and intolerance would itself be punished. The combination of extreme tightness and extreme looseness appears to make for a vibrant community that "walks the walk" with respect to environmentally sustainable practices and provides a high quality of life for members of the group. We realize that this example is conjectural, along with Jackson and Gelfand's example of Singapore, and that more research is required to understand the constraints on varying tightness and looseness within any given culture.

Cultural diversity vs. religious diversity. What does the cultural ecosystem approach have to say about religious diversity per se, as opposed to cultural diversity? We subscribe to Bloch's (2008) statement quoted by Tucker that religion is "nothing special," i.e., a subset of something more general, which Tucker aptly describes as "cultural cognition" and "part of the human ability to imagine 'other worlds', which forms the basis of most social institutions, including kinship." We sometimes use the more compact term "meaning system" in the same way. A strength of the cultural ecosystem approach is that it studies religious groups and non-religious groups as part of the same cultural ecosystem, no matter what specific definition of religion is used. This makes it possible to ask a host of questions concerning the advantages of religious groups compared to secular groups in their immediate vicinity, the movement of individuals in and out of religious groups (as discussed in the target article), and so on. A good example concerns the growth of strict churches and decline of lax churches in America chronicled by Kelly (1972; while the strict–lax axis is not exactly the same as the tight–loose axis, the same statement could be made about tight and loose churches). We think that the appeal of a lax church depends upon the social acceptability of not belonging to any church. In a culture where it was necessary to belong to a church to be socially respected, such as America during the nineteenth and early twentieth centuries, then lax churches were very popular. It was the availability of a third option (no church) that made lax churches weak. This is another specific hypothesis that emerges from the cultural ecosystem approach. We agree with Johnson that syncretic religions and new age spiritual movements are fascinating to study, as we are starting to do with our study of the Interspiritual and Intentional Communities movements described above.

We hope that our target article and the commentaries promote the study of cultural diversity as like biological diversity. We look forward to what future research employing the cultural ecosystem approach will bring.

References

Acemoglu, D., & Robinson, J. (2012). *Why nations fail: The origins of power,prosperity,and poverty. 2012*. New York: Crown.

Bloch, M. (2008). Why religion is nothing special but is central. *Philosophical Transaction of the Royal Society B*, *363*, 2055–2061.

Bodkin, B. B. (1990). *Discordant harmonies: A new ecology for the twenty-first century*. New York: Oxford University Press USA.

Henrich, J., Boyd, R., & Richerson, P. J. (2008). Five misunderstandings about cultural evolution. *Human Nature*, *19*, 119–137.

Johnson, K., & Ord, D. (2013). *The coming interspiritual age*. Vancouver: Namaste.

Kelly, D. M. (1972). *Why conservative churches are growing: A study in the sociology of religion*. Macon, GA: Mercer University Press.

Lockyer, J., & Veteto, J. R. (2015). *Environmental anthropology engaging ecotopia: Bioregionalism, permaculture, and ecovillages*. Oxford, NY: Berghahn Books.

Margalef, R. (1963). On Certain unifying principles in ecology. *American Naturalist*, *97*, 357–374.

O'Brien, D. T., Gallup, A. C., & Wilson, D. S. (2012). Residential mobility and prosocial development within a single city. *American Journal of Community Psychology*, *50*(1–2), 26–36. http://doi.org/10.1007/s10464-011-9468-4

O'Brien, D. T., & Wilson, D. S. (2011). Community perception: The ability to assess the safety of unfamiliar neighborhoods and respond adaptively. *Journal of Personality and Social Psychology*, *100*(4), 606–620. http://doi.org/10.1037/a0022803

Paul, R. A. (2015). *Mixed messages: Cultural and genetic inheritance in the constitution of human society*. Chicago: University of Chicago Press.
Richerson, P. J., & Boyd, R. (2006). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.
Wilson, D. S. (2007). *Evolution for everyone: How Darwin's theory can change the way we think about our lives*. New York: Delacorte.
Wilson, D. S. (2011a). *The neighborhood project: Using evolution to improve my city, one block at a time*. New York: Little, Brown.
Wilson, D. S. (2011b). The design your own park competition: Empowering neighborhoods and restoring outdoor play on a citywide scale. *American Journal of Play*, *3*, 538–551.
Wilson, D. S. (2013). Human cultures are primarily adaptive at the group level (with comment). *Cliodynamics: The Journal of Theoretical and Mathematical History*, *4*(1), 102–138.
Wilson, D. S. (2015). *Does altruism exist? Culture, genes, and the welfare of others*. New Haven: Yale University Press.
Wilson, D. S., Geher, G., Waldo, J., & Chang, R. (2011). The EvoS consortium: Catalyzing evolutionary training in higher education (introductory article to a special issue of evolution: Education and outreach) devoted to EvoS . *Evolution: Education and Outreach*, *4*(1), 8–10.
Wilson, D. S., Kauffman, R. A., & Purdy, M. S. (2011). A program for at-risk high school students Informed by evolutionary science. *PLoS ONE*, *6*(*11*), e27826. http://doi.org/10.1371/journal.pone.0027826
Wilson, D. S., O'Brien, D. T., & Sesma, A. (2009). Human prosociality from an evolutionary perspective: Variation and correlations at a city-wide scale. *Evolution and Human Behavior*, *30*(3), 190–200. http://doi.org/10.1016/j.evolhumbehav.2008.12.002
Wilson, D. S., Ostrom, E., & Cox, M. E. (2013). Generalizing the core design principles for the efficacy of groups. *Journal of Economic Behavior & Organization*, *90*, S21–S32. http://doi.org/10.1016/j.jebo.2012.12.010