ESA CENTENNIAL PAPER

Ecological Monographs, 85(3), 2015, pp. 287–331
© 2015 by the Ecological Society of America

Ecology in an anthropogenic biosphere

Erle C. Ellis[1]

Department of Geography and Environmental Systems, University of Maryland, Baltimore County, 1000 Hiltop Circle, Baltimore, Maryland 21250 USA

Abstract. Humans, unlike any other multicellular species in Earth's history, have emerged as a global force that is transforming the ecology of an entire planet. It is no longer possible to understand, predict, or successfully manage ecological pattern, process, or change without understanding why and how humans reshape these over the long term. Here, a general causal theory is presented to explain why human societies gained the capacity to globally alter the patterns, processes, and dynamics of ecology and how these anthropogenic alterations unfold over time and space as societies themselves change over human generational time. Building on existing theories of ecosystem engineering, niche construction, inclusive inheritance, cultural evolution, ultrasociality, and social change, this theory of anthroecological change holds that sociocultural evolution of subsistence regimes based on ecosystem engineering, social specialization, and non-kin exchange, or "sociocultural niche construction," is the main cause of both the long-term upscaling of human societies and their unprecedented transformation of the biosphere. Human sociocultural niche construction can explain, where classic ecological theory cannot, the sustained transformative effects of human societies on biogeography, ecological succession, ecosystem processes, and the ecological patterns and processes of landscapes, biomes, and the biosphere. Anthroecology theory generates empirically testable hypotheses on the forms and trajectories of long-term anthropogenic ecological change that have significant theoretical and practical implications across the subdisciplines of ecology and conservation. Though still at an early stage of development, anthroecology theory aligns with and integrates established theoretical frameworks including social–ecological systems, social metabolism, countryside biogeography, novel ecosystems, and anthromes. The "fluxes of nature" are fast becoming "cultures of nature." To investigate, understand, and address the ultimate causes of anthropogenic ecological change, not just the consequences, human sociocultural processes must become as much a part of ecological theory and practice as biological and geophysical processes are now. Strategies for achieving this goal and for advancing ecological science and conservation in an increasingly anthropogenic biosphere are presented.

Key words: anthropocene; anthropogenic landscapes; anthrosequence; archaeology; biodiversity; Centennial Paper; cultural inheritance; disturbance; Extended Evolutionary Synthesis; human-dominated ecosystems; human ecology; human impacts; natural history.

> *It would be difficult, not to say impossible, to draw a natural line between the activities of the human tribes which presumably fitted into and formed parts of "biotic communities" and the destructive human activities of the modern world.*
>
> —Tansley 1935

> *The vast bulk of the impact that human beings have made on this planet has undoubtedly resulted directly from socially transmitted knowledge.*
>
> —Odling-Smee and Laland 2012

> *Changes in human societies over the past 12,000 years can be understood as constituting a single complicated earth-wide event of spiraling globalization.*
>
> —Chase-Dunn and Lerro 2013

INTRODUCTION

Human societies have been altering ecological and evolutionary processes across the Earth for millennia (Butzer 1982, Redman 1999, Grayson 2001, Kirch 2005,

Manuscript received 26 November 2014; revised 11 March 2015; accepted 12 March 2015. Corresponding Editor: A. M. Ellison.

Editors' Note: This paper was commissioned by the journal editors to commemorate the ESA Centennial celebration. A virtual Table of Contents with links to all the centennial papers will be available on the journals' web site (esajournals.org) by the fall of 2015.

[1] E-mail: ece@umbc.edu

Barnosky 2008, Ellis 2011, Doughty 2013, Ruddiman 2013, Smith and Zeder 2013, Barnosky 2014). As behaviorally modern *Homo sapiens* spread out of Africa more than 50 000 years ago (Klein 2013), their advanced hunter-gatherer societies helped to cause the extinction of more than half of Earth's mammalian megafauna, yielding trophic cascading effects on ecosystems coupled with the direct effects of landscape burning to enhance hunting and foraging success (Grayson 2001, Barnosky 2008, Estes et al. 2011, Doughty 2013, Barnosky 2014). More than 10 000 years ago, agricultural societies accelerated these early defaunation and land clearing processes, ultimately replacing them with even more novel ecological transformations, including the culture of domesticated species, widespread soil tillage, sustained societal growth, and ever-increasing scales of material exchange, leading to globally significant transformation of the terrestrial biosphere by at least 3000 years before the present time (Fig. 1A; Kirch 2005, Ellis 2011, Ellis et al. 2013*b*, Smith and Zeder 2013).

Human societies have now caused global changes in atmospheric composition and climate (IPCC 2013), hydrology (Vörösmarty and Sahagian 2000), geomorphology (Wilkinson 2005, Syvitski and Kettner 2011), fire regimes (Bowman et al. 2011), and other Earth systems (Zalasiewicz et al. 2012). Human societies have caused widespread species extinctions (Barnosky 2008, Dirzo et al. 2014, Pimm et al. 2014) and species invasions (Vitousek et al. 1997*a*, Ricciardi 2007, Lockwood et al. 2013), and changes in the local and global patterns of net primary production (Vitousek et al. 1986, Krausmann et al. 2013) and in the local and global biogeochemical cycles of carbon, nitrogen, phosphorus, and other elements (Vitousek et al. 1997*b*, Falkowski et al. 2000, Galloway et al. 2004, Elser et al. 2007).

Humans have also introduced a wide array of entirely new ecological processes to the Earth system (Ellis and Haff 2009), including species domestication by artificial selection (Larson et al. 2014), direct genetic modification of organisms (Dale et al. 2002), large-scale combustion of fossilized photosynthates (Boden et al. 2012), artificial lighting (Longcore and Rich 2004), and the chemical synthesis of reactive nitrogen (Gruber and Galloway 2008) together with a vast number of artificial chemicals, plastics, and other synthetic materials, many of which are used to control other species (Alloway and Ayres 1997, Corcoran et al. 2014). Humans have facilitated the release and utilization of nuclear energy and radionuclides (Harrison et al. 2011, Hancock et al. 2014, Zalasiewicz et al. 2015). Humans engage in annual soil tillage and produce large-scale earthworks, channels, tunnels, and boreholes (Richter et al. 2011, Edgeworth 2014, Zalasiewicz et al. 2014), including massive vertically built structures (Frolking et al. 2013), and artificial structures interconnected across continents (e.g., canals, roads, railways [Forman and Alexander 1998, Verburg et al. 2011]). Humans have also introduced increasingly rapid, massive, and mechanized aerial, terrestrial, and hydraulic transport of material and biota across the Earth (Mooney and Cleland 2001, Steinberger et al. 2010, D'Odorico et al. 2014), and these transport processes are beginning to extend beyond Earth's atmosphere (Crowther 2002, Gorman 2014). Rates and scales of these processes continue to accelerate, driven by increasing use of nonbiological energy and the mechanization and automation of human activities, from food production and construction to trade and communications (Smil 2008, Baccini and Brunner 2012, Brynjolfsson and McAfee 2014).

Taken together, these anthropogenic global environmental changes have been characterized as the emergence of humans as a "great force of nature" that is transforming the Earth system, shifting the planet into a new epoch of geologic time: the Anthropocene (Crutzen 2002, Steffen et al. 2007, Ellis 2011, Steffen et al. 2011, Zalasiewicz et al. 2012, Smith and Zeder 2013, Barnosky 2014). Whether or not the Anthropocene is formally recognized, there is no question that the scale, rate, intensity, and diversity of anthropogenic environmental changes are unprecedented in comparison with those caused by any prior multicellular species. The question for ecology is not whether, when, or even how humans have transformed the biosphere, but rather, why?

Evolutionary theorists and social scientists have made substantial progress toward explaining the exceptional growth and development of human societies and their unprecedented capacity for environmental transformation, especially in archaeology, anthropology, and sociology (e.g., Butzer 1982, Laland et al. 2000, Kirch 2005, Nolan and Lenski 2010, Chase-Dunn and Lerro 2013). Yet ecology remains without a widely accepted causal theory that can explain how a single multicellular species gained the capacity to transform an entire planet; though such theories have a long history (e.g., Marsh 1865, de Chardin 1955, Vernadsky 1998) and are of increasing interest to ecologists (e.g., Barnosky 2008, Collins et al. 2011, Steffen et al. 2011, Barnosky et al. 2012, Costanza et al. 2012, Smith and Zeder 2013, Malhi 2014).

It is no longer possible to explain or predict ecological patterns or processes across the Earth without considering the human role in these (Ellis and Ramankutty 2008, Ellis and Haff 2009, Barnosky et al. 2012). More than three-quarters of the terrestrial biosphere has already been transformed into anthropogenic biomes (anthromes) by human populations and their use of land (Fig. 1B; Ellis and Ramankutty 2008). In a biosphere increasingly transformed by human societies, ecology cannot advance as a predictive science without gaining the basic theoretical tools needed to investigate and understand the ultimate causes, not just the consequences, of human transformation of ecological pattern, process, and change.

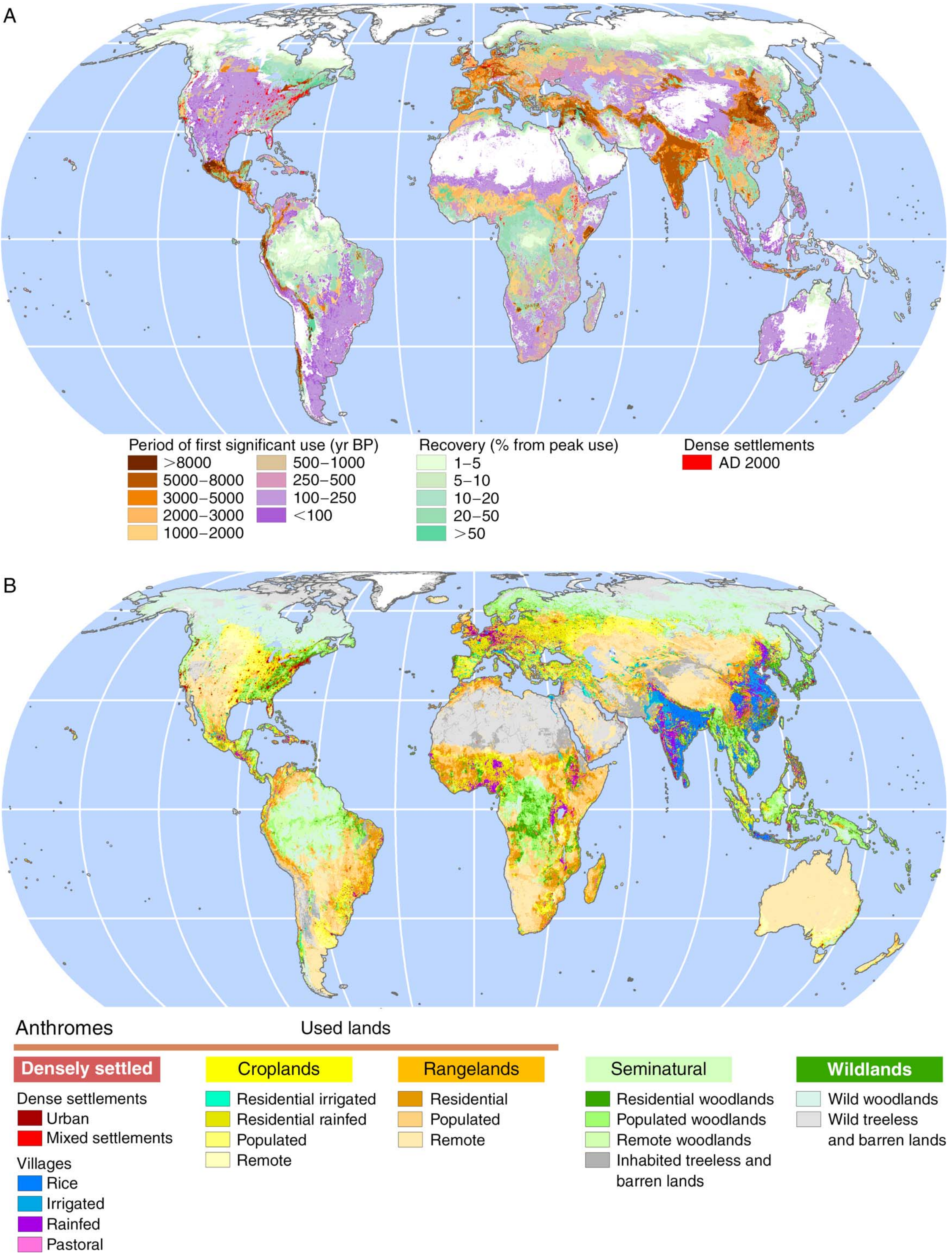

FIG. 1. Human transformation of the terrestrial biosphere. (A) Time period of first significant human use of land for agriculture and settlements in regions with sustained use (years before present [BP]), urban and densely settled areas in year 2000, and the percentage of recovery from peak land use in regions without sustained use (modified from Ellis et al. 2013*b*). (B) Anthropogenic biomes (anthromes; year 2000; modified from Ellis et al. 2010). Anthromes are organized into five levels in the legend. The map is an Eckert IV equal area projection.

Toward a General Theory of Anthropogenic Ecological Change

This paper introduces a general causal theory of long-term anthropogenic ecological change ("anthroecology theory") based on a synthesis of contemporary evidence and theory across the ecological, evolutionary, and social sciences. The evidence will show that the ultimate causes of unprecedented human transformation of the biosphere are social and cultural; not biological, chemical, or physical. As a result, an understanding of human sociocultural processes is central to understanding anthropogenic ecological change. Disciplinary barriers to this understanding are formidable (Laland and Brown 2011). Yet there is no other way forward.

Human societies have emerged as a global force that is reshaping the biosphere, atmosphere, hydrosphere, and lithosphere (Steffen et al. 2007). To understand this massive and sustained human transformation of Earth's ecology, it is necessary to consider human societies as a global force capable of interacting with and reshaping ecology across the Earth in ways analogous to that of the climate system (Ellis and Haff 2009, Lucht 2010, Steffen et al. 2011). Just as a causal understanding of climate and weather is needed to understand the ecological patterns, processes, and dynamics produced by these across the Earth, a causal understanding of human sociocultural processes, analogous to a "human climate and weather," is required to understand the long-term ecological patterns and processes resulting from sustained interactions with human societies.

Social–ecological systems (SES) theory has developed into a useful framework for understanding, predicting, and addressing the dynamics of a "human weather," in which human societies interact directly with populations and ecosystems locally and regionally with direct feedbacks over years to decades (Folke et al. 2005, Alessa and Chapin 2008, Carpenter et al. 2009, Chapin et al. 2011, Collins et al. 2011, Levin et al. 2013). SES frameworks have become especially useful for understanding the dynamic interplay of coupled social and ecological systems in practical settings generally with the aim of promoting resilient system interactions together with stakeholders (Folke 2006, Chapin et al. 2011, Collins et al. 2011).

Here the goal is more basic: to explain the emergence and long-term dynamics of the "human climate system" that has been reshaping the terrestrial biosphere for more than 50 000 years and that will likely continue reshaping it into the foreseeable future. This explanation has two parts. The first is to explain how human societies initially gained their unprecedented capacity to transform ecological and evolutionary processes. The second is to explain how this capacity has scaled up and changed as a transformative force on ecology as human societies themselves have changed and diversified over human generational time, from small bands of hunter-gatherers to globalized industrial societies. To gain this understanding, it is necessary to see beyond the short-term local and regional dynamics of the "human weather" to focus on the "human climate system"; the long-term processes by which human societies act as a global force transforming Earth's ecology.

A detailed global understanding of social–ecological changes over the past 50 000 years is certainly beyond the scope of any single published work. The ultimate purpose here is to guide ecological science toward a general causal framework explaining why long-term societal changes reshape ecology and evolution, with the goal of generating ecologically useful hypotheses. To build this framework, terms are borrowed from the social and evolutionary sciences, and some are defined specifically here; Table 1 provides definitions of key terms. A practical distinction is made here between "natural" patterns and processes, defined as those unaltered by humans, and anthropogenic patterns and processes that have been altered, or introduced de novo by human sociocultural systems, representing the "human climate system."

The way forward begins with a simple question. Why and how did a single species of hominin, so biologically and ecologically similar to others in its genus (Sterelny 2011, Antón et al. 2014), originate, scale up (social upscaling; Table 1), and sustain for generations the culturally complex societies capable of transforming an entire planet? The answer begins with a review of recent evolutionary theory explaining how socially transmitted behavioral strategies that transform environments and enable societies to scale up through processes of social specialization and non-kin social exchange can evolve across generations by enhancing the adaptive fitness of individuals, progeny, populations, and societies. As will be seen, the emergence of behaviorally modern human societies as a global force transforming the biosphere has resulted from an unprecedented ability for these societies to scale up socially and to accumulate capacity for ecosystem engineering while harnessing nonhuman and even abiotic energy in this process.

To understand why and how a single biological species gained the capacity to transform the biosphere requires an evolutionary theory of anthroecological change based on "sociocultural niche construction" (Table 1), an integrative theory constructed from existing theories of ecosystem engineering, niche construction, ecological inheritance, inclusive inheritance, cultural inheritance, cultural evolution, and ultrasociality. Elements of this theory are outlined in Box 1 and presented in detail in the remainder of this section. Background readings are listed in Table 2.

Ecosystem engineering, niche construction, and ecological inheritance

Many species transform their physical environments by processes of "ecosystem engineering" (Jones et al. 1994, 2010, Wright and Jones 2006, Erwin 2008, Matthews et al. 2014). Yet the evolutionary consequences of this transformation have only recently been incorporated into ecological theory (Lewontin 1983, Odling-Smee 1988, Matthews et al. 2014). Niche construction theory, introduced in the 1990s, links environmental alterations by organisms to changes in their adaptive fitness, and that of their progeny, and also that of other species within these altered environments (Odling-Smee et al. 1996, 2003*c*, Laland et al. 1999). Niche construction theory challenges one of the most basic assumptions underlying modern evolutionary theory, that organisms must adapt solely within environmental conditions that they cannot alter, and replaces this with a "two-way street" (Ellison 2004) in which organisms alter environments and must in turn adapt to these altered environments, generating complex feedbacks in both ecological and evolutionary processes. The theory has strong empirical and mathematical support (Laland et al. 1999, Odling-Smee et al. 2003*c*), applies broadly across taxa, and is increasingly well connected with existing theory in ecology and evolution (Odling-Smee et al. 2003*b*, 2013, Erwin 2008, Matthews et al. 2014, Scott-Phillips et al. 2014).

Niche construction theory holds that, by enhancing or degrading environments in ways that increase or decrease the adaptive fitness of later generations, or that of other species interacting with a given environment, organisms produce an "ecological inheritance" (Table 1; Odling-Smee et al. 2003*c*). Well-documented examples of ecological inheritance include the positive fitness benefits received by a species through the construction of protective burrows, nests and webs, and the buildup of nutrients and organic material in soils, and also the negative fitness, or detrimental effects, of depleting soil nutrients, soil erosion, and the buildup of harmful chemicals in soil and water (Odling-Smee et al. 2003*c*). Given the many pathways by which species may alter environments and their varied consequences, it is useful to first characterize these as either direct (environmental alteration by a species directly affects a species, the same or not; e.g., toxic accumulation in soils) or indirect (environmental alteration by a species affects the same or another species by altering an additional environmental process; e.g., production of flammable leaves increases fire frequencies, causing a fire effect), and then to characterize their effects on the adaptive fitness of the acting species and/or other species as either beneficial, detrimental, or compound (beneficial and detrimental) ecological inheritance. For example, fires produced by the buildup of flammable leaves would simultaneously yield indirect beneficial ecological inheritance to a fire-dependent plant species and indirect detrimental ecological inheritance to a fire-intolerant species in the same environment.

One major evolutionary consequence of ecological inheritance is that environment-altering traits that produce fitness benefits for a given species (e.g., burrowing, nest building, web construction, nutrient-rich leaves, or allelopathic chemicals) or that help a species adapt to the detrimental effects of environmental changes (e.g., enhanced nutrient uptake or recycling, metabolism of toxics) or that increase the beneficial effects of these changes (e.g., burrow and nest re-use, root systems adapted to nutrient-rich soils), will be selected for in these altered environments and therefore increase or decrease in frequency in populations by processes of natural selection, causing these "recipient traits" to evolve over generational time (Odling-Smee et al. 2013). The second, and perhaps even greater consequence of ecological inheritance is that species engaging in niche construction tend to increasingly alter the environments and adaptive fitness experienced by other species, generating broad changes in the ecology and evolution of entire communities (Odling-Smee and Laland 2012). For example, niche construction by bioturbation, biostabilization, bioerosion, and bioconstruction are increasingly recognized as globally significant forces shaping both biotic and geomorphic processes across the Earth over the long term (Erwin 2008, Corenblit et al. 2011). The oxygenation of Earth's atmosphere by photosynthetic microorganisms is perhaps the ultimate example of the global transformative power of niche construction (Odling-Smee et al. 2003*c*).

The behavioral traits of active allogenic ecosystem engineers, like dam building by beavers and nest construction by termites, with their direct adaptive fitness benefits, are among the clearest examples of how ecological inheritance can drive the evolution of environmental altering traits (Matthews et al. 2014). To understand the evolution of ecosystem engineering by humans, "the ultimate ecosystem engineers," the effects of directly beneficial ecological inheritance are paramount (Laland et al. 2000, Odling-Smee et al. 2003*a*, Smith 2007*b*).

Inclusive inheritance, cultural inheritance, and the Extended Evolutionary Synthesis (EES)

Ecological inheritance is now integrated with other forms of nongenetic inheritance, including heritable modifications of gene activation (epigenetic inheritance), heritable parental effects, and the inheritance of cultural traits, into an "Extended Evolutionary Synthesis" (EES; Table 1) that expands the "Modern Synthesis" beyond genetics to explain the evolution of complex phenotypic traits across a variety of taxa (Bonduriansky and Day 2009, Danchin et al. 2011, Bonduriansky 2012, Danchin 2013, Mesoudi et al. 2013). The EES combines all forms of heritable phenotypic information into a vector of "inclusive inheritance" (Table 1) that can be transmitted across generations from parent to progeny (vertical transmission), from older to younger generations (oblique transmission), and among siblings, kin, and non-kin within a generation (horizontal transmission) (Danchin et al. 2011, Danchin 2013). In this way, evolution by natural selection has been extended beyond the vertical genetic inheritance of higher organisms to the oblique and horizontal inheritance common in microbes and generalized to all forms of vertical,

TABLE 1. Definition of terms, in order of appearance in the text. Terms in italics are either newly defined or redefined for use here. This table is set on three pages.

Term	Definition
Anthropogenic	Altered or influenced by human sociocultural systems. Anthropogenic alteration of ecosystems and evolutionary processes may be direct or indirect, intended or unintended, and have neutral, beneficial, detrimental, or combined consequences for humans and/or nonhumans.
Behaviorally modern humans	Human populations engaging in a suite of complex and symbolic social behaviors that emerged fairly rapidly ~60 000 years ago in Africa as evidenced by major shifts in tool sophistication, diversity, and standardization, personal ornaments, pigments, symbolic inscriptions, a broadening of the subsistence base, increasing settlement and population size, and long-distance trade. Linkage with anatomical or other genetic adaptations remains controversial (Nowell 2010).
Anthrome, anthropogenic biome	Globally significant ecological patterns produced by sustained direct human interactions with ecosystems (Ellis and Ramankutty 2008). A globally significant anthroecosystem pattern.
Anthropogenic biosphere	The biosphere as reshaped by sustained direct interactions with humans (Ellis and Ramankutty 2008). The global anthroecosystem. The system formed by the interactions of a world system and the biosphere.
Sociocultural processes	Processes sustaining sociocultural systems, including both internal processes and those connected with the natural world.
Sociocultural system, *human system*	A system composed of a human population and its social institutions, culture, and material products: a human society (Nolan and Lenski 2010) or *human system*. Sociocultural systems generate, transmit, reproduce, select for, and accumulate cultural, material, and ecological inheritance. Sociocultural systems can be identified at multiple scales, from small bands and tribes, to small social groups within a society to an entire world system.
Natural processes, natural systems, natural state	Processes, systems, or states unaltered by human sociocultural systems, e.g., natural ecosystems or natural landscapes; "pristine."
Niche construction	Organismal alteration of ecological patterns and processes in ways that confer heritable advantages and/or disadvantages to individuals or populations (ecological inheritance). Niche construction likely applies to all species in some form. Ecosystem engineers engage in niche construction only to the extent that their environmental alterations yield heritable consequences. Examples: soil acidification by nitrifying bacteria, termite nest building, beaver dams, rice paddy systems, pollution.
Ecological inheritance	Heritable ecological patterns and processes capable of conferring adaptive advantages and/or disadvantages to individuals, populations, and sociocultural systems. The constructed niche that is inherited. Examples: degraded or improved habitats, nests, dams, burrows, buildup of nutrients or toxins in soils or water, eroded soils, co-evolved species (flowers of pollinators), domesticates, planted forests.
Extended Evolutionary Synthesis (EES)	An extension of the Modern Synthesis of evolutionary theory to include nongenetic inheritance together with genetic inheritance ("inclusive inheritance"). Also called the "Inclusive Evolutionary Synthesis" (Danchin et al. 2011, Danchin 2013).
Nongenetic inheritance	"The part of variation in a trait that is transmitted to offspring through mechanisms other than genetic variation" (Danchin 2013). Includes epigenetic, parental, cultural, and ecological characteristics transmitted across generations as part of the EES.
Inclusive heritability	The degree to which phenotypic characteristics are transmitted between generations, whatever the mechanism of transmission. Includes both genetic and nongenetic characteristics inherited across generations, and processes of inheritance from parent to offspring (vertical inheritance), from older to younger generations (oblique transmission) as defined in the EES (Danchin et al. 2011).
Inclusive inheritance	The inheritance of both genetic and nongenetic phenotypic information between generations, whatever the mechanism of transmission. Phenotypic inheritance as defined in the EES (Danchin et al. 2011).
Culture	Information transmitted across individuals through social learning (Danchin et al. 2011). Examples: bird song, tool use, subsistence strategies, languages, social roles and institutions, advanced tool-making "recipes," and other complex technologies (Mesoudi and O'Brien 2008*a*).
Technology	Cultural information enabling or enhancing the behavioral capacity of organisms beyond their biological capabilities. Technology enables the production and use of tools and machines, but is not the same as the tools and machines themselves, which are defined as material culture. Examples: tool use, tool-making recipes, control of fire, techniques for machine and computer manufacture, computer software.
Cultural inheritance	Information transmitted across generations through social learning by vertical or oblique transmission processes. Examples: subsistence strategies, tool-making knowledge, languages, family planning.

TABLE 1. Continued.

Term	Definition
Cultural evolution	Processes by which variations in cultural information are produced, transmitted, selected for, change in frequency and accumulate across generations. Cultural macroevolution explains variations across societies; cultural microevolution explains variations within societies and social groups. This definition is consistent with the EES and other theory explaining cross-generational cultural inheritance, and is not the definition used in theory explaining horizontal transmission of cultural information within generations, such as memetics.
Cultural niche construction	Alteration of ecological patterns and processes by organisms through socially learned behaviors that produce heritable advantages and/or disadvantages to individuals or populations (ecological inheritance). Examples: tool use, agriculture, pollution.
Ultrasociality	Dependence on non-kin social cooperation for survival and the biological and sociocultural adaptations enabling this (e.g., Hill et al. 2009, Tomasello 2014).
Cooperative engineering	Processes of ecosystem and material culture engineering that require non-kin social cooperation to enact, including collaborative manufacture of tools and other material culture, large-scale landscape modifications for hunting, irrigation, and transportation infrastructure, and complex agricultural and industrial systems.
Social upscaling	Regime shifts in the scale of a society, in terms of number of interacting individuals sustained within a sociocultural system, from smaller to larger. Transitions from smaller- to larger-scale societies (e.g., hunter-gatherers to horticultural societies; see Table 3)
Energy substitution	Substitution of one form of energy for another, such as the substitution of fire or animal traction for human labor in clearing land, or use of nuclear energy to substitute for coal.
Sociocultural niche	The heritable sociocultural, material, and ecological conditions within which human individuals, groups, and populations reproduce and sustain themselves. Applies only to species dependent on socially learned exchange relations.
Sociocultural niche construction (SNC)	Alteration of sociocultural, ecological, or material patterns and processes by human individuals, groups, or populations through socially learned behaviors, exchange relations, and cooperative engineering in ways that confer heritable benefits and/or detriments to these individuals, groups, or populations. Examples: agriculture, pollution, the marketplace, electrical grids, nuclear power, genetic engineering.
Shared intentionality	The ability to interpret the intentions of others and to act cooperatively with these intentions; a capacity for intentionality and social cognition not shared by any other species (Tomasello et al. 2005).
Sociocultural evolution	Processes by which variations in cultural information are produced, transmitted, selected for, change in frequency, and accumulate across generations and across sociocultural systems. Sociocultural evolution includes processes of change not only in cultural information relevant to individuals, but also the cultural information, organization, and exchange relations that structure societies themselves. As with biological evolution, cross-generational changes in the frequencies of culturally based individual and population behaviors within and across sociocultural systems are influenced by their heritable advantages and/or disadvantages to individuals, populations, and groups.
Material culture	Artificial materials produced by sociocultural systems, ranging from stone tools and other small artifacts to the advanced technologies and built infrastructure of industrial societies; these are key evidence in archaeology (Eerkens and Lipo 2007). Examples: tools, artificial materials and chemicals, built structures, roads and other infrastructure.
Anthroecosystem, anthropogenic ecosystem	A system composed of sustained interactions among human sociocultural systems, nonhuman biota and abiotic environment (Fig. 2). A sociocultural system interacting with an ecosystem.
Material inheritance	Heritable artificial material products of behaviorally modern human societies that confer advantages or disadvantages to human individuals, populations, or sociocultural systems and that cannot be produced outside of human societies. Examples: tools, machines, artificial materials and chemicals, built structures, roads and other infrastructure. Similar to "material culture," but only when heritable and selectable.
Subsistence strategy	Behaviors that sustain organisms, including foraging strategies, ecosystem engineering, and subsistence exchange.
Subsistence exchange	Exchange of materials, labor, energy, and/or information among individuals that assist in their survival and reproduction.
Subsistence regime	Socially learned subsistence strategies implemented within and by sociocultural systems. Sociocultural subsistence regimes may be simple or complex (composed of multiple interacting subsistence strategies) and may or may not produce ecological, cultural, and/or material inheritance. Examples: tool-making techniques, cultivation of crops, trading networks, craft industries (more in Table 4).
World system	A sociocultural system formed from interacting sociocultural systems. Analogous to the interacting ecosystems comprising the biosphere.

TABLE 1. Continued.

Term	Definition
Abiotic energy	Energy not derived from any biological process, past or present, including solar, wind, geothermal, tidal, and nuclear. Excludes fossil fuels and biological products of any kind.
Land use	Intentional alteration of terrestrial ecosystems by sociocultural systems, including harvesting, extracting, cultivating, grazing, building on, restructuring, managing, conserving, and restoring ecosystem pattern and process. Land use produces ecological inheritance such as the intentional direct benefits of food production by agricultural ecosystem engineering and detrimental effects from overhunting, soil erosion, and pollution.
Wildlands	Landscapes or ecosystems that are not currently intentionally altered by sociocultural systems. Free of agriculture and permanent human settlements. Wildlands anthromes are defined as having no evidence of land use or human populations (Ellis et al. 2010)
Seminatural lands, seminatural ecosystems	Landscapes or ecosystems which show low levels of intentional alteration by sociocultural systems. Seminatural anthromes are defined as having <20% land use for agriculture and settlements (Ellis et al. 2010).
Used lands	Lands significantly altered intentionally by sociocultural systems. Or, in anthrome classification, landscapes with >20% land in use for agriculture and settlements (Ellis et al. 2010).
Novel ecosystem	An ecosystem altered permanently by interactions with sociocultural systems.
Anthrosequence	Anthrosequences depict hypothetical patterns in ecological processes caused by variations in sociocultural niche construction by different societies acting on a given biome, analogous to the patterning of ecological processes by time (chronosequence), terrain (toposequences), and climate (climosequences). Fig. 5 is an example of a woodland biome anthrosequence.
Telecoupling	The capacity of human populations to exert ecological effects over long distances by means of non-kin exchange relations, especially the demands for materials, biota, and energy expressed through markets (Liu et al. 2013).
Decoupling	Increasing the efficiency of resource production or extraction in ways that reduce direct utilization or harvesting of primary resources and transformation of natural ecosystems (Ausubel and Waggoner 2008, Fischer-Kowalski and Swilling 2011). Examples: the use of less fossil fuel per mile traveled by a vehicle, the substitution of fossil fuels for biomass energy, reducing use of land for biomass production, or production of food by more productive agricultural systems instead of hunting and foraging.

oblique, and horizontal transmission of genetic, epigenetic, parental, cultural, and ecological inheritances (Danchin et al. 2011, Danchin 2013).

The EES was developed to better understand the evolution of complex phenotypic traits in nonhuman taxa, such as bird song, tool use, and active allogenic ecosystem engineering that are not readily explained without multigenerational feedbacks among cultural, ecological, and/or genetic/epigenetic inheritances (Danchin et al. 2011, Danchin 2013). Nevertheless, by building ecological and cultural inheritance into evolutionary theory, the EES paves the way for major advances in understanding the evolution and ecology of human societies. Though many species exhibit cultural inheritance, which is defined as the transmission of information across generations through social learning (i.e., "learning from others"; Danchin et al. 2011), human capacity for social learning and accumulating cultural inheritance across generations is unrivaled by any other species (Tomasello 1999). By bringing cultural, ecological, and other inheritances together within a single evolutionary model, the EES provides a mechanistic framework for understanding the coupled evolution of human cultural and ecological inheritance over generational time.

One major prediction of the EES is that genetic and epigenetic inheritances will tend to predominate in environments that remain stable across generations and become less important in transmitting phenotypic variation across generations as environmental variation increases (Danchin 2013). As cross-generational environmental variation increases, cultural and then ecological inheritances become increasingly important modes of phenotypic trait transmission, as traits that enhance phenotypic plasticity are favored over the inheritance of traits adaptive only under prior environmental conditions (Danchin 2013). Given that ecosystem engineers generally reshape environmental patterns and processes at levels that alter environmental conditions experienced by later generations, the role of ecological and cultural inheritance in the evolution of phenotypic traits in ecosystem engineers would be expected to increase, even more so in the case of culturally inherited traits for ecosystem engineering, such as tool use and domestication (O'Brien and Laland 2012). To understand long-term anthropogenic ecological changes caused by culturally transmitted traits for ecosystem engineering, it is necessary to understand how these cultural traits evolve, supported by exceptional human capacities for social learning and sociality that have

Box 1. Elements of human sociocultural niche construction (SNC) theory.

Points in boldface correspond to sections in the text with the same heading. Terms are defined in Table 1.

1) Ecosystem engineering, niche construction, and ecological inheritance

1.1) Allogenic ecosystem engineers engage in environment altering behaviors, including nest building, bioturbation, and agriculture.

1.2) To the extent that ecosystem engineering behaviors produce adaptive advantages and disadvantages, this constitutes niche construction, and produces ecological inheritance.

2) Inclusive inheritance, cultural inheritance, and the Extended Evolutionary Synthesis (EES)

2.1) Natural selection acts on a combined vector of inheritances (inclusive inheritance) comprising not only genetic and epigenetic inheritance (heritable alterations of gene expression), but also nongenetic inheritances, including parental effects, cultural inheritances, and ecological inheritances.

2.2) Inheritances may be transmitted vertically (parent to offspring), obliquely (older to younger), and horizontally (across individuals). Natural selection can act on all of these transmission pathways.

2.3) When environments remain stable across generations, genetic and epigenetic inheritances tend to be the predominant form of adaptive trait transmission.

2.4) When environments change substantially between generations, nongenetic inheritances, especially cultural and ecological inheritances, become increasingly important for adaptive trait transmission.

2.5) Ecosystem engineers cause environmental change. As a result, ecological and cultural inheritances are favored mechanisms for adaptive trait transmission in ecosystem engineering species, especially those with culturally inherited traits for ecosystem engineering, like humans.

2.6) To the extent that socially learned ecosystem engineering behaviors produce adaptive benefits or detriments, this is cultural niche construction.

3) Cultural evolution

3.1) Cultural inheritances evolve by processes of natural selection acting on traits transmitted vertically, obliquely, and horizontally.

3.2) Human cultural inheritances include languages, technologies, social strategies for ecosystem engineering, foraging, societal organization and interaction, material and labor exchange, warfare, and defense.

3.3) Cultural traits can evolve far more rapidly than genetic and epigenetic traits owing to natural selection acting on horizontal inheritances within a single generation, because selection can act on novel combinations of preexisting cultural inheritances (e.g., the "recipe" for manufacturing a tool"), and because selection can also act at the scale of interacting social groups or societies.

4) Human ultrasociality and the human sociocultural niche (see also Box 2)

4.1) Behaviorally modern humans are ultrasocial, with unrivalled capacity for high-fidelity transmission of cultural traits, exemplified by human capacity for language together with unrivaled capacity to form, sustain, and depend for survival on complex non-kin social relationships and cooperative material and labor exchanges within and across social groups and societies.

4.2) Behaviorally modern humans occupy a sociocultural niche, as cultural traits enable individuals to sustain themselves and their progeny within social groups and societies (sociocultural systems) and to form and sustain the structure and functioning of both the sociocultural systems and the engineered ecosystems, exchange networks, and other subsistence regimes that support human populations.

4.3) The human niche evolves in response to changes in social organization brought about both by cultural evolution and the environmental changes caused by cultural niche construction.

4.4) The unique human capacity for shared intentionality enables individual choices to scale up to larger group decisions; individual humans and social groups act as agents deciding and acting within culturally inherited but dynamic sociocultural systems that emerge from these interactions.

5) The ratchet effect and runaway cultural niche construction.

5.1) Cultural traits have overwhelmed genetic traits in shaping the human niche, in part because of more rapid processes of cultural evolution, including horizontal trait selection, the ratchet effect, and runaway cultural niche construction.

6) Human sociocultural niche construction (SNC).

6.1) Long-term changes and diversification of the human niche and the upscaling of human societies and their capacity to transform the biosphere (Box 2) can be explained by combining cultural niche construction, culturally mediated social organization, and cultural evolution into a single theory of sociocultural niche construction.

TABLE 2. Recommended readings.

Topic	Reference
Niche construction theory	
Core book	Odling-Smee et al. (2003*c*)
Review for ecologists	Matthews et al. (2014)
Extended Evolutionary Synthesis	
General review	Danchin et al. (2011)
Research challenges	Danchin (2013)
Cultural evolution	
Core book	Richerson and Boyd (2005)
Research synthesis	Mesoudi et al. (2006)
Brief summary	Castro and Toro (2010)
Evolution and human behavior	Laland and Brown (2011)
Human ultrasociality	
Behavioral sciences	Tomasello et al. (2005)
Anthropology	Hill et al. 2009)
Human niche construction	
Social learning and sociality	Sterelny (2011)
Domestication	Smith (2012)
Social sciences	
Societal types, macrosociology	Nolan and Lenski (2010)
Social change, world systems theory	Chase-Dunn and Lerro (2013)
Archaeology	
Human ecology theory	Butzer (1982)
Environmental change	Redman (1999)
Anthropocene	
Global change	Steffen et al. (2007)
Terrestrial ecology	Ellis (2011)
Archaeology	Smith and Zeder (2013)
Paleontology	Barnosky (2014)
Geology	Zalasiewicz et al. (2012)

enabled the emergence and evolution of sociocultural systems of unprecedented scale, complexity, and power.

Cultural evolution

Darwin used cultural analogies to explain biological evolution (Darwin 1859, Mesoudi et al. 2004) and addressed human cultural evolution directly (Darwin 1871), helping to spark the production of a superabundance of theory: much of it incorrectly interpreting Darwin (Mesoudi et al. 2004, Laland and Brown 2011). At least three major theoretical frameworks now address human cultural evolution (Laland and Brown 2011): sociobiology (Wilson 1975), gene–culture coevolution (Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985, Durham 1991), gene–culture coevolution plus niche construction (closely related to the EES; Laland et al. 2000), and a fourth framework, less popular among evolutionary theorists, of "memetics," with "memes" serving as the cultural equivalent of genes (Dawkins 1976, Blackmore 1999, Laland and Brown 2011). Sociobiology explains behavior genetically, avoiding cultural inheritance, while noting that "the most spectacular cultural advances [of humans] were impelled by the invention of new ways to control the environment" (Wilson 1975). Memetics applies evolutionary theory to socially learned information ("memes"), focuses primarily on horizontal, not cross-generational transmission, and generally ignores interactions with ecological processes (Henrich et al. 2008). Gene–culture coevolution, or "dual-inheritance" theory, explains the coupled evolution of genetic and cultural traits, such as lactose tolerance in dairy farming societies, without incorporating ecological inheritance (Laland and Brown 2011).

Gene–culture coevolution plus niche construction integrates genetic, cultural, and ecological inheritances in a form capable of explaining the evolution of cultural traits for ecosystem engineering. The theory was developed by integrating gene–culture coevolution (Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985) with ecological inheritance (Laland et al. 2000, Mesoudi et al. 2006, 2013, Bonduriansky and Day 2009) to explain genetic changes in societies engaged in ecosystem engineering, such as increased frequencies of malaria-resistance genes in rainforest yam-cultivating societies; an adaptive genetic response to malaria-carrying mosquitos that are an indirect detrimental ecological inheritance of cultivating yams in rainforests (Laland et al. 2000). By considering this theory as a subset of the EES (setting aside epigenetics and parental effects) in which genetic, cultural, and ecological inheritances interact in producing phenotypic outcomes, we obtain a mechanistic basis for explaining cross-generational changes in cultural niche construction (Table 1): the engineering of ecosystems by socially transmitted behaviors that produce heritable adaptive benefits and/or detriments (Laland et al. 2000, 2001, Mesoudi et al. 2006, 2013, Smith 2007*a*, Bonduriansky and Day 2009, Boyd et al. 2011, Kendal et al. 2011, Laland and O'Brien 2012, O'Brien and Laland 2012).

Mechanisms of cultural evolution.—Culture is "the part of phenotypic variation that is inherited socially (that is, learnt from others)" (Danchin et al. 2011). Four criteria distinguish whether a specific trait, or variant, is culturally inherited and therefore capable of undergoing evolution by natural selection (Danchin et al. 2011). First, a cultural trait must be socially learned and not inherited by another transmission pathway or acquired by individual ("asocial") learning. Second, cross-generational transmission of the trait must occur, generally from older to younger generations (vertical or oblique transmission). Third, organisms must exhibit the trait for sufficient time and in such a way that others are capable of learning it. And fourth, the trait must be expressed and selected for under differing environmental conditions, because traits expressed or selected for only within a single non-repeating environmental condition cannot be selected for across generations. By these criteria, cultural inheritance is evident in many nonhuman animal species, including the social learning of foraging strategies, tool use, mate choice, and song dialects, though comprehensive evidence meeting all four criteria is still lacking in nonhumans (Tomasello et al. 1993, Danchin et al. 2011). In humans, however, evidence for cultural inheritance and cultural evolution is overwhelming (Henrich and McElreath 2003, Laland and Brown 2011, Mesoudi 2011, Whiten et al. 2011). Primary among the cultural inheritances that humans have specialized in are languages and technology, defined here as cultural information enabling or enhancing the behavioral capacity of organisms beyond their biological capabilities, from the use of tools and the control of fire, to the manufacture of advanced machines and computers (Table 1; Pfaffenberger 1992).

Macro- and microevolution of human cultural traits across generations including toolmaking and other technologies has been confirmed by mechanistic and empirical investigations both across societies (macroevolution) and within societies and social groups (microevolution) (Basalla 1988, Henrich and McElreath 2003, Mace and Holden 2005, Mesoudi et al. 2006, Bettinger 2009, Boyd et al. 2011, Mace and Jordan 2011, Mesoudi 2011, Whiten et al. 2011). That many human behavioral traits are cultural is beyond question; individuals of different cultures readily acquire and maintain cultural traits learned from each other (Laland and Brown 2011). While the units of cultural inheritance remain subject to ongoing scientific debates, it has been demonstrated that the existence of cultural "replicators" analogous to genes (e.g., memes) is not an absolute requirement for culture to be inherited, only some form of copying behavior that leads to some level of cross-generational transmission, whether vertical, oblique, or horizontal (Mesoudi et al. 2004, Henrich et al. 2008, O'Brien et al. 2010).

For cultural traits to evolve by natural selection across human generational time requires that these traits must vary within generations, be transmissible across generations, and cause differential effects on fitness, such that the frequencies of cultural traits vary over generations in response to selective pressures. All of these properties are well confirmed for cultural traits (Henrich and McElreath 2003, Mesoudi et al. 2006, Mesoudi 2011, Whiten et al. 2011). The generation of novel and variant cultural traits by asocial processes of innovation and trial and error experimentation provides a source of cultural trait variation analogous to the role of mutation in biological evolution (Cavalli-Sforza and Feldman 1981, Laland et al. 2000, Mesoudi and O'Brien 2008*b*, Laland and Brown 2011). Cultural traits are transmitted with high fidelity both vertically and obliquely by human behaviors that include the copying of common cultural traits (conforming), the imitation of high-performing cultural traits, and the teaching of traits to progeny and non-kin individuals (Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985, Tomasello et al. 1993, Richerson and Boyd 1998, Eerkens and Lipo 2007, Laland et al. 2007, 2010, Chudek and Henrich 2011, Laland and Brown 2011, Lewis and Laland 2012). Long-term trends in cultural traits also show patterns analogous to those observed for genetic traits (Cavalli-Sforza and Feldman 1981, Mesoudi et al. 2006, Laland and Brown 2011: Table 6.1), including long-term phylogenetic trends in languages and material culture, such as arrowheads (Table 1; Mace and Holden 2005, Eerkens and Lipo 2007, O'Brien et al. 2010, Gray et al. 2011, Mace and Jordan 2011, Shennan 2011*a*), the accumulation of cultural information, diversity, and complexity (Mesoudi et al. 2004, Foley and Mirazón Lahr 2011), convergent patterns such as writing and domestication (Mesoudi et al. 2004), extinctions (Mesoudi et al. 2006), and the persistence of vestigial patterns like the QWERTY keyboard (Basalla 1988).

Studies of African tribes have demonstrated that most human cultural trait transmission may be vertical, not horizontal (Guglielmino et al. 1995). Nevertheless, high levels of horizontal cultural trait transmission occur especially in larger scale societies, and frequencies of cultural traits can vary dramatically within generations and within and across human social groups and societies (Mesoudi et al. 2006, Henrich et al. 2008, Laland and Brown 2011, Godfrey-Smith 2012). Selection processes acting on horizontally transmitted cultural traits within the span of a human generation can enable cultural traits to evolve far more rapidly than genetic traits (Henrich and McElreath 2003). While the horizontal transmission of genetic traits is important in microorganisms, rates of horizontal transmission of human cultural traits and their selection at group and population levels adds new levels of complexity to evolutionary patterns and processes (Henrich et al. 2008, Laland and Brown 2011, Godfrey-Smith 2012). For example, horizontal exchanges of words and technologies across societies ("cultural borrowing") challenges phylogenetic analysis of human cultural history, blending together the branches of otherwise tree-like cultural lineages (Gray et al. 2010). And that is only the beginning of the evolutionary complexities introduced by cultural inheritance.

Cultural inheritances may amalgamate other cultural inheritances; for example, the knowledge needed to manufacture a complex tool, which archaeologists conceive of as "recipes," combining the preparation of raw materials, tool construction, use, repair, and maintenance (Mesoudi and O'Brien 2008*a*). Even greater complexity is added by the potential for cultural inheritance to alter the adaptive fitness of entire groups or societies, with the result that natural selection has the potential to act at the level of entire competing groups of kin and/or non-kin individuals through the adaptive advantages of social foraging, collective strategies for warfare and defense, material exchange, and even the collaborative advantages of language (Boyd and Richerson 1985, Henrich 2004, Bowles 2006, 2009, Laland et al. 2010, Apicella et al. 2012, Rand and Nowak 2014). Given the clear adaptive fitness benefits for individuals, groups, and individuals within groups engaging in collaborative social behaviors, it is not surprising that selective processes acting at all of these levels are implicated in the evolution of the unprecedented social behaviors present in humans (Boyd and Richerson 1985, Chudek and Henrich 2011, Rand and Nowak 2014).

Human ultrasociality and the human sociocultural niche

Two exceptional patterns of human social behavior are needed to explain the emergence of humans as a global force transforming the biosphere. The first is the unrivalled capacity of humans to transmit information by social learning, exemplified by human use of language (Tomasello 1999, Hill et al. 2009, Pinker 2010, Dean et al. 2012, Morgan et al. 2015). Compared even with close relatives, including chimpanzees and apes, humans are far more capable of social learning across both kin and non-kin individuals, and especially across generations (Tomasello 1999, Pinker 2010, Laland and Brown 2011, Dean et al. 2012, Morgan et al. 2015). Second, humans have unparalleled capacity to form, sustain, and depend for survival on complex non-kin relationships, easily marking humans as the most ultrasocial species on Earth (Campbell 1983, Richerson and Boyd 1998, Fehr and Fischbacher 2003, Tomasello et al. 2005, Boyd and Richerson 2009, Hill et al. 2009, Boyd et al. 2011, Apicella et al. 2012, Turchin et al. 2013, Tomasello 2014).

There is increasing evidence that some aspects of the exceptional human capacity for social learning, including use of languages, is supported by genetic traits, some of which have been identified recently as specific to *Homo sapiens*, including a variant of FoxP2 (a protein involved in brain development and language), among others (Enard et al. 2002, Tomasello et al. 2005, Laland et al. 2010, Dean et al. 2012, Fisher and Ridley 2013, Pääbo 2014). Gene–culture coevolution is strongly implicated in the early evolution of human genetic traits supporting both social learning and ultrasociality (Boyd and Richerson 1985, Laland et al. 2010, Chudek and Henrich 2011, Gintis 2011, House et al. 2013), and molecular genetic comparisons among extant humans, extinct hominins, and other close relatives is enabling unprecedented breakthroughs in understanding the evolution of human genetic traits relating to social learning and ultrasociality over thousands to millions of years (Pääbo 2014).

Yet the role of genetics in explaining the emergence of modern human behaviors ~60 000 years ago in Africa has remained controversial (Henshilwood and Marean 2003, Mellars 2005, Nowell 2010, Fisher and Ridley 2013, Klein 2013, Sterelny 2014). Some experts argue that a genetic mutation or other major genetic change is required to explain the relatively sudden and widespread emergence of the suite of modern human behaviors (Klein 2013), which include symbolic inscriptions, lithic projectile point weapons, personal ornaments, rapid changes in tools and technologies, more highly structured settlements, and long-distance trade (Mellars 2005, Hill et al. 2009, Nowell 2010). Others explain this based on the need to adapt to rapid environmental changes or heterogeneous environmental conditions (Mellars 2005, Stiner and Kuhn 2006, Potts 2012), to changes in social conditions conducive to social learning (Sterelny 2011), including demographic shifts toward higher population densities enabling greater accumulation of cultural information (Shennan 2001, Powell et al. 2009, Derex et al. 2013), the emergence of exchange-based economies (Sterelny 2014), increased intergroup conflict or cooperation (Mellars 2005, Stiner and Kuhn 2006), and by other factors and combinations of factors (Powell et al. 2009).

Despite disagreements on the role of genetics in the emergence of behavioral modernity, there is broad consensus that the behaviorally modern human populations that spread out of Africa more than 50 000 years ago possessed genetic capacities for social learning and sociality that were functionally equivalent to those of human populations today (Sterelny 2011, Pääbo 2014). Human genetic evolution continues to respond to ecological pressures including diseases and environmental conditions, some of which have resulted from human sociality, such as high population densities, trading networks, and engineered environments (Laland et al. 2010, Richerson et al. 2010, Rendell et al. 2011). Nevertheless, genetic changes cannot explain long-term changes in modern human behaviors that support social learning and sociality or their effects on the structural organization of human societies.

Human cultural traits for sociality have evolved over the long term. For example, common social behaviors within hunter-gatherer societies, such as high degrees of resource sharing, are incompatible with those common in industrial societies (Richerson and Boyd 1998, 1999, Henrich et al. 2001, Smith et al. 2010*a*). Human social institutions, including formal and informal rules, conventions, and other forms of socially learned information that regulate and structure human relationships within societies and sometimes across societies, have also changed significantly over the long term and also show great diversity across and sometimes within societies (Richerson and Boyd 1999, Hodgson 2002, Boyd and Richerson 2008, Kaplan et al. 2009, Pinker 2010, Henrich 2015).

Cultural traits are what enable behaviorally modern humans to sustain themselves and their progeny within social groups and societies and cultural traits also produce and sustain the social organization of these groups and societies; both are the product of ongoing cultural evolution (Richerson and Boyd 1999, Henrich et al. 2001, Hodgson 2002, Hill et al. 2009, Kaplan et al. 2009, Smith et al. 2010*a*, Boyd et al. 2011, Sterelny 2011). As a result, the human niche is largely sociocultural; defined within the patterns and processes of sociocultural systems together with the altered ecosystems that sustain them. Further, the human niche is also dynamic in response to changes in social organization brought about both by cultural evolution and the environmental changes caused by cultural niche construction.

Human agency and intentionality.—Sociocultural systems emerge and reproduce through the interactions of individual humans and social groups as agents deciding and acting within culturally inherited social structures ("structuration theory"; Giddens 2013). While the actions of individuals within sociocultural systems can depend largely on culturally inherited traits (Richerson and Boyd 1999, Henrich et al. 2001), individuals and groups choose among and adopt cultural traits in different ways, such as copying the most common traits in a population or group vs. copying those of high-status individuals or groups or even low-status groups, yielding substantial variance and unpredictability in individual, group, and societal behavior (Henrich 2001, Macy and Willer 2002, Brown et al. 2011*a*, Chudek and Henrich 2011, Gelfand et al. 2011, Wolf and Krause 2014). Though human capacity for cooperative behavior is exceptional, so is human cognitive capacity and behavioral flexibility (Roth and Dicke 2005, Brown et al. 2011*a*). As a result, human agency and individuality of choice are key determinants of the emergent behavior of sociocultural systems and groups, such that culturally inherited social structures and behaviors alone are incapable of fully predicting individual, group, or societal behavior (Macy and Willer 2002, Brown et al. 2011*a*, Gelfand et al. 2011, Smith 2013*b*). Further, humans have a capacity for shared intentionality not present in any other species (fourth-order intentionality): the ability to interpret the intentions of others and to act cooperatively with these intentions, enabling individual choices to scale up to larger group decisions (Dunbar 1998, Tomasello et al. 2005, Dean et al. 2012). This unrivalled ability to act intentionally and cooperatively adds another dimension to the consequences of human agency: intended vs. unintended consequences, together with social responsibility for these consequences. For example, ecosystem engineering by tilling soils might yield a combination of its intended beneficial direct consequence, enhanced food supply, together with unintended detrimental direct consequences, such as a long-term decline in soil fertility, and unintended indirect detrimental consequences, such as water pollution, with sediments affecting human populations downstream.

The ratchet effect and runaway cultural niche construction

Though human individuals and social groups can act intentionally to alter sociocultural systems and ecosystems, long-term, cross-generational changes in sociocultural systems and human-engineered ecosystems are shaped largely by processes of cultural evolution. The overwhelming importance of cultural over genetic traits in human niche construction is explained partly by the observation that cultural traits can evolve much faster than genetic traits. While cultural traits have been observed to evolve slowly, at rates similar to those of genetic traits (for example, the evolution of technologies for stone tool manufacture by early hominins [Laland et al. 2000, Nolan and Lenski 2010: Table 5.1]), the hypothesis that cultural traits can evolve far more rapidly than genetic traits has had wide support since it was first proposed by Darwin (Mesoudi et al. 2004, Richerson and Boyd 2005, Eerkens and Lipo 2007). Horizontal transmission and selection among cultural traits within a single human generation is one process that can enable cultural traits to evolve faster than genetic traits (Henrich and McElreath 2003). The "ratchet effect" is a further cause of rapid cultural evolution, as cultural traits can build upon and combine earlier cultural traits to produce increasingly complex and powerful cultural traits such as cultural institutions (e.g., languages, legal systems) and advanced technologies (projectile weapons, the automobile) that enable cultural accumulation to accelerate across generations (Tomasello 1999, Laland et al. 2000, Dean et al. 2014).

Perhaps the most powerful mechanism supporting rapid cultural change is "runaway" cultural evolution, in which changes in culture must be adapted to by further changes in culture, which in turn require additional cultural adaptations, generating accelerating rates of cultural change across generations (Boyd and Richerson 1985, Laland et al. 2000, Richerson and Boyd 2005). This runaway effect can even increase the frequency of maladaptive cultural traits, such as when individuals copy the prestige-seeking behaviors of influential or successful members of their society, such as costly adornments, grave monuments, and other forms of conspicuous consumption (Boyd and Richerson 1985, Boyd et al. 2011).

Rates of evolution of cultural traits for ecosystem engineering (cultural niche construction) appear to have become so rapid that they have overwhelmed natural selection for human genetic adaptations to environments (Laland et al. 2000, 2001). The central mechanism proposed to explain this is runaway cultural niche construction, in which socially learned traits for ecosystem engineering cause environmental changes that must be adapted to by additional cultural traits (Rendell et al. 2011, Laland and O'Brien 2012). For example, tillage of soils to produce crops reduces soil productivity over time, requiring fallowing, manuring, or other cultural practices to maintain the productivity of soils across generations. The use of antibiotics and the development of antibiotic resistance, requiring further antibiotic development, is another. By processes of runaway cultural niche construction combined with the ratchet effect, cultural traits for niche construction tend to become increasingly adaptive, complex, and powerful across generations, the evolution of these traits is accelerated, and populations become more and more dependent on cultural traits for ecosystem engineering to sustain themselves (Laland et al. 2007, Rendell et al. 2011).

There are further explanations for increasing human dependence on cultural niche construction. Socially learned traits for ecosystem engineering have the potential to support larger human populations, and larger populations have the potential for more rapid cultural evolution, especially in small-scale societies (Shennan 2001, Kline and Boyd 2010, Derex et al. 2013). Population pressures in themselves can drive demand for cultural adaptations to larger and denser populations, a potential explanation for observed relationships between cultural complexity and population among hunter-gatherers (Keeley 1988, Powell et al. 2009, Muthukrishna et al. 2014, Vegvari and Foley 2014). But no matter what the mechanisms, there is no question that socially learned practices of ecosystem engineering have changed dramatically over the past 50 000 years and increased in their transformative capacity and complexity together with the diversity, scale, and complexity of human sociocultural systems and their transformations of the biosphere.

Human sociocultural niche construction

By combining cultural niche construction, culturally mediated social organization (ultrasociality), and cultural evolution into a single theory of sociocultural niche construction (SNC; Tables 1 and 2, and Boxes 1 and 2), the observation of dramatic long-term changes in and diversification of the human niche can be explained, together with the capacity of human societies, to transform the biosphere. Just as species engage in cultural niche construction when their socially learned behaviors alter environments in ways that produce heritable adaptive consequences, humans engage in sociocultural niche construction when their socially learned behaviors are enacted socially, altering both the organization of their societies and the environments that sustain them in ways that produce heritable adaptive consequences. As with cultural niche construction, sociocultural niche construction, unfolding across generations, tends to cause increasing dependence on cultural traits for survival and reproduction, including technology, socially learned subsistence strategies for cooperative ecosystem engineering, and non-kin subsistence exchange (the socially mediated exchange of materials, labor, and information to meet subsistence needs; Table 1). To the extent that subsistence strategies for cooperative ecosystem engineering and subsistence exchange are socially learned and socially enacted (dependent on cooperative efforts across groups or societies rather than individuals acting alone), these are "subsistence regimes" (Table 1), or cooperative processes that sustain social groups and societies that cannot be implemented by individuals alone.

Evidence for human sociocultural niche construction is presented in Box 2. As processes of sociocultural niche construction have evolved across generations, the human niche has broadened dramatically, diversified within and across social groups and societies, and has become increasingly social, such that most human individuals have come to depend more and more on complex networks of social interaction and non-kin subsistence exchange for their survival and they do this at increasing spatial scales (Hill et al. 2009, Kaplan et al. 2009). Increasing dependence on non-kin subsistence exchange networks has, in turn, enabled human societies to become increasingly specialized, complex, and hierarchical (Hill et al. 2009, Nolan and Lenski 2010, Chase-Dunn and Lerro 2013), with individuals specialized in different socially learned productive capacities cooperating with unrelated and often unknown individuals through long-distance exchange networks to accomplish complex tasks. One example is the production of shell-bead garments, which require shell harvest and preparation in coastal areas, long-distance trade (social exchange), the production of hides or textiles in an upland area, and their integration by a skilled bead worker in another area. Specialization and exchange in subsistence regimes have made it possible for human individuals to subsist apart from any direct interactions with ecosystems (though not without indirect interactions, or telecoupling; Table 1), with all subsistence needs met through exchange networks of subsistence producers (i.e., farmers, fisherman), processors (food preparation), providers (traders), and potentially many more specialists (tool makers, irrigation experts, bankers) in complex and dynamic subsistence supply chains ("subsistence webs") inviting further study as "sociotrophic relations."

As specialization and exchange have increased, human interactions with ecosystems have increasingly become societal interactions based on subsistence regimes enacted by ever-larger groups of cooperating specialized individuals and groups guided by accumulated cultural inheritances of social organization, social exchange, and technological capacities far beyond those of any human individual. The human sociocultural niche is a function of the accumulated cultural inheritance of societies and is therefore the product of and subject to cultural evolution (Hill et al. 2009, Kaplan et al. 2009, Boyd et al. 2011).

SOCIAL CHANGE: SOCIETAL SCALE, COMPLEXITY, TECHNOLOGY, AND INTERACTION

As with biological evolution, there is no simple progressive pathway describing the rise, diversification, and extinction of societies, or the observed tendency toward increasing scale and complexity. Some of the earliest forms of sociocultural systems, such as hunter-gatherer societies, are remarkably complex and have endured to the present day, sometimes in the face of pressures from larger scale societies (Marlowe 2005). Yet, as with the convergent evolution of similar phenotypes across taxa, human sociocultural systems, while tremendously diverse, complex, and heterogene-

Box 2. Evidence for human sociocultural niche construction (SNC).

1) The human ecological niche has changed dramatically over time.
    1.1) Rates of change in the human niche appear to be more rapid than possible by biological evolution, and these rates of change appear to be generally increasing over time.
2) The human ecological niche is not predictable from human biology.
    2.1) Human genetic variation does not account for variation in human subsistence strategies or habitat preferences, over space or time.
    2.2) Genetically similar, demographically equivalent human individuals and populations within the same environment can engage in extremely different livelihood strategies based on socially learned behaviors.
    2.3) Human use of biotic and abiotic resources and alteration of ecosystems is not strictly density dependent. Profoundly different demands and effects are observed at similar population densities in similar environments. These differences are generally associated with differences in sociocultural systems.
3) The human ecological niche is broader and more diverse than that of any other species.
    3.1) Humans live under a broader range of environmental conditions than any other multicellular species and are more widely distributed across the Earth.
    3.2) Humans utilize a wider range of biotic, abiotic, and energy resources than any other species.
    3.3) Humans engineer ecosystems and apply selective pressures to species by a larger number of diverse practices and at levels and scales greater than that of any other species.
4) Different human societies and social groups transform ecology in a variety of different ways.
    4.1) When one socioculturally distinct group displaces another across a given region, ecological pattern and process generally tend to change as well.
    4.2) Human populations and their effects can be dynamic in stable environments, stable in dynamic environments, and vice versa.
    4.3) Human populations and their effects can be heterogeneous across homogeneous environments or homogeneous across heterogeneous environments, and may or may not follow pre-existing environmental patterns.
5) Humans depend on non-kin subsistence exchange far more than any other species.
    5.1) Humans engage in prosocial non-kin interactions at the expense of individual fitness. This trait shows both genetic and cultural inheritance.
    5.2) Humans regularly exchange materials, biota, energy, and information across extensive, complex, and dynamic non-kin networks. These social exchanges may now be daily, global, and even extraterrestrial.
    5.3) Human populations can depend entirely on non-kin exchanges of food and other necessary material and energy resources with other populations for survival.
    5.4) Non-kin exchange can sustain the long-term growth and development of human populations, decoupling them from the use of local ecological, material, and energy resources.
    5.5) Non-kin exchange can facilitate the utilization and accumulation of resources at much higher levels than possible by utilizing local resources.
    5.6) Subsistence and other demands of human populations can exert ecological effects over long distances by means of non-kin exchange relations (trade/telecoupling).
    5.7) The relative scale and distance of trade/telecoupling has tended to increase over time.
6) Socially learned subsistence strategies for ecosystem engineering and non-kin exchange exhibit cross-generational heritability and evolution by natural selection.
    6.1) Selection for desired traits has been applied to some species for millennia, yielding domesticates with little resemblance to ancestral species that reproduce poorly without human help (e.g., maize, wheat, dogs).
    6.2) Anthropogenic ecosystems requiring high levels of human maintenance have been sustained for centuries to millennia (e.g., rice paddy irrigation systems, cities).
    6.3) Socially learned subsistence strategies for ecosystem engineering and specialized exchange including agriculture and craft industries have been transmitted with high fidelity across large numbers of generations and disparate populations and societies.
    6.4) Variants of socially learned subsistence strategies, including technologies, tools, and institutions governing social exchange show long-term changes in frequencies and phylogenetic relationships demonstrating that competition, selection, and accumulation of variations in these strategies have occurred over generations.
7) The scale, structural complexity, specialization, and ecological transformative capacity of human societies and their subsistence strategies vary tremendously and have tended to increase over the long term.
8) Human alteration of local and global environments is now greater than that of any other multicellular species.

TABLE 3. Human sociocultural systems classified by primary subsistence regime, in order of historical emergence, based on Lenski (1966), and updated by Nolan and Lenski (2010) using data from Murdock and White (1969, 2006).

A) Qualitative

Sociocultural system	Subsistence regime†	Technological innovations†	Cultural and institutional innovations‡
Hunter-gatherer	hunting, foraging	land clearing using fire, social hunting, food processing and cooking, projectiles, ceramics	languages, barter, permanent settlements, tribes
Simple horticultural	long fallow shifting cultivation	domestication, tillage (hoe)	land ownership, trade, villages
Herding	nomadic pastoralism	horse warfare	extended trading networks
Advanced horticultural	short fallow shifting cultivation, conquest	nonferrous metals (weapons), manuring, terracing	warfare/raiding, chiefdoms
Simple agrarian	continuous subsistence agriculture, handicrafts	plow, animal traction	taxation, writing, numeracy, cities, states
Advanced agrarian	subsistence and commercial agriculture, specialized crafts	iron (tools), irrigation, roads, printing, regional trade	coined money, empires
Industrial	commercial agriculture, manufacturing	fossil energy, synthetics, rapid bulk transport, telecommunication	capitalist states, banking, global trade, science
Post-industrial	commercial agriculture, services	nonbiological energy, internet, genetic engineering, robotics	international governance, global peer exchange

B) Quantitative

Sociocultural system	Scale§ (median population)	Social complexity¶ (% complex)	Specialization# (% specialized)	Energy|| (GJ·person^{-1}·yr^{-1})		Density†† (persons/km^2)
				Total	Food	
Hunter-gatherer	40	0	0	8	5	2
Simple horticultural	1500	1	2	nd	5	35
Herding	6000	nd	9	nd	6	nd
Advanced horticultural	5000	7	22	nd	5	110
Simple agrarian	$>10^5$	51	34	18	6	>250
Advanced agrarian	...	...	...	40	9	urban
Industrial	$>10^7$	100	100	118	11	urban
Post-industrial	$>10^9$	100	100	350	15	urban

Notes: Hybrid systems are common (e.g., "industrializing agrarian" equates to industrial plus agrarian), especially in larger and more complex societies. Fishing, maritime, and other less common societies are not included; "nd" represents no data. Some data shown in the simple agararian sociocultural system row apply to an "agrarian" system, and could not be separated into advanced and simple agrarian sociocultural systems (shown in the advanced agrarian row with ellipses).

† Based on Nolan and Lenski (2010): Table 4.1.

‡ Cultural system where earliest form of cultural and institutional innovations have been observed (Chase-Dunn and Lerro 2013).

§ Median population size of societies, by type of society, from Nolan and Lenski (2010): Table 4.2.

¶ The percentage of societies having complex status systems, from Nolan and Lenski (2010): Fig. 4.3.

The average frequency of craft specialization across societies, by type of society, from Nolan and Lenski (2010): Table 4.3.

|| Approximate total and food energy consumption per capita from Table 6.1 in Christian and McNeill (2004). Total energy = home + agriculture + commerce + industry + transport. Food energy = food + animal feed. Industrial estimates ca. 1850.

†† Median population density, by type of society, from Table 6.1 in Nolan and Lenski (2010). "Urban" refers to societies in which high-density urban populations are spatially distant from the lower density agricultural lands that sustain them (decoupling).

ous, also show some converging patterns over time. These basic patterns have been categorized by social scientists into societal types based on major differences in their primary subsistence regimes, as described in Table 3 (Lenski 1966, Nolan and Lenski 2010).

To understand the emergence and divergence of sociocultural systems over time, it must first be noted that the data available in Table 3 are neither complete, nor exclusive: Some societal types are missing, societies regularly intermingle to generate hybrid forms, and the patterns of a given societal type are generally not shared by all societies of the same type. Still, some general patterns of long-term sociocultural change are evident when societal types are ordered in relation to the order of their appearance (Table 3; Lenski 1966, Nolan and Lenski 2010). Over time, the scale of societies has increased by more than five orders of magnitude from the small-scale societies of hunter-gatherers to large-scale industrial societies, and as societal scales have increased, so have societal complexity, specialization, and technological capacity, along with inequality among individuals within societies in the distribution of resources, social power (the capacity to act independently), and access to environments (Mulder et al. 2009, Nolan and Lenski 2010, Smith et al. 2010*b*, Chase-Dunn and Lerro 2013).

Lenski (1966) introduced a theory of sociocultural evolution to explain these patterns in which the social organization of societies, including their institutions, beliefs, complexity, and degree of specialization are seen as responses to the population sizes and densities sustainable by their primary subsistence technologies "which define the limits of what is possible for a society" together with the accumulation of these and other cultural inheritances over time through cultural evolution (Nolan and Lenski 2010). In other words, technological innovation and its accumulation through cultural inheritance are theorized as the ultimate drivers of long-term social change. Lenski's theory also holds that societies evolve over the long-term both through internal processes and by competition, exchange, and other interactions among societies within a "world system" (Table 1). While Lenski's (1966) theory of sociocultural evolution has not garnered mainstream support, his identification of long-term societal trends and theory of world systems remain core elements of contemporary sociology and anthropology (Chase-Dunn 2006, Nolan and Lenski 2010, Hall et al. 2011, Chase-Dunn and Lerro 2013).

Of the many theories explaining long-term societal change, all tend to incorporate relationships among human demographics, subsistence technologies, and other cultural inheritances (cultural complexity), social organization, and institutions (social complexity and inequality), and some also include energy use (White 1959, Flannery 1972, Butzer 1982, Redman 1999, Redman et al. 2004, Sanderson 2006, Tainter 2006*b*, Abrutyn and Lawrence 2010, Nolan and Lenski 2010, Tainter 2011, Butzer 2012, Chase-Dunn and Lerro 2013, Fischer-Kowalski et al. 2014). Another agreement across theories is that most change tends to be gradual, punctuated by relatively abrupt societal transitions or regime shifts (Geels 2002), including episodes of relatively rapid growth and societal collapse, in which populations, technological capacity (linked to energy use), cultural complexity, and social organization tend to change together (Tainter 2006*b*, 2011). The degree to which innovations in technology in themselves determine the long-term patterns of sociocultural change has long been debated without resolution, with theories ranging from "technological determinism" (Smith and Marx 1994) to "social construction of technology" (Bijker et al. 1987) to coevolutionary models of social and technological change (Basalla 1988, Nelson 1994, Redman 1999, Geels 2002, Geels and Schot 2007, Hodder 2011, Brynjolfsson and McAfee 2014, Haff 2014, Morgan et al. 2015). For a variety of reasons, especially the challenge of establishing appropriate models, causal relations among population, technology, cultural inheritances, and social complexity have yet to be established scientifically (Hedström and Ylikoski 2010). Nevertheless, their tight linkage across societal scales and their tendency to change together in regime shifts does imply that these are mechanistically coupled in multicausal relationships.

Interactions among societies also help to explain general long-term trends of societal change. Analogous to competition among individuals, competition among societies, including warfare, should select for cultural traits that enhance adaptive fitness in the face of intersocietal competition, such as weaponry, strategies for warfare, raiding, defense, and avoidance, together with larger scales of social organization (Nolan and Lenski 2010, Chase-Dunn and Lerro 2013, Turchin et al. 2013, Scott 2014). That larger societal scales can become an adaptive advantage over smaller scales is summarized by the "law of cultural dominance," which holds that "larger scale societies tend to destroy or radically alter the cultures of smaller scale societies" (Sahlins et al. 1960, Nolan and Lenski 2010, Chase-Dunn and Lerro 2013). Beyond its strong empirical support and the obvious advantage of numbers, the law of cultural dominance has also been explained by the theory that larger populations have greater capacity for cultural innovation, cultural accumulation, and stronger social organization (Powell et al. 2009, Nolan and Lenski 2010, Chase-Dunn and Lerro 2013, Turchin et al. 2013).

Two other elements of intersocietal interaction are important: subsistence exchange and cultural exchange (Chase-Dunn and Lerro 2013). Starting with the first societies of behaviorally modern humans, exchange through long-distance trade of prestige goods is evident, such as shell beads (Mellars 2006), and this exchange has grown dramatically in bulk and extent as exchange of subsistence goods developed, with an early example being the exchange of wheat from southern European farmers to northern European hunter-gatherers 8000 years ago (Chase-Dunn and Lerro 2013, Smith et al. 2015). The horizontal exchange of cultural information and populations among societies has likely also been a feature of behaviorally modern human societies since the beginning (Bellwood 2001, Mesoudi et al. 2006, Skoglund et al. 2012, Chase-Dunn and Lerro 2013, Barceló et al. 2014). These processes of material and cultural exchange and the intermingling of populations and societies through warfare and emigration have, together with the internal processes of societies, sustained a long-term trend of increasing societal scales, complexities, diversification, interconnection, the accumulation of technology and other cultural inheritances, and ultimately, the emergence of a diverse and complex global-scale world system (Chase-Dunn and Lerro 2013).

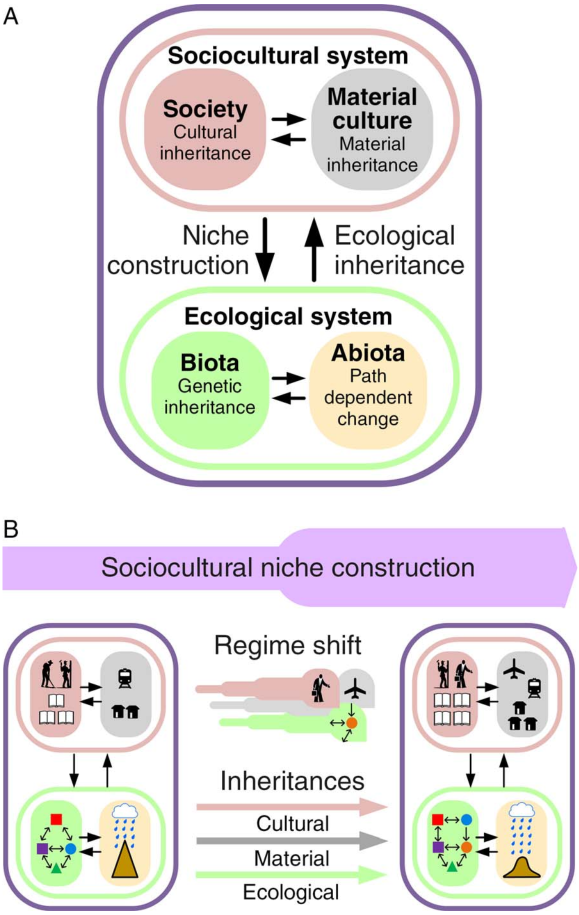

FIG. 2. Conceptual model of (A) an anthroecosystem combining sociocultural and ecological systems through heritable and path-dependent interactions, and (B) long-term, cross-generational changes in anthroecosystems caused by sociocultural niche construction both through gradual variations in inheritances and by regime shifts caused by novel and transformative inheritances and combinations of inheritances. The regime shift illustrated here depicts new trading system (cultural + material inheritance) + facilitated species invasion (orange circle) + new biotic interactions (arrows between shapes in the green oval). The boldface type denotes major systems, and regular type indicate processes. Widening purple bar depicts the increasing role of sociocultural niche construction in shaping anthroecosystem structure and function. Path-dependent abiotic change is depicted here by erosive reshaping of brown landform.

AN EVOLUTIONARY THEORY OF LONG-TERM ANTHROECOLOGICAL CHANGE

By weaving together existing theories of ecosystem engineering, niche construction, inclusive inheritance, cultural evolution, ultrasociality, and social change, we have the basis for a theory explaining the long-term upscaling of human societies and their unprecedented capacity to transform the biosphere through long-term changes in human sociocultural niche construction (Table 1, Boxes 1 and 2). The next step is to integrate these within an evolutionary framework in which sociocultural systems, ecosystems, and sociocultural niche construction are coupled with their cultural, ecological, and material inheritances, as "anthroecosystems" (Fig. 2A). Material inheritances represent the heritable adaptive benefits and detriments of artificial materials and constructs, such as buildings, roads, and pollutants that are produced exclusively by behaviorally modern human societies and are incapable of being produced by natural processes.

In the anthroecosystem framework, sociocultural systems and the biota within ecosystems coevolve through the sustained direct interactions of sociocultural systems and ecosystems across human generational time (Fig. 2A). Anthroecosystems are formed of these systems and their cross-generational interactions, and change through processes of natural selection acting on their cultural, material, and ecological inheritances, with inheritances conferring adaptive benefits to individuals, groups, and societies being selected for, and those producing detriments, against. In such a way, anthroecosystems change through evolutionary processes acting on sociocultural niche construction over the course of human generations, accumulating, losing, and combining cultural, material, and ecological inheritances through gradual processes of selection, accumulation, attrition, and recombination, and also more rapidly by regime shifts in subsistence regimes and social organization (Fig. 2B).

Patterns of long-term change in sociocultural niche construction

By applying the anthroecosystem framework (Fig. 2), we may examine major regime shifts in sociocultural niche construction associated with major societal transitions (Table 3) in terms of their relative cultural, material, ecological, and human genetic inheritances as depicted in Fig. 3A and also their long-term effects on ecosystem transformation and energy use (Fig. 3B). Examples of subsistence regimes producing the cultural, material, and ecological inheritances in Fig. 3A are detailed in Table 4. The emergence of anatomically modern *Homo sapiens* about 200 ka BP (thousands of years before present) is depicted at the far left in Fig. 3, highlighting that control of fire, meat-eating, rudimentary cooking, and the manufacture of stone tools were already established cultural traits of multiple hominin species long before the emergence of our species (Ambrose 2001, Antón et al. 2014). A global timeline of changes in human societies, populations, and ecosystem transformation is presented in Fig. 4.

Hunter-gatherers.—The rise of behaviorally modern human populations in Africa >50 ka BP is associated with a major expansion in the adaptive role of cultural inheritance as a wide array of novel subsistence regimes emerged then, including landscape modification for hunting, use of lithic projectile point weapons for hunting, symbolic and aesthetic expression (symbolic

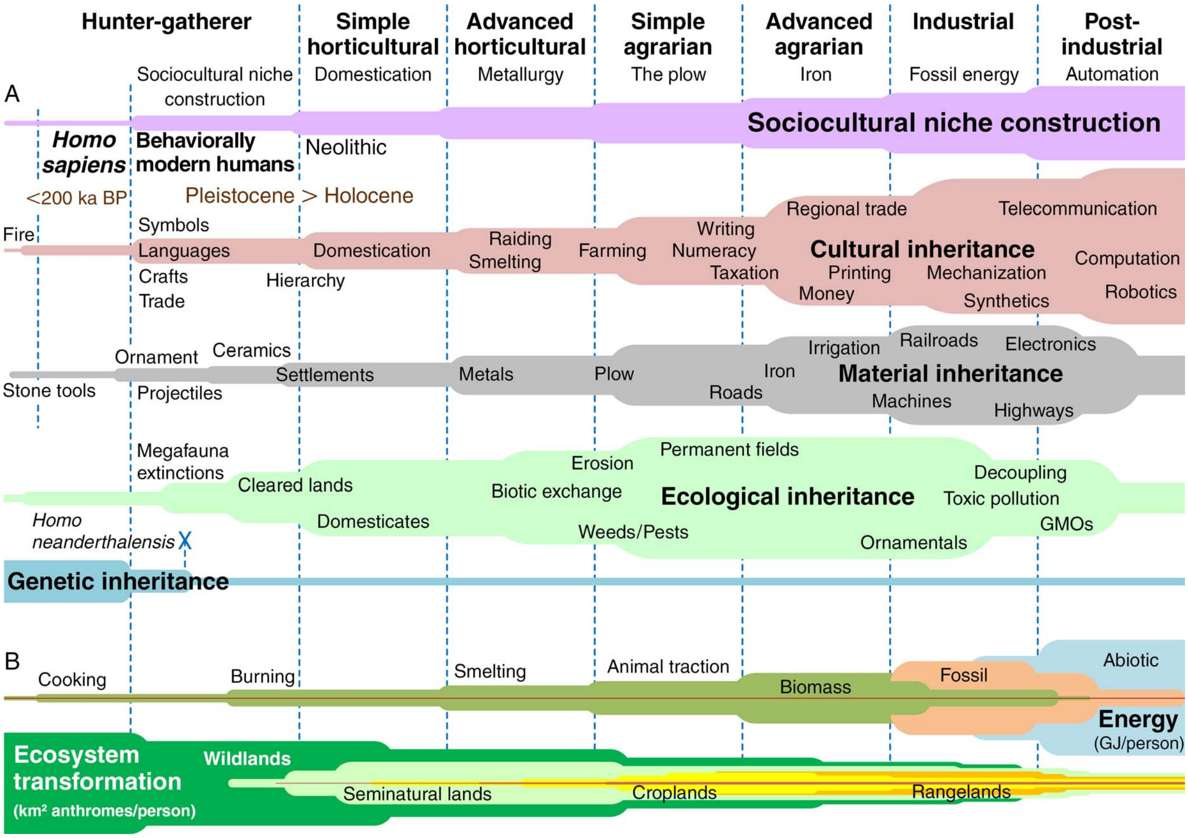

FIG. 3. Conceptual model of regime shifts in human sociocultural niche construction across major types of sociocultural systems (see Table 3). All *y*-axes indicate relative, not absolute, changes. (A) Increasing scales of sociocultural niche construction (widening purple bar); also a proxy for societal scale, median population size and degree of specialization of individuals within societies (Table 3), and their relative production of cultural, ecological, material, and genetic inheritance (relative heights of pink, gray, and green bars). Nonhuman genetic inheritances are incorporated within ecological inheritance. (B) Relative per capita energy expenditure and per capita ecosystem transformation in terms of relative anthrome area used across different types of sociocultural systems (anthrome levels are the same as in Fig. 1B: densely settled is shown with red, cropland is yellow, rangeland is orange, seminatural lands are light green, and wildlands are dark green.

markings, cave paintings, ochre, beads), increasingly complex and standardized tools made from a widened variety of materials, and likely the use of languages to enhance cooperation in foraging, trade, and other social exchange and social organization (Sterelny 2014). Genetic inheritance in hominins narrows through the extinction of *Homo neanderthalensis*, most likely as a result of competition and displacement by larger populations of behaviorally modern humans (Klein 2009). More importantly, runaway sociocultural niche construction begins, with cultural and ecological inheritances surpassing genetic traits in adapting to the environmental alterations and social challenges of living in culturally complex hunter-gatherer societies (Sterelny 2014). The adaptive benefits of material inheritances also began to accumulate through the manufacture and intergenerational exchange of increasingly labor-intensive and complex ornaments, tools, clothing, and other material goods.

Before the Pleistocene had ended and the Holocene began, behaviorally modern human hunter-gatherer societies became established on every continent, initiating the global role of sociocultural niche construction as a force transforming the biosphere through early forms of cooperative ecosystem engineering and other socially learned and implemented subsistence regimes (Kirch 2005, Doughty 2013, Ellis et al. 2013*b*). Early hunter-gatherers introduced anthropogenic fire regimes across the continents, both unintentionally and with the intention to create and maintain open landscapes and early successional ecosystems to enhance their success in hunting and foraging (Cronon 1983, Grayson 2001, Bird et al. 2005, Bowman et al. 2011, Rowley-Conwy and Layton 2011, Smith 2011, Ellis et al. 2013*b*). More complex and sedentary hunter-gatherer societies developed larger populations, a degree of social inequality and hierarchy (Ames 2007, Shennan 2011*b*), and some developed ceramic technologies, the first artificial minerals produced by humans (Craig et al. 2013). Larger populations put greater pressure on plant and animal resources, helping to drive megafauna extinct (Barnosky 2008) and requiring the broadening of

TABLE 4. Sociocultural subsistence regimes and their cultural, material, and ecological inheritance. This table continues on the next page.

Subsistence regime	Cultural inheritance	Material inheritance	Ecological inheritance		Citations
			Human	Nonhuman	
Cooperative hunting	social networking, hunting	none	*+foraging† efficiency (labor + land)*, **overharvest**	**extinctions‡**	Zimov et al. (1995), Stiner and Kuhn (2006)
Cooking	fire, cooking	hearths	*+nutrients from existing foods, new foods, −disease (meat)*, **smoke inhalation, degraded woodlands (fuelgathering)**	+**wildfire, biomass removal**	Wrangham and Conklin-Brittain (2003)
Food processing	food processing, toolmaking	grindstones	*+nutrients from existing foods, new foods (e.g., grasses)*		Wollstonecroft (2011)
Hunting with lithic projectile point weapons	toolmaking	launchers, projectiles	*+foraging efficiency (labor + land)*, **overharvest**	**extinctions**	Shea (2006)
Landscape modification for hunting (corralling, pits, wiers)	hunting, territorial relations	stone traps	*+foraging efficiency (labor + land), steady food,* **overharvest**	**extinctions**	Bar-Oz and Nadel (2013), Smith (2013*a*)
Broadened hunting/foraging strategies (broad-spectrum revolution)	biota identification, utilization	traps, storage systems	*+foraging efficiency (labor + land), new foods*, **overharvest**	**extinctions**	Stiner (2001), Zeder (2012)
Land clearing using fire to enhance hunting/foraging	burning	none	*+foraging efficiency (labor + land), steady food source,* **soil erosion/degradation**	**habitat loss, extinctions, invasions,** habitat gain	Bliege Bird et al. (2008), Bowman and Haberle (2010), Rowley-Conwy and Layton (2011), Smith (2011), Archibald et al. (2012), Lightfoot et al. (2013)
Propagation of desired species	propagation	none	*crops, livestock, +land productivity, steady food*	**invasions**	Smith and Wishnie (2000), Smith (2007*a*, 2011), Fuller et al. (2014), Larson et al. (2014)
Artificial selection for desired traits	breeding, traits	none	*crops, livestock, +land productivity, steady food*	**invasions**	Smith (2007*a*), Fuller et al. (2014), Larson et al. (2014)
Shifting cultivation	farming, toolmaking	digging sticks	*crops, +land productivity, steady food,* **soil erosion/degradation**	**habitat loss, invasions, erosion,** habitat gain	Bellwood (2004), Smith (2007*a*)
Raiding	warfare	weapons	*horses,* **communicable disease**	**invasions**	Turchin et al. (2013)
Dairy pastoralism§	livestock care	pens	*livestock, steady food, pastures*, **zoonotic disease, degraded pastures**	**grazing competition**	Bellwood (2004)
Household livestock (meat)	livestock care	pens, manure storage	*livestock, steady food,* **zoonotic disease**	**habitat loss** (livestock feed)	Larson and Fuller (2014)
Annual cultivation	farming	plows, paths	*crops,* **weeds, soil erosion/degradation**	**habitat loss**	Grigg (1974), Bellwood (2004)
Manuring	farming	manure storage	*+land productivity, soil fertility,* **polluted water/eutrophication**	**nutrient saturation (soil, water)**	Grigg (1974)
Irrigation	farming, hydrology, social networking	irrigation systems	*steady food, +land productivity,* **waterborne disease**	**salt accumulation, water pollution, invasions**	Grigg (1974)
Trade	tradecraft (literacy, numeracy, trading), social networks, **prestige culture,** urban lifeways	paths, roads, transport networks, cities	*steady food, +labor productivity,* **communicable disease**	**invasions**	Smith (2004), Oka and Kusimba (2008), Earle (2010), Feinman and Garraty (2010), D'Odorico et al. (2014)

TABLE 4. Continued.

Subsistence regime	Cultural inheritance	Material inheritance	Ecological inheritance		Citations
			Human	Nonhuman	
Specialized crafts	craft skills, toolmaking, trade	tools, crafts, specialized workplaces	*steady food, +labor productivity*	unknown	Costin (1991, 2001), Smith (2004)
Rent extraction from production and/or exchange (e.g., governing elites, landlords, bankers, investors)	social organization, *infrastructure investment,* **rent extraction**, **taxation**	large-scale dwellings, luxury goods, centralized infrastructures (ornamental, functional)	unknown	unknown	Smith (2004), Nolan and Lenski (2010), Chase-Dunn and Lerro (2013)
Industrial production (general)	industrial sciences, engineering, tradecraft, social organization	industrial infrastructure, industrial products (machines to plastics), roads, railways	*steady food, surplus production,* **pollution (toxic, nutrient, carbon)**	**pollution (toxic, nutrient, carbon), extractive industrial damage**	Basalla (1988), Nolan and Lenski (2010)
Mechanized crop production	industrial sciences, farming, tradecraft	Industrial infrastructure, machinery, storage infrastructure	*+labor productivity*, **energy impacts, erosion**	**carbon pollution**	Grigg (1974)
Synthetic nitrogen fertilizer	nitrogen synthesis, plant nutrition	industrial infrastructure	*+land productivity, +labor productivity*, **polluted water/ eutrophication, energy impacts**	**nitrogen saturation, carbon pollution**	Smil (1991)
Pesticides	chemistry, pests	industrial infrastructure	*steady food, +labor productivity*, **resistant pests**, **polluted water**	**toxic pollution (soil, water)**	Grigg (1974)
Service economy	service, tradecraft	communication systems	*+labor productivity*	unknown	Buera and Kaboski (2009)

Notes: Benefits are shown in italic type, detriments are shown in boldface type, and unknown, dual consequence, and neutral characteristics are shown in regular type. Plus symbols indicate an increased characteristic. Citations add detail on subsistence strategies and may not describe inheritances.

† Foraging here refers to both hunting and foraging.

‡ Extinctions and invasions also include ecological inheritance from long-term population changes and trophic cascade effects on communities and ecosystems (Estes et al. 2011).

§ Evidence of gene–culture coevolution.

hunting and foraging strategies to obtain adequate nutrition once preferred prey and plant resources became rare (Stiner 2001, Zeder 2012). Technologies for food processing, including grinding and boiling, increased the nutrients extractable from plant and animal foods, boosting food returns from limited land and potentially making small seeds and tubers worth exploiting at high levels for the first time, putting them on course to later domestication (Fuller et al. 2011, Wollstonecroft 2011).

Sedentary populations of complex hunter-gatherers, especially those occupying the most productive parts of landscapes, began to propagate desirable species of plants and animals by a wide array of pre- and proto-agricultural niche construction strategies (Price and Bar-Yosef 2011, Smith 2011, 2012). By the early Holocene, most human populations likely lived in societies that had adapted to denser populations by processes of sociocultural niche construction that boosted the productivity of land through ecosystem engineering (Smith 2007*b*, 2011) and an array of other subsistence regimes including the cooperative exchange of these technologies and their material products, enabling their populations to grow even more in both scale and complexity (Marlowe 2005, Hamilton et al. 2007, Nolan and Lenski 2010, Ellis et al. 2013*b*).

Horticultural and agrarian societies.—The first agrarian societies emerged in the early to mid-Holocene in more than a dozen centers of origin and spread across the continents by diverse trajectories from coevolution in situ to cultural exchange, and from mobile and sedentary hunter-gatherers to shifting cultivation and herding (Fuller 2010, Fuller et al. 2011, 2014, Price and Bar-Yosef 2011, Rowley-Conwy and Layton 2011, Ellis et al. 2013*b*, Larson et al. 2014). The domestication of desirable species is an especially important form of sociocultural niche construction in which genetic changes in populations are induced through generations of selective breeding for desired traits in environments engineered through land clearing and tillage, ultimately producing major beneficial ecological inheritances for both humans and domesticates (Smith 2007*a*, *b*, 2011, 2012, Fuller et al. 2014, Larson et al. 2014). Through early forms of agriculture, horticultural societies reached much greater scales of population and cultural accumulation than those of hunter-gatherers, and this led to further population growth, the spread of agricultural populations into new areas and the displacement of hunter-gatherers, and to more and more complex forms of farming and other technologies, including manuring, terracing, and the development of smelting to produce nonferrous metal ornaments, weapons, and later other tools including farm implements (Bellwood 2004, Bocquet-Appel 2011, Gignoux et al. 2011). Horticultural societies developed more complex and hierarchical forms of social organization, with some advanced horticultural societies developing subsistence regimes based on raiding and trade with other societies (Nolan and Lenski 2010, Chase-Dunn and Lerro 2013).

As populations grew and agricultural and other technologies continued to accumulate, societies continued to scale up, with agrarian societies dependent on animal traction combined with the plow displacing earlier horticultural and hunter-gatherer societies from the most productive lands, while also displacing and exchanging with each other through warfare, trade, emigration, disease, land degradation, and periodic collapse (Grigg 1974, Ellis and Wang 1997, Butzer and Endfield 2012, Ellis et al. 2013*b*, Turchin et al. 2013). Over millennia, on most continents, agrarian societies developed remarkably productive technologies for boosting and sustaining productivity from the same lands to support large and growing populations, including irrigation, multiple cropping, and the use of a wide range of fertilizers (Grigg 1974, Ellis and Wang 1997, Ellis et al. 2013*b*). As populations and land productivity increased, cultural innovations including numeracy, writing, money, the state, absentee land ownership, and systems of unequal intergenerational wealth transfer made possible subsistence regimes based on the extraction of agricultural surplus by trade and taxation, supporting the rise of nonagricultural populations in urban settlements separated from productive lands and specializing in craft production, trade, and the extraction of rent from land, trade, and other subsistence resources by governing and land-owning elites (Table 4; Smith 2004, Nolan and Lenski 2010, Shennan 2011*b*, Chase-Dunn and Lerro 2013, Turchin et al. 2013). Technological innovations including irrigation systems, improved roads, iron tools and weaponry, and ships capable of sea trade further enhanced the beneficial cultural, material, and ecological inheritances of advanced agrarian societies, aiding in their spread, their subjugation and annexation of other societies, and ultimately their interconnection into a global world system by about 1600 AD through trade, tribute, and other intersocietal exchange relations (Smith 2004, Nolan and Lenski 2010, Chase-Dunn and Lerro 2013, Turchin et al. 2013).

Urban and industrial.—Urban populations dependent on trade and other exchange-based subsistence regimes first arose in the Near East more than 6000 years ago, and small cities became common in advanced agricultural societies by 3500 yr BP, with major cities (populations >100 000) appearing by 2000 yr BP (Cowgill 2004, Kirch 2005, Ellis et al. 2013*b*). The concentrated populations, specialized elites, marketplaces, networks of exchange, and wealth of cities in advanced agrarian societies, such as that of the Romans, likely facilitated remarkable cultural and technological advances and increased incomes and opportunities as they do in contemporary cities, despite their relatively small share of overall population prior to the past few centuries (Cowgill 2004, Smith 2004, Bettencourt et al. 2007, Bettencourt and West 2010, Ortman et al. 2014, 2015). As industrial societies arose over the past two centuries, the scale and rate of urbanization accelerated dramatically, with the global percentage of human populations living in cities growing from about 7% in 1800, to 16% in 1900, to more than 50% today (Klein Goldewijk et al. 2010). To meet the large-scale demands of wealthy and growing urban industrial populations, high levels of agricultural surplus production and trade were met by ever-larger scales of farming operations, trading systems, and technological infrastructure and institutions sustained by large energy subsidies from fossil fuels and other industrial inputs (Grigg 1974, Lambin et al. 2001, Ellis et al. 2013*b*). Attendant with the rise and centralization of large-scale urban and industrial societies has also been a continued trend toward the systematic generation of material, cultural, and political inequality within societies and the systematic subjugation and extraction of resources from the smaller scale and less central societies within world systems by larger scale societies, though these trends also include considerable rise and fall dynamics, geographic heterogeneity, and near continuous processes of societal and ecological restructuring (Harvey 1996, Chase-Dunn and Manning 2002, Smith 2008, Brenner and Schmid 2011, Moore 2011, Chase-Dunn and Lerro 2013).

Evolutionary trends in sociocultural niche construction

The behaviorally modern hunter-gatherer societies of 50 000 years ago had already gained cultural and technological capacities for ecosystem transformation beyond those of any other multicellular species in history (Kirch 2005, Hill et al. 2009, Doughty 2013). As societies scaled up from hunter-gatherers to industrial societies, they also accumulated technological and organizational capabilities for ecosystem engineering and subsistence exchange that enabled their populations to grow well beyond the capacity of unaltered ecosystems to support them (Ellis et al. 2013*b*). Through the evolution of sociocultural niche construction over hundreds of human generations, human societies became a global force capable of transforming the biosphere. Three main forces of human sociocultural

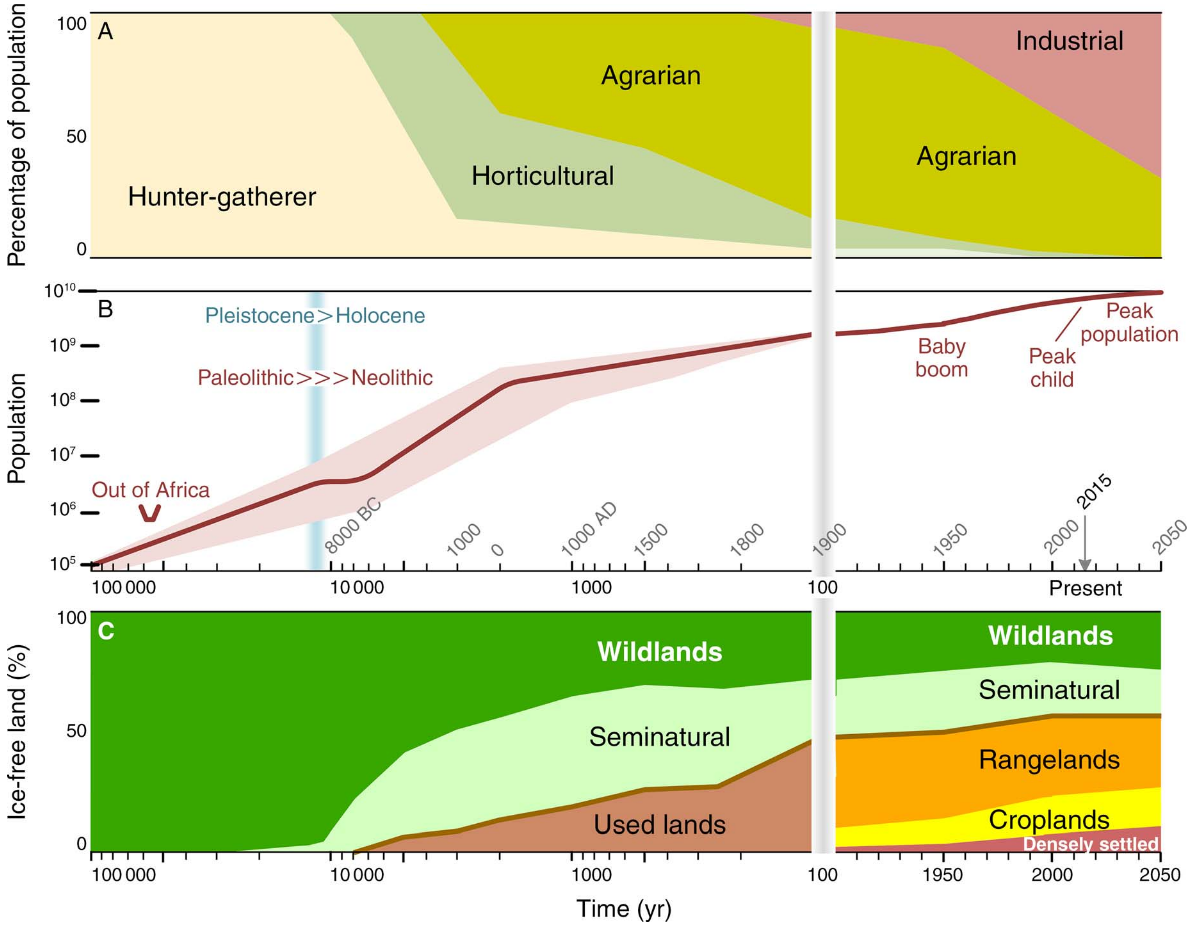

FIG. 4. Long-term global changes in (A) major categories of sociocultural systems (based on Nolan and Lenski [2010]), (B) human populations based on U.S. Census Bureau 2013, *available online*: http://www.census.gov/population/international/data/worldpop/table_history.php), and (C) anthropogenic transformation of the terrestrial biosphere (based on Ellis et al. [2013*b*]). Multiple arrows indicate that Paleolithic to Neolithic transitions are regional, not global. Time scale prior to 1900 is logarithmic years BP, after 1900 is linear calendar years.

niche construction explain this unprecedented capacity and its dynamics across the biosphere in time and space: cooperative engineering, social upscaling, and energy substitution (Table 1).

The general long-term trend in sociocultural niche construction is toward the evolution of subsistence regimes capable of supporting ever-larger and denser human populations in increasingly unequal, hierarchical, and complex societies by increasing land productivity over time through cooperative ecosystem engineering, increasing dependence on subsistence exchange over larger and larger distances, and by increasing use of nonhuman energy (Tables 3 and 4). The early evolution of increasingly productive cooperative engineering strategies and technologies to produce more food from limited land resources by growing populations, or "land use intensification," has been explained in two ways: optimal foraging strategies and cultural niche construction (Bird and O'Connell 2006, Price and Bar-Yosef 2011, Shennan 2011*b*, Smith 2012, Ellis et al. 2013*b*). Optimal foraging theory explains early forms of land use intensification, including dietary broadening, use of fire to clear land, and species domestication, as the adoption of energy-efficient strategies for food procurement by growing populations faced within increasingly limiting land and biotic resources, with demographic pressures considered as the direct cause of intensification (Bird and O'Connell 2006). Cultural niche construction theory explains land use intensification not in terms of demographic pressures, but "as the result of deliberate human enhancement of resource-rich environments in situations where evidence of resource imbalance is absent" (Smith 2012). Contemporary archaeological evidence favors cultural niche construction as the driver of early innovations in land use intensification (Price and Bar-Yosef 2011, Smith 2012). In either case, land use intensification represents the intentional cooperative engineering of ecosystems to produce direct beneficial ecological inheritance for human populations, generally to the detriment of other species.

Social upscaling, centrality, and urbanization

In general, societies concentrated on and used the most productive and accessible lands first, such as lowland floodplains, in processes of central place foraging (Dyson-Hudson and Smith 1978, Bird and O'Connell 2006, Smith 2007*a*, Price and Bar-Yosef 2011), migrating to and using more distant and/or lower productivity lands (land use extensification) only when population pressures built up or local resources became degraded (Hamilton et al. 2009, Barbier 2010, Ellis et al. 2013*b*). Sociocultural niche construction by ecosystem engineering in the most suitable environments enabled more sedentary lifestyles, but also induced populations to grow, requiring more productive land-use practices to sustain them or migrations to new areas, including wildlands (Hamilton et al. 2009, Ellis et al. 2013*b*). Over time, as populations grew, societies scaled up and shifted to subsistence regimes capable of sustaining even larger scale societies, and these were implemented both on lands already altered by earlier populations (central places) and through expansion from earlier sites of settlement and land use intensification. Subsistence regimes incapable of supporting larger scale societies or producing detrimental cultural, ecological, or material inheritances were selected against, both within societies and across them, by warfare, population growth, and cultural exchange.

As early societies scaled up, supported by increasingly intensive use of the most suitable lands and by extensification of populations across regions, the importance of central places increased as well, as sites of denser, more resource rich, and more culturally rich populations sustained increasingly by cooperative strategies of subsistence exchange (Dyson-Hudson and Smith 1978, Hamilton et al. 2009, Kaplan et al. 2009, Burnside et al. 2012). The central places of hunter-gatherers were not cities, nor were their lifestyles urbanized through specialized subsistence regimes, the unequal distribution of resources, hierarchical social organization, or dependence on subsistence exchange. Yet central places still played a significant functional role in sedentary hunter-gatherer societies as the optimal loci of networks of cultural and material exchange (Redman 1999, Hamilton et al. 2009, Kaplan et al. 2009, Burnside et al. 2012, Brughmans 2013, Ortman et al. 2014). Long before the rise of cities and urban lifeways, the importance of social networks and centrality in structuring the processes of sociocultural niche construction, cultural and material accumulation and subsistence exchange were established (Dyson-Hudson and Smith 1978, Cowgill 2004, Hamilton et al. 2009, Kaplan et al. 2009, Feinman and Garraty 2010, Burnside et al. 2012, Brughmans 2013, Ortman et al. 2014).

Over time, as societies scaled up, the populations of some central places became the first cities, increasing in density, wealth, inequality, social organization, cultural accumulation, and importance in focusing and guiding subsistence exchange processes across regions (von Thünen and Schumacher-Zarchlin 1875, Christaller 1933, Stewart 1947, Redman 1999, M. E. Smith 2004, Barbier 2010, Therborn 2011, Verburg et al. 2011, Rivers et al. 2013, Ortman et al. 2014, M. L. Smith 2014, Ortman et al. 2015). The density of cities in itself provides advantages through the economies of scale, increasing opportunities for wealth creation, cultural innovation, and social connectivity, while at the same time increasing demands for energy to sustain this concentration of resources and increasing potential for disease (Redman 1999, Bettencourt 2013, Ortman et al. 2014, 2015). As the opportunities provided by cities increase with scale, they ultimately begin to restructure the distribution of human populations, attracting rural immigrants in contemporary processes of urbanization that have shifted populations from countryside to city (Lambin et al. 2001, Klein Goldewijk et al. 2010, Smith 2014). The sustained upscaling of societies is therefore associated with an enhancement of social centrality in structuring and concentrating the forces of sociocultural niche construction within landscapes and across regions and globally through the telecoupling of resource demand and migration (Grimm et al. 2008, Bruckner et al. 2012, Seto et al. 2012).

As societies have scaled up and increased in wealth, there has also been a long-term trend toward increasing use of nonhuman energy per capita; a long-term upscaling of social metabolism (Fig. 3B, Table 3; White 1959, Smil 2008, Burnside et al. 2012, Fischer-Kowalski et al. 2014). Beginning with the use of fire to cook food, reducing the energy costs of digestion (Wrangham and Conklin-Brittain 2003), humans have increasingly harnessed nonhuman energy to support their subsistence regimes, using harvested biomass to heat and to cook, by substituting animal traction for human labor, and ultimately by using fossil biomass fuels and abiotic sources of energy as substitute for labor and even for soil fertility, through nitrogen synthesis and the mining and transport of phosphorus and other limiting nutrients (Smil 2008, Brown et al. 2011*b*, Fischer-Kowalski et al. 2014). From the beginning, energy substitution has been essential in sustaining the upscaling of societies and their subsistence regimes, enabling human societies to increase in scale from small bands to telecoupled global societies sustained by increasing scales of social exchange of materials, energy, services, and information.

Sociocultural niche construction as the driver of long-term anthroecological change

Three fundamental processes of sociocultural niche construction drive long-term ecological change. The first is cooperative ecosystem engineering, defined as the ability of social groups and societies to alter ecosystems to preferentially sustain human populations over other species. The second is social upscaling through culturally

PLATE 1. A living metaphor for our anthropogenic biosphere, this tree (*Tetrameles nudiflora*) is firmly rooted within the ancient material cultures of past societies. Anthroecology theory couples ecology and society just as deeply through sociocultural niche construction, an evolutionary framework explaining the emergence of behaviorally modern human societies as a global force transforming the biosphere. To deepen the metaphor, the cultural, material, and ecological inheritances represented in this socially shared image from Wikimedia Commons are embedded within a UNESCO World Heritage Site. Photograph by Francisco Anzola at Ta Promh Temple, Angkor Wat, Siem Riep, Cambodia (103.890423E,13.434959N) (CC BY 2.0).

mediated changes in social organization and increasing scales of subsistence exchange, and the third is the harnessing of nonhuman energy sources to sustain these processes of ecosystem engineering, social upscaling, and subsistence exchange. To explore the ecological consequences of these three processes of sociocultural niche construction as they have unfolded across the Earth, it is critical to consider their patterning in space and time. As societies have scaled up, so have rates of cultural evolution, enabling human subsistence regimes and their transformation of ecology to evolve more rapidly than rates of biological evolution, putting nonhuman species at an extreme disadvantage. Social upscaling has not only increased scales of populations and the use of energy and other resources, but has also shaped sociocultural niche construction in space, with land use intensifying in the most suitable lands, and populations increasingly concentrated in central places dependent on subsistence exchange, where populations become decoupled from direct interactions with ecosystems, while increasing their influence at regional and global scales through telecoupling.

ECOLOGICAL PREDICTIONS OF ANTHROECOLOGY THEORY

The most general prediction of anthroecology theory is that the spread of behaviorally modern human societies across the Earth caused sociocultural niche construction to emerge as a global process of ecological change that has transformed the terrestrial biosphere (see Plate 1). While contemporary industrial societies have certainly developed unprecedented capacities for biospheric transformation (Steffen et al. 2007), evidence from archaeology, paleoecology, and environmental history confirms that human societies have been reshaping the terrestrial biosphere, and perhaps even global climate, for millennia (Kirch 2005, Sherratt and Wilkinson 2009, Ellis 2011, Doughty 2013, Ellis et al. 2013*b*, Ruddiman 2013, Smith and Zeder 2013). Even before the Holocene began, sociocultural niche construction by behaviorally modern hunter-gatherers had produced major ecological changes across Europe, Australasia, and the Americas by their hunting and trophic displacement of megafauna, causing regime shifts in ecosystem structure (Fig. 3A; Barnosky 2008, Estes et al. 2011, Doughty 2013, Gill 2014, Sandom et al. 2014).

The long-term upscaling, intensification, and extensification of sociocultural niche construction would be expected to begin as a relatively low-level, but widespread transformation of ecosystems across the Earth followed by a gradually accelerating intensification of this transformation over time, as illustrated in Fig. 3B. Contemporary evidence indicates that this is indeed the case (Ellis et al. 2013*b*). Though the global extent and dynamics of this transformation remain poorly understood, hunter-gatherer societies used fire to clear land long before the emergence of agriculture, transforming wildlands into the open landscape mosaics of seminatural anthromes (Figs. 3B and 4C; Williams 2008, Ellis et al. 2013*a*, *b*). With the rise of horticultural societies, the first cropland anthromes appear and then the scale, intensity, and sophistication of ecosystem engineering escalates from propagation and domestication to the sustained tillage, irrigation, manuring, and other practices required to support the ever-larger scales of agrarian societies and later, the first urban populations subsisting on trade and other exchange processes (Figs. 1, 3, and 4; Redman 1999, Bellwood 2004, Kirch 2005, Ellis et al. 2013*b*).

Though the small-scale horticultural and agrarian societies of prehistory had much lower populations than those of today, their per capita land requirements were orders of magnitude greater (Table 3). As a result, anthropogenic transformation of the terrestrial biosphere begins much earlier and is far more extensive than the low populations of the past would predict (Figs. 1 and 4; Ruddiman and Ellis 2009, Kaplan et al. 2011, Ellis et al. 2013*b*). As large-scale industrial societies arose, sustained by global networks of exchange and increasing use of fossil fuels, populations grew from one billion in 1800 to more than seven billion today, ultimately transforming more than three-quarters of the terrestrial biosphere from biomes into anthromes (Figs. 1 and 4; Ellis et al. 2010, 2013*b*). Human sociocultural niche construction became established as a global force transforming ecological pattern and process across the terrestrial biosphere.

Biomes to anthromes: anthropogenic transformation of the biosphere

A suite of more specific ecological predictions emerge from the proposition that human sociocultural niche construction is the main cause of long-term anthropogenic changes in ecological pattern and process. To explore these predictions and develop them into testable hypotheses, we begin by considering sociocultural niche construction as a force acting on the biosphere analogous to that of a dynamic "human climate" interacting with ecosystems and species.

Human societies first emerged within and continue to act upon the biomes and ecosystems formed by long-term interactions with natural climate systems. We therefore begin by expressing the formation of the natural global patterns of the biomes and the ecosystem processes within them at regional landscape scales (10^2 to 10^5 km^2; Noss 1990, Ellis et al. 2012), as a function of global variations in temperature and precipitation acting on biota within heterogeneous terrain and soil parent material (Pm) over time (e.g., Olson et al. 2001, Ellis and Ramankutty 2008), as

$$\begin{aligned}&\text{Biomes, ecosystems}\\&\quad = f(\text{temperature, precipitation, biota, terrain, Pm, time})\end{aligned} \tag{1}$$

To describe the formation of anthromes and anthroecosystems through sustained processes of sociocultural niche construction acting on the heterogeneous landscapes and Pm of biomes, we first express the "human climate" produced by sociocultural niche construction as function of two sociocultural variables, society type and social centrality, and a third variable, land suitability, as

$$\begin{aligned}&\text{Sociocultural niche construction}\\&\quad = f(\text{society, centrality, suitability})\end{aligned} \tag{2}$$

$$\begin{aligned}&\text{with land suitability}\\&\quad = f(\text{society, biome, terrain})\end{aligned} \tag{3}$$

Land suitability expresses the potential productivity of a specific area of land in sustaining a given society, which depends on the potential productivity attainable through application of the societies' ecosystem engineering practices and subsistence regimes to a specific biome and terrain, where terrain is considered as a factor varying within each biome, rather than at the scale of biomes. For most societies in most biomes, flatter areas with accessible water tend to be the most suitable (Silbernagel et al. 1997, Huston 2005), but this can differ greatly across societies and biomes. By combining the variables defining sociocultural niche construction with those defining biomes, we obtain an expression defining the formation of anthromes and anthroecosystems over time:

$$\begin{aligned}&\text{Anthromes, anthroecosystems}\\&\quad = f(\text{biome, society, centrality, suitability, time})\end{aligned} \tag{4}$$

This last function provides the basis for predictions of the anthropogenic ecological patterns and processes emerging within a given regional landscape in response to sociocultural niche construction by a specified society, degree of social centrality, and land suitability. Simply put, anthroecology theory predicts that the ecological patterns, processes, and dynamics within and across regional landscapes inhabited by or otherwise subject to direct interactions with behaviorally modern humans will be predicted more accurately by Eq. 4 than by Eq. 1. In other words, anthromes will predict ecological pattern and process more accurately than biomes alone (Ellis and Ramankutty 2008).

Ecosystems to anthroecosystems: anthrosequences

Variations in ecological patterns and processes can be conceptualized as "sequences," as in chronosequences (time), toposequences (terrain), and climosequences (climate). In this way, "anthrosequences" (Table 1) depict variations in ecological patterns and processes caused by variations in sociocultural niche construction acting on a given biome. Fig. 5 uses this approach to illustrate hypothetical variations in ecological patterns and processes in response to broad differences in types of societies (Table 3) and variations in social centrality (horizontal axis) and land suitability (vertical axis) across a stylized woodland biome landscape (Fig. 5A).

Patterns depicted from left to right in Fig. 5 might be interpreted as a chronosequence, and settlement patterns are drawn to allow this. However, it must be remembered always that societal transitions may occur in different sequences (e.g., hunter-gatherer to industrial) and that societal types are rarely homogeneous or fully consistent. The hypothetical anthrosequences depicted in Fig. 5 are also based on patterns of anthropogenic transformation in old-world temperate woodland biomes; very different anthrosequences would be expected in different woodland biomes, such as tropical moist woodlands, and in savannas, grasslands, deserts, and other biomes. The purpose here is only to demonstrate the utility of anthroecology theory in generating testable hypotheses on anthropogenic transformation of ecological patterns and processes based on the three main forces of human sociocultural niche construction, cooperative engineering, social upscaling, and energy substitution, and their spatial patterning across landscapes in terms of social centrality and land suitability.

As illustrated in Fig. 5, all types of societies alter land cover across woodlands, fragmenting the more continuous patterns of tree cover in natural woodlands into the complex heterogeneous mosaics of land cover typical of most anthrome landscapes (Ellis and Ramankutty 2008). Nevertheless, different societies do this in very different ways, ranging from the burning of woodland patches by more sedentary hunter-gatherers, to the wholesale clearing, cultivation, and grazing of land by agrarian populations, to the construction of built infrastructure by dense industrial populations and their refocusing of cultivation in the most suitable lands remaining, abandoning the rest to woodland recovery and grazing (Fig. 5A, C).

The transformation of wildland biomes into anthromes by sociocultural niche construction is depicted in Fig. 5B, illustrating a general trend toward the increasingly intense use of land for agriculture and settlements from wildlands and seminatural lands to croplands, rangelands, and dense settlements (Fig. 5C). While sociocultural niche construction is the ultimate cause of direct anthropogenic transformation of terrestrial ecological pattern and process, human populations and their use of land are the proximate causes of these transformations, as illustrated in Fig. 5C. As societies increase in scale (left to right in Figs. 3 and 5, and top to bottom in Table 3), human populations become larger and denser and become more concentrated, first into larger and larger villages and then into towns and urban settlements of increasing size and density. Following the same trend, extractive use of land for hunting and foraging by early hunter-gatherers transitions into increasingly intense and complex forms of engineered ecosystem management, from the use of fire to enhance success in hunting and foraging and to protect the encampments of hunter-gatherers, to the shifting cultivation of crops and increasingly permanent encampments, villages and early urban settlements of advanced horticultural societies. Land use by agrarian and industrial societies continues the trend toward increasingly intense and diverse use of land, introducing continuous cropping, irrigated agriculture, and the pasturing of livestock, and in industrial systems, the management and conservation of forested lands, and the introduction of ornamental land uses such as parks and yards (Fig. 5C).

Anthroecological succession and anthrobiogeography

By combining the ultimate and proximate causes of anthropogenic transformation of terrestrial ecosystems depicted hypothetically in Fig. 5A and 5C, relative changes in ecosystem (Fig. 5D) and biogeographic (Fig. 5E) processes are predicted in terms of sociocultural niche construction as processes of anthroecological succession (Janzen 1983, Balée 2006, Ellis et al. 2012). Primary anthroecological succession is the response of ecosystems and communities to their first exposure to and transformation by sociocultural niche construction, while secondary anthroecological succession represents the responses of transformed ecosystems and communities to subsequent regime shifts in societal type or centrality. The spatial patterning and dynamics of species and communities within and across anthromes at global and regional scales by processes of sociocultural niche construction and anthroecological succession is anthrobiogeography. For example, the patterns of sociocultural niche construction depicted in Fig. 5A–C and their influence on habitat patch size, isolation, megafauna biomass, plant species richness, and ecosystem novelty in Fig. 5E are anthrobiogeographic patterns. The diversity of anthropogenic ecological effects on nonhuman species is further evident in the wide array of ecological inheritances produced by the sociocultural subsistence regimes listed in Table 4.

Anthroecological succession in anthromes formed by hunter-gatherer societies is caused primarily by the

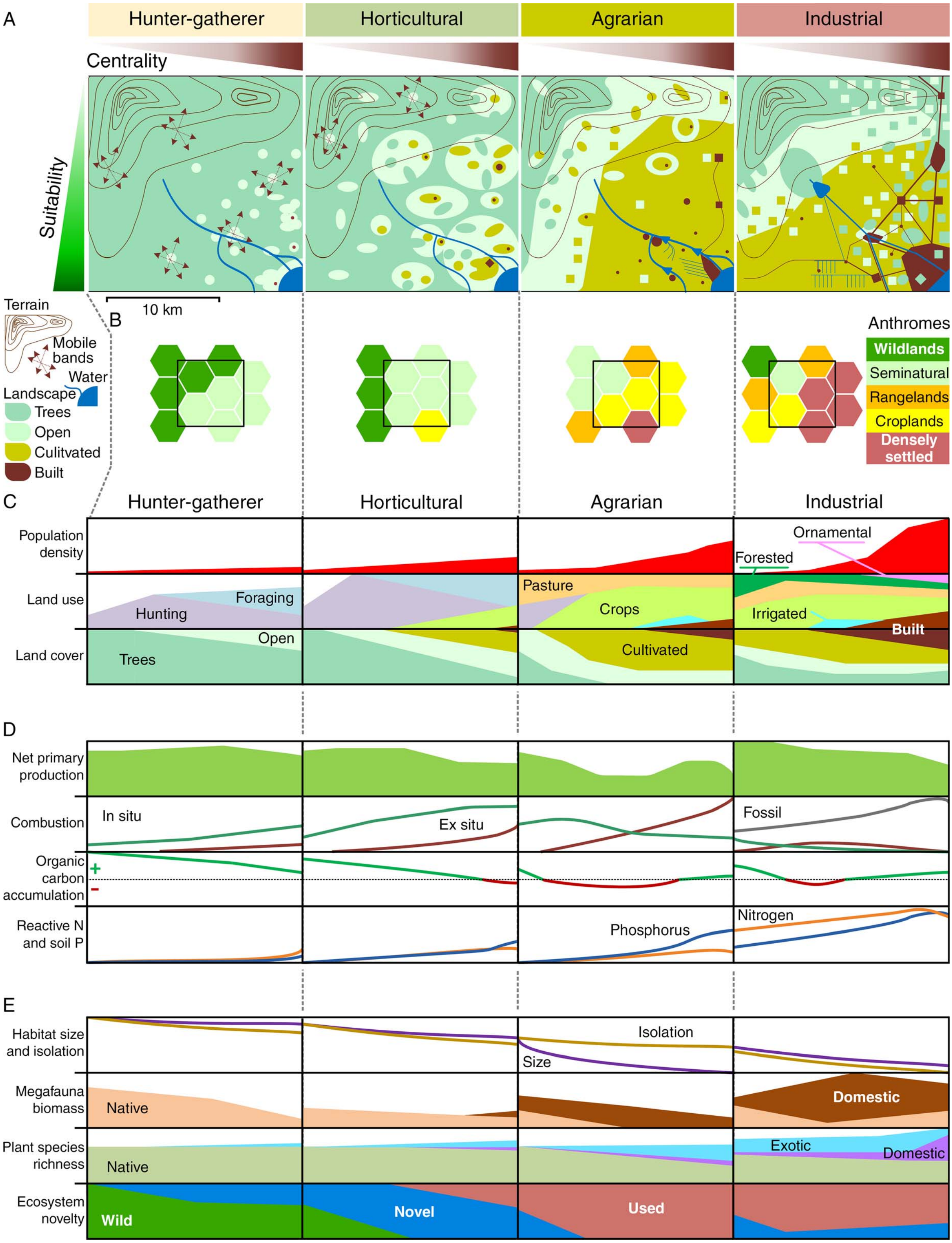

FIG. 5. Anthrosequence in a stylized temperate woodland biome illustrating conceptual relationships among society types and social centrality and their interactions with land suitability for agriculture and settlements in shaping the spatial patterning of human populations, land use, and land cover, and their ecological consequences. Settlement patterns are drawn to allow interpretation as a chronosequence of societies from left to right; however, alternate transitions are also likely, e.g., from hunter-gatherer to industrial. (A) Anthropogenic transformation of landscapes under different sociocultural systems (top) relative to

pressures of hunting and foraging, together with land clearing using fire and the propagation of desired wild plants (Fig. 5). Ecological patterns and processes strongly resemble those of wildland biomes, with the main alterations being the formation of open woodlands and reduced organic carbon accumulation by burning (Fig. 5D), and reductions in megafauna biomass (Fig. 5E), slight increases in species richness through the introduction of desired plant species and enhanced rates of species introduction and establishment in burned areas and shifts toward novel species assemblages at the highest levels of social centrality in the most suitable lands, where sedentary hunter-gatherer settlements are located.

Sociocultural niche construction by horticultural societies produces much more substantial transformation of ecological pattern and process. In the least central and suitable parts of landscapes, patterns of succession resemble those of sedentary hunter-gatherer societies. However, in the most central and suitable parts of landscapes, shorter fallow shifting cultivation and denser sedentary populations become established, producing the used lands of cropland anthromes (Fig. 5B). In these areas, habitat is fragmented into smaller sized patches and communities of exotic and domestic plants develop in response to declining habitat isolation and size (Fig. 5E) caused by increasing social exchanges and human land use in these areas. Losses of native megafauna biomass continue, accompanied by gains in domesticated megafauna. Biomass harvested across landscapes for food and fuel is moved to and consumed within settlements (ex situ combustion, hunting, gathering, crop harvest), leading to modest accumulations of reactive N and P, enriching soils in the vicinity of the most sedentary settlements (Fig. 5D).

Agrarian societies cause far more profound shifts in ecosystem and community patterns and processes. The larger scales and dense populations of these societies generally eliminate and displace native megafauna, replacing them with domestic livestock (Fig. 5E). Continuous cultivation of suitable lands in the most socially central areas reduces primary productivity and carbon balance through nutrient loss through the harvest of crops for food and feed and crop residues for fuel, causing N and P to become concentrated near settlements (Fig. 5D). Low levels of agricultural productivity require near complete cultivation of land in the most central areas where populations are concentrated, greatly reducing habitat patch size, almost to zero in the most central and suitable areas (Fig. 5E). This causes substantial loss of native plant species, supplanted by smaller numbers of domesticates, and substantial exotic establishment, mostly of weedy plants introduced through increasing levels of social and subsistence exchange that reduce habitat isolation (Fig. 5E).

Sociocultural niche construction by industrial societies focuses agricultural production in the most suitable landscapes as commercial agriculture, mechanization, and rural to urban migration concentrates dense populations in cities and reduces rural populations (Fig. 5C). Use of synthetic N and mined P for fertilizer, together with reactive N release by fossil fuel combustion cause high levels of available N and P across landscapes, increasing primary production across all vegetated land cover (Fig. 5D). High levels of domestic livestock are sustained, in part through the production of feed crops. In less suitable areas for agriculture, woodlands recover, further enhancing net primary production. However, native plants species are reduced significantly, and supplemented by large numbers of exotic plant species, including high levels of domesticates in urban areas, where large numbers of horticultural species are maintained in yards and parks, and most habitats are smaller in size and exposed to high volumes of human transport, reducing their isolation from other regions to very low levels (Fig. 5E).

Nonhuman ecological inheritance and adaptations to sociocultural niche construction

In general, the conversion of wildlands to anthromes through sociocultural niche construction by increasingly larger scales of societies produces both ecosystems intentionally engineered for production and managed with increasing intensity, and patches of remnant and recovering habitats with increasing levels of ecosystem novelty in the parts of landscapes not directly engineered for production (Fig. 5E; Hobbs et al. 2014). To understand the patterning of ecological communities emerging through these patterns of anthroecological succession in anthromes, it may be useful to consider

---

←
spatial variations in social centrality (horizontal axis; same for all charts below) and land suitability (vertical axis). Landscape legend is at far left. (B) Anthrome level patterns across regional landscapes (black box frames landscape in A). (C) Variations in human population densities and relative land use and land cover areas (white represents no human use of any kind; ornamental land use includes parks, yards). (D) Relative variations in ecosystem processes, including net primary production, combustion of biomass in situ (natural fires, unintended anthropogenic fires, and intended fires, e.g., land clearing), ex situ (hearth fires, cooking, heating), and fossil fuels, organic carbon accumulation in vegetation and soils, and reactive nitrogen and available soil phosphorus. (E) Relative variations in biogeographic and evolutionary processes, including woodland habitat patch size and relative isolation from other biotic communities, megafauna biomass (not including humans; native and domesticated), plant species richness of native, exotic, and domesticated plants, and relative area of landscape without human populations or land use (wild), used directly by human populations ("used"; e.g., crops, grazing, settlements), and transformed by human influences, but not used directly (novel).

species as comprising functional groups in terms of their adaptations to and fitness within the used and novel habitats of anthromes, analogous to the grouping of species in terms of environmental adaptations (e.g., xerophytes, mesophytes, halophytes, hydrophytes) and guilds (e.g., frugivorous birds, insectivores, ruderals, understory trees). For example, five simple groups might be recognized, anthropophagics (preferred wild foods and other used wild species not adapted to human harvest), domesticates, anthropophiles (species tending to establish well and outcompete other species in used and novel ecosystems), anthropophobes (species tending not to establish in and to be outcompeted by others in used and novel ecosystems), and anthropoagnostics (no consistent difference in establishing populations and competing with other species in wild vs. novel and used ecosystems) (Bohac and Fuchs 1991, Speight and Castella 2001, Bradley et al. 2010). By grouping species in this way, it might be increasingly possible to predict species assemblages in the used and novel habitats of anthrome mosaics under different societal conditions and levels of social centrality.

Primary anthroecological succession in wildlands and seminatural anthromes produces detrimental ecological inheritances for anthropophagic species and their predators in all societal types except industrial, where wild foods are uncommon. The exceptional survival of megafauna in Africa may best be explained by their long-term coevolution with hominins through the gradual emergence of modern human behaviors and sociocultural niche construction. For this reason, primary anthroecological succession could be considered to have never truly occurred in Africa, as species there were not confronted all at once by behaviorally modern human societies but rather experienced a form of secondary anthroecological succession acting on species that may already have evolved the adaptive traits of anthropoagnostic and/or anthropophilic species. In the engineered used habitats of anthroecosystems, sociocultural niche construction intentionally produces direct beneficial ecological inheritance for domesticates, indirectly benefits anthropophiles and filters out anthropophobes. For anthropoagnostic species, the rise of sociocultural niche construction has, in theory, produced no ecological inheritance or population effects. However, as sociocultural niche construction has increased in extent and intensity with the rise of agrarian and industrial societies, the populations of domesticates and anthropophiles have benefitted, while anthropophobes have lost habitat, tending to become threatened and endangered, while anthropophagics may be recovering, if they are not already extinct.

Species are generally considered native based on their history of establishment within biomes and ecoregions. Domesticates and anthropophiles have similar relationships with anthromes and anthroecosystems and might thus be considered native to these in the same way. To treat such species as invading exotics within the anthromes to which they are adapted seems both ecologically incorrect and wildly impractical, even though this will appear to be the case when such species become established for the first time during early stages of primary anthroecological succession. In considering the forces of sociocultural niche construction as equivalent to a "human climate," the question of where some species "belong" shifts from ecoregions to the novel habitats of urban landscapes, croplands, rangelands, and seminatural anthromes (e.g., Del Tredici 2010). With the glaring exception of most megafauna, island species, flightless birds, and anthropophagic species, there is evidence that high levels of both native and introduced biodiversity are generally sustained in the multifunctional mosaic landscapes of anthromes through high levels of biotic exchange (telecoupling; Helmus et al. 2014), albeit in novel assemblages, habitats, and ecosystems that may have little resemblance to prior native forms (Smith and Wishnie 2000, Kowarik 2003, 2011, Stork 2010, Ellis et al. 2012, Dornelas et al. 2013, Ellis 2013, Thomas 2013, Mendenhall et al. 2014).

SHIFTING THE BASELINE: ECOLOGY IN AN ANTHROPOGENIC BIOSPHERE

The call to integrate humans into ecology is older than the discipline itself and has been loud and clear for generations (e.g., Darwin 1859, Tansley 1935, Hawley 1944, Odum 1953, Pickett and McDonnell 1993, Redman et al. 2004, Collins et al. 2011). Major progress has been made by theory on social–ecological systems (Redman et al. 2004, Folke et al. 2005, Folke 2006, Hornborg and Crumley 2007, Alessa and Chapin 2008, Carpenter et al. 2009, Chapin et al. 2011, Collins et al. 2011, Levin et al. 2013), social metabolism (Baccini and Brunner 2012, Fischer-Kowalski et al. 2014, Malhi 2014), coupled human and natural systems (Liu et al. 2007), human ecology (Boyden 2004, Dyball and Newell 2014), urban ecology (McIntyre et al. 2000, Pickett et al. 2001, Grimm et al. 2008), agroecology (Tomich et al. 2011, Gliessman 2015), countryside biogeography (Daily et al. 2001, Mendenhall et al. 2014), novel ecosystems (Hobbs et al. 2006), anthromes (Alessa and Chapin 2008, Ellis and Ramankutty 2008), and Anthropocene island biogeography (Helmus et al. 2014). Anthroecology theory builds on these with the aim of going further.

To advance the science of ecology in an increasingly anthropogenic biosphere, it is useful to begin with "The First Law of the Anthropocene": the ecological patterns, processes, and dynamics of the present day, deep past, and foreseeable future are shaped by human societies. Anthroecology theory takes this law as given, and integrates human societies into ecology globally across geologic time through an evolutionary framework of human sociocultural niche construction directed at explaining ecological pattern, process, and change within and across an increasingly anthropogenic terrestrial biosphere. In this way, human societies are integrated into ecological science in much the same way as climate systems, which powerfully shape the patterns, processes, and dynamics of ecology, while also being influenced, but less so, by these interactions. As with the classic frameworks of biogeography, succession, evolution, and ecosystem structure and function that are structured within climate systems and the biomes formed by these, anthroecology theory frames ecology within the "human climate" systems of sociocultural niche construction and the anthromes formed by these. Further, anthroecology theory suggests substantial changes are needed in ecological science, conservation, and pedagogy if these are to advance in understanding, conserving, and adapting to life in an increasingly anthropogenic biosphere.

Ecological science in an anthropogenic biosphere

Anthroecology theory challenges the conventional research practices of ecological scientists in four significant ways.

The baseline is anthropogenic.—It is common practice in ecology to define the ecological context of research sites without incorporating either historical or contemporary social conditions. As a result, even though most field research is conducted in sites situated in and transformed by sustained direct interactions with human societies, this is rarely considered or reported (Martin et al. 2012). Given that most of the terrestrial biosphere has likely been transformed by primary and even secondary anthroecological succession, it is likely that the ecological patterns and processes recognized as natural at these sites are in fact substantially altered by sociocultural niche construction (Rackham 1980, Cronon 1983, Redman 1999, Grayson 2001, Briggs et al. 2006, Sih et al. 2011, Cuddington 2012, Higgs et al. 2014). While this bias might seem a minor issue, it has already been shown to influence scientific understanding of paleoclimate and long-term changes in community structure in response to anthropogenic fire regimes and other forms of early land use (Grayson 2001, Briggs et al. 2006, Jackson and Hobbs 2009, Archibald et al. 2012, Li et al. 2014). Similarly, the tendency of ecologists to seek out the most isolated parts of landscapes to conduct their research, such as the siting of most permanent forest field plots in forest interiors, biases results against understanding anthroecological pattern and process in the small patches of trees and other fragmented habitats that now likely represent the majority of woodlands globally (Ellis 2011).

To advance scientific understanding of ecology in an anthropogenic biosphere, sites for field research should be selected by more random and less biased criteria than convenience or "the absence of readily observable anthropogenic disturbance." Further, the trajectory of sociocultural conditions driving primary and secondary anthroecological succession should be characterized and included in the ecological descriptions of field sites in the same way that soil type or plant association usually are, including at minimum, the anthrome context at time of observation (see information *available online*)[2] and ideally, but far more challenging, the dynamics of human populations, land use, cultural history, and social centrality starting with the earliest societies present at sites to the present, assessed in terms of relative travel times to nearest large settlements or markets (Verburg et al. 2011). By including such information in ecological research, new types of questions might be answered. For example, genomic or metagenomic tests might determine whether there are genetic traits associated with anthropophilia or anthropophobia, if the anthroecological context of species is known (Allendorf et al. 2010, Sih et al. 2011).

The context is global.—Perhaps the most fundamental challenge in understanding the anthroecological context of observations is poor reporting of their global geographic context, which is widespread in ecological publications (Martin et al. 2012, Dornelas et al. 2013, Karl et al. 2013). Given the free availability of powerful geographic tools, such as Google Earth, there is no excuse for all ecological observations not to be described geographically, not just in the general terms of a nearby point location, but precisely, using a polygon outlining the extent of each observation unit for which data are reported (Kwan 2012, Karl et al. 2013). By linking all ecological observations with their precise geographic context, the global and local patterns, processes, and dynamics of sociocultural niche construction may be connected with these observations at a later time. Further, it is useful, if possible, to make observations across landscapes at spatial scales large enough to represent regional to global patterns (Noss 1990) and to investigate ecological patterns, processes, and dynamics across the full spectrum of anthromes and anthropogenic landscapes (Martin et al. 2012). Not to do this reduces the generalizability of ecological observations overall, and especially their relations with anthroecological processes and their dynamics, which are now unfolding globally through telecoupling (Kwan 2012, Martin et al. 2012, Dornelas et al. 2013, Liu et al. 2013, Gerstner et al. 2014, Murphy and Romanuk 2014, McGill et al. 2015).

People are data.—While the challenges of incorporating humans into ecological research are many, so are the opportunities. Especially exciting are recent advances in techniques for citizen science and for sensing, cataloging, and sharing ecological data from local to global (Fraser et al. 2013, Crain et al. 2014, Cristescu 2014, Turner 2014, McGill et al. 2015). Macroecological study of anthroecological processes (Burnside et al. 2012) is increasingly supported by powerful tools for "big data" analytics, including the rise and spread of behaviorally modern humans using paleogenomics (Pääbo 2014) and the structure of human social networks, including

---

[2] http://anthromes.org

changes in social centrality (Schich et al. 2014), the crowdsourcing of ecological questions and experiments (Fraser et al. 2013, Sutherland et al. 2013), and new methods for integrative global synthesis, including more powerful forms of meta-study (Magliocca et al. 2015) and global geospatial data and analytics (Verburg et al. 2011, Martin et al. 2012, Schmill et al. 2014). Ecologists have much to gain by further embracing these new larger scale methods for socio-ecological data acquisition and synthesis.

Ecology is a human experiment.—There are many good reasons why it is difficult to experiment with human interactions with ecosystems. Nevertheless, efforts to do this show increasing promise (Felson and Pickett 2005, Felson et al. 2013), and experimentally replicating human influences is well developed in ecology (Debinski and Holt 2000, Fraser et al. 2013). There are real limits to these experimental approaches however, especially in establishing cause and effect in human–environment interactions at larger scales and over longer time frames (Hedström and Ylikoski 2010, Cuddington 2012). To develop mechanistic theory on human transformation of ecology requires approaches that are nondeterministic, multicausal, path-dependent, and probabilistic, so as to model the emergent anthroecological patterns and processes produced by human individuals, groups, and societies interacting with each other in transforming ecology across landscapes and regions, and responding to and learning from these changes (Macy and Willer 2002, Hedström and Ylikoski 2010, Magliocca et al. 2013, 2014, Turchin et al. 2013). Agent-based modeling is ideal for this, especially using a virtual laboratory approach applied to the anthroecological patterns observed in real-world landscapes (Magliocca et al. 2013, 2014). These techniques show great promise for testing basic hypotheses on sociocultural niche construction as a force reshaping ecological pattern and process within and across landscapes under different societal and ecological conditions; for example, the long-term patterning of habitat quality and fragmentation under different strategies for cooperative engineering of multifunctional landscapes, enabling theory validation, scenario generation, and interactive assessments in the field together with stakeholders (Matthews et al. 2007, Willemen et al. 2012).

Sustaining nonhuman nature in an anthropogenic biosphere

The challenges of sustaining nonhuman species and habitats in an anthropogenic biosphere have never been greater as the scale, extent, and intensity of sociocultural niche construction by industrial societies is already without precedent and continues to accelerate. Perhaps the greatest challenge for conserving nonhuman species and habitats is that human harm to these is generally not intentional, but rather results as the unintended consequences of intentional human-benefitting sociocultural niche construction, including ecosystem engineering for agriculture and resource extraction (habitat loss and degradation, pollution), industrial production and infrastructure (pollution, hydrologic change), social exchange (facilitated biotic exchange, wildlife trade), and energy substitution (pollution, climate change, ocean acidification). Yet the increasing global scale, interconnection, and capacity for engineering of human societies may yet prove to be powerful forces driving major societal shifts in both valuing and conserving nonhuman nature. The societal benefits of sustaining nonhuman species and habitats have likely never been clearer, as the ecological linkages among human health, social systems, and engineered environments are increasingly understood both theoretically and with the aim of advancing intentional management by societies (Millennium Ecosystem Assessment 2005, Mooney et al. 2013). Perhaps the most potent example is the recent discovery and rapid scientific advances in understanding the novel global ecology of the human microbiome, in which humans serve as both host environments and biological recipients of microbial benefits and detriments (Smillie et al. 2011, Kembel et al. 2012, O'Doherty et al. 2014). Just as today's globalizing and urbanizing societies are growing more concerned with the need to conserve nonhuman nature, they are becoming more and more capable technologically, culturally, and socially of accomplishing this (Inglehart 2000, Rosenzweig 2003, Ellis 2015).

Engage with planetary opportunities.—The scale of human societies is increasingly global, with telecoupling linking the resource demands of increasingly wealthy urban populations with transformative ecological change across the biosphere (Lambin and Meyfroidt 2011, Fairhead et al. 2012, D'Odorico et al. 2014, Nepstad et al. 2014). It is also highly unlikely that human populations will decline significantly in the foreseeable future (Bradshaw and Brook 2014). Strategies for conserving nonhuman nature will therefore have little chance of succeeding if they depend on halting the growth and development of human societies. The way forward for conservation requires strategies that can engage beneficially with global trends toward increasing societal scales, globalization, and urbanization.

Urbanization, land use intensification, and decoupling are planetary opportunities to conserve more nonhuman nature (Fischer-Kowalski and Swilling 2011, Tilman et al. 2011, DeFries et al. 2012). While urbanization transforms ecology more than any other form of land use, urban areas have the potential to be the most compact and resource efficient form of human settlement (Grimm et al. 2008, Bettencourt and West 2010, Bettencourt 2013). As the wealth, lifestyles, and other opportunities afforded by urban living attract populations from the countryside, opportunities are arising for woodland recoveries in lands less suitable for industrial agriculture (Foster et al. 1998, Rudel et al. 2009, Meyfroidt and Lambin 2011, Ellis et al. 2013*b*, Queiroz et al. 2014). While the challenges are certainly as great as the opportunities, there is good evidence that even more land can be spared for nonhuman nature as urbanization and societal upscaling continue, depending on the productivity gains attainable in agriculture and forestry through sustained land use intensification combined with more equitable distribution to meet growing societal demands for food, feed, housing, and energy (Neumann et al. 2010, Foley et al. 2011, Tilman et al. 2011, Tomich et al. 2011, Loos et al. 2014). To succeed in these efforts, it is essential to avoid the mere displacement of societal demands from one region to another by monitoring and improved governance of agricultural supply chains and environmental programs (Fairhead et al. 2012, D'Odorico et al. 2014, Nepstad et al. 2014, Scales 2014).

Embrace change, beware domestication.—Anthropogenic climate change, together with other indirect and direct forces of sociocultural niche construction are causing ecological changes that are likely more rapid than in any other recent period of Earth history (Steffen et al. 2007, Hoffmann and Sgro 2011). To sustain nonhuman nature, it will be necessary to assist species and ecosystems in changing, for example, by translocating species together with their habitats as these shift toward the poles; a very different paradigm than the classic view of ecological conservation as the preservation of historical patterns in situ (Bengtsson et al. 2003, Waltner-Toews et al. 2003, Jackson and Hobbs 2009, Hobbs et al. 2011, 2014, Hoffmann and Sgro 2011, Thomas 2011, Robbins and Moore 2013, Balaguer et al. 2014, Gillson and Marchant 2014, Higgs et al. 2014, Ellis 2015). Most importantly, it will be essential to sustain processes of evolution by natural selection in the face of powerful human tendencies to select the traits of and even to domesticate the native species we are trying to conserve as wild (Western 2001, Ellis et al. 2012, Palkovacs et al. 2012, Smith et al. 2014). The need to refocus conservation science on sustaining evolutionary processes and their dynamics requires efforts and expertise that go far beyond simply preserving or restoring historical states of ecosystems, habitats, or populations, and this need can only grow as environments become ever more dynamic (Antrop 2006, Hoffmann and Sgro 2011, Hobbs et al. 2014), technological advances enable more precise management of population genetics, the revival of extinct species, and the creation of novel life forms, and these technological capacities are confronted with expanded social demands for rewilding, conservation beyond protected areas, and other unconventional, controversial, and poorly understood strategies for restoring and sustaining nonhuman nature (Hobbs et al. 2011, 2014, Redford et al. 2013, Robbins and Moore 2013, Marris 2014, Sandler 2014, Smith et al. 2014).

Bring people in: codesigning anthromes and multifunctional landscapes.—The future of nonhuman nature depends both on meeting human needs and inspiring human desires toward greater efforts at Earth stewardship (Chan et al. 2007, Chapin et al. 2011, Marris 2011, Felson et al. 2013, Mooney et al. 2013, Ives and Kendal 2014, Mace 2014, Palomo et al. 2014). To accomplish this, it is more necessary than ever to integrate sociocultural understanding into conservation (Waltner-Toews et al. 2003, Mooney et al. 2013, Redpath et al. 2013, Ives and Kendal 2014, Kueffer and Kaiser-Bunbury 2014, Mace 2014, Palomo et al. 2014, Poe et al. 2014), and to consider flexible strategies enabling the sustained integration of nonhuman species into the novel habitats of anthromes as part of multifunctional landscape management approaches (Antrop 2006, Bennett et al. 2006, Kleijn et al. 2011, Tomich et al. 2011, van Noordwijk et al. 2012, Ellis 2013, Hobbs et al. 2014, Jantz et al. 2014, Martin et al. 2014, Marvier 2014, Quinn et al. 2014).

To the extent that trade-offs among production, biodiversity, and ecosystem services are considered (Bergen et al. 2001, DeFries et al. 2004, Naidoo et al. 2008) and the people and societies with a stake in the results are involved in codesigning and cooperating in these efforts (Berkes et al. 2000, Olsson et al. 2004, Antrop 2006, Reed 2008), multifunctional landscape approaches have the potential to sustain nonhuman nature in the face of unprecedented anthropogenic ecological change (Rosenzweig 2003, DeFries and Rosenzweig 2010, DeFries et al. 2012, Ellis 2013, Hobbs et al. 2014, Martin et al. 2014). Toward this end, ecologists will need to more actively embrace their role in informing and helping to shape the work of policymakers, planners, engineers, and designers, as these are the societal realms in which larger scales of human intentionality are engaged in the processes of sociocultural niche construction that generate ecological inheritance for nonhuman species. To make this possible, ecologists must become more active in observing and informing on, if not collaborating directly in, the full range of human engagements with ecology beyond conservation, including agriculture, industry, and the built environment, the creative and experimental processes of design and policy, and even the decision to allow novel ecological patterns and processes to emerge without human intervention.

Pedagogy is destiny: teach the future

With current rates of social and environmental change, pedagogy has never been more important; teaching is the most powerful process of social learning and is potentially capable of shifting the cultural and ecological trajectory of societies (Wilson et al. 2014). Moreover, the teaching of ecology and conservation needs to change if it is to successfully assist societies in influencing the trajectories of global anthroecological change.

Accepting sociocultural systems as a global force of nature represents a paradigm shift across the natural sciences that is no less significant than evolution by natural selection or plate tectonics (Steffen et al. 2011).

For ecologists, the meaning should be very clear. The forces of humanity are now akin to those of climate geophysics or biology and therefore as fundamental to understanding the processes that shape life on Earth as the sciences of climate, soils, or biology. To engage in scientific study of ecological pattern, process, and change as it exists today and for the foreseeable future demands a firm grasp of the human sciences and their deep integration into ecological theory and practice. It is no longer adequate merely to study the consequences of human transformation of ecological pattern and process: Ecology must become a science of their ultimate causes.

In the teaching of ecology, humans are generally presented as operating entirely within a biological world, sustained by natural ecosystems, in statements like "humanity is a biological species in a biological world" (Wilson 2012) and "that man is, in fact, only a member of a biotic team is shown by an ecological interpretation of history" (Leopold 1949). Human alteration of ecology tends to be depicted as a recent crisis brought on by modern industrial societies and their rapid population growth, disturbing fragile natural ecosystems, and threatening both humanity and nonhuman nature, with such framing usually accompanied by a call to return to or maintain some prior balance of nature (Rockstrom et al. 2009, Simberloff 2014). As with the seemingly perpetual need for ecology to reject the balance of nature concept, these romantic notions should have no place in ecological science (Cronon 1983, Briggs et al. 2006, Pickett 2013).

There are important pedagogical consequences to this erroneous portrayal. Beyond its incorrect interpretation of environmental history, it implies that behaviorally modern human populations and their transformation of ecology might be understood, as with other species, as a matter determined simply by population size in relation to fixed environmental limits, an incorrect understanding of the processes that sustain societies and cause anthropogenic ecological change (Cohen 1995, Tainter 2006*a*, Ellis et al. 2013*b*). The ecological niche, carrying capacity, and environmental impacts of behaviorally modern human populations are the product of sociocultural niche construction and are therefore defined more by sociocultural processes than by environmental constraints (Cohen 1995, Gurney and Lawton 1996, Odling-Smee et al. 2003*c*, Sayre 2008, Ellis et al. 2013*b*, Odling-Smee et al. 2013). Moreover, by singling out industrial technologies as the primary cause of environmental harm, the fact that these are now required to sustain existing populations is ignored, together with the fact that these have already enabled far less land to be used per capita over the long term (Butzer 2012, Ellis et al. 2013*b*). Further advances in ecosystem engineering efficiency combined with more equitable subsistence regimes are the only way that growing and thriving human populations will be able to use less of the biosphere to produce food, fiber, energy, and other resources. It is pedagogical malpractice to teach that contemporary human populations might somehow sustain themselves by going back to earlier, less efficient technologies, such as Paleolithic lifeways, a full transition to traditional organic farming, or an increasing dependence on harvesting biomass for energy.

Behaviorally modern humans have always used technology to engineer their ecosystems and have never lived in ecosystems unaltered by their societies (Smith and Wishnie 2000, Ellis et al. 2013*b*). The human niche is not defined by human biology. Humans live within a sociocultural niche constructed by cooperative ecosystem engineering and culturally mediated subsistence exchange. In an increasingly anthropogenic biosphere, it is essential to shift the paradigm. Humans are a sociocultural species living in a sociocultural world on a used planet. It is time to go beyond balances of nature and even fluxes of nature to embrace the "cultures of nature" in ecology.

The paradigm must shift. Cultures create and sustain natures. Individual humans act intentionally, but they do so within their social contexts and depend on cultural values, perceptions, and actions (Dyball and Newell 2014, Ives and Kendal 2014, Mace 2014, Medin and Bang 2014). The question is not how to stop "others" from destroying nature, or finding a way to "get back to nature," but how to engage societies toward shaping nature more beneficially for both humans and nonhumans (Mace 2014, Palomo et al. 2014). Sociocultural niche construction in an increasingly anthropogenic biosphere is neither new nor disastrous, but the perpetual activity of human societies engaged in the intentional cooperative engineering of ecosystems since prehistory (Smith and Wishnie 2000, Ellis et al. 2013*b*).

To incorporate human sociocultural niche construction at the core of ecological pedagogy, the framing of humans as destroyers of nature must transition to narratives of societies as nature sustainers (Chapin et al. 2011). In moving toward this goal, the work of archaeologists, natural historians, agroecologists, urban ecologists, conservationists, engineers, and designers all have much to offer and much to gain.

The teaching of ecology has always appealed to a sense of wonder about the natural world. As educators we must build a new sense of wonder and discovery about the "tangled bank" of human sociocultural systems and the diversity of ecosystems they create and sustain together with the traditional ecologies of cultures, cultural landscapes, and cities. By embracing sociocultural evolution and teaching it, current and future generations of ecologists and the public will be better equipped to guide societies toward better outcomes for both people and nonhuman nature.

Thinking globally in an anthropogenic biosphere

The call to recognize the Anthropocene as a new epoch of geologic time confronts ecologists and other environmental scientists with the need to understand, visualize, and model the emergence and dynamics of human societies as a global force reshaping the biosphere, atmosphere, and the other "spheres" of the Earth system (Ellis 2011, Steffen et al. 2011). Anthroecology characterizes these global forcings and dynamics through the analogy of a "human climate system." Just as Earth's climate system shapes the dynamics of energy and material flow across the atmosphere, hydrosphere, and other spheres, human sociocultural systems shape the dynamics of energy, material, biotic, and information flow across the biosphere and other spheres, including those of a newly emerged anthroposphere comprised of human societies and their material cultures (Ellis and Haff 2009, Lucht 2010, Steffen et al. 2011, Baccini and Brunner 2012). Human systems and their interactions with the biosphere and anthroposphere are responsive to feedbacks with other Earth systems and are dynamic in response to evolutionary changes in sociocultural niche construction. In this way, long-term changes in human social organization, cooperative ecosystem engineering, exchange relationships, and energy systems are coupled with long-term changes in the Earth system. It remains to be seen whether intentional efforts by societies to intervene in the dynamics of human systems at global scales can or will ultimately generate more beneficial and less detrimental ecological inheritance for both human societies and nonhuman species.

Conclusions: The Natures We Create

Behaviorally modern humans are Earth's first ultrasocial species, requiring social learning to survive and to reproduce within the sociocultural systems and cooperatively engineered ecosystems that sustain them. Behaviorally modern human societies began transforming terrestrial ecology more than 50 000 years ago and emerged as a global force as their populations spread out of Africa and across the Earth. While contemporary rates and scales of anthropogenic ecological change are unprecedented, behaviorally modern human societies began permanently reshaping the terrestrial biosphere countless generations before the rise of industrial societies.

This paper introduces a causal theory explaining the emergence and dynamics of human transformation of the biosphere based on sociocultural niche construction, an evolutionary theory combining socially learned cooperative ecosystem engineering, the upscaling of societies through culturally mediated changes in social organization and subsistence exchange, and the harnessing of nonhuman energy sources to sustain these processes. In developing this theory, archaeological, paleoecological, anthropological, sociological, historical, and evolutionary evidence have been presented demonstrating that the ultimate causes of human transformation of the biosphere are inherently social and cultural, not biological, chemical, or physical.

The emergence of sociocultural niche construction by behaviorally modern human societies represents a novel evolutionary process in the Earth system that has reshaped the biosphere and will likely continue reshaping both the biosphere and human societies for the foreseeable future. Building on this "first law of the Anthropocene," anthroecology theory generates novel ecological hypotheses together with strategies for testing them using new theoretical frameworks including anthroecosystems, anthrosequences, anthrobiogeography, and anthroecological succession. By engaging these frameworks together with sociocultural niche construction theory, the emergence and long-term dynamics of anthropogenic ecological patterns and processes in biogeography, ecological succession, ecosystems, and landscapes, including the reshaping of biomes into anthromes, can be more effectively investigated and understood in an increasingly anthropogenic biosphere.

Ultimately, anthroecology theory aims to shift the science and pedagogy of ecology beyond the classic paradigm of "natural systems with humans disturbing them" to a new paradigm of "societies sustaining an anthropogenic biosphere." In applying anthroecology theory, it is critical to remember that like biological evolution, sociocultural evolution is a process, not a destiny, and that the future remains fully open to surprise. Perhaps the only guarantee is that the future will likely include societies and ecosystems that bear little resemblance to those of today. Nevertheless, it is hoped that, as ecological science advances in its capacity to investigate and understand the ultimate causes, not just the consequences, of human transformation of the biosphere, that this capacity will help to guide societies toward sustaining nonhuman natures more successfully in a thriving anthropogenic biosphere that future generations across the world will be proud of.

Acknowledgments

The author thanks Aaron Ellison for inviting this work with the question: How would ecological concepts and ideas have to change if we (re)focused our attention on anthromes, not biomes, as an underlying biogeographic organizing schema? This work would not have been possible without the sustained support of Ariane de Bremond. The author also thanks Jared Margulies, Nicholas Magliocca, David Lansing, Robert Dyball, Michael Perring, and three anonymous reviewers for their very helpful comments on the manuscript. Support for Erle Ellis was provided by U.S. NSF grants CNS 1125210 and DBI 1147089.

Literature Cited

Abrutyn, S., and K. Lawrence. 2010. From chiefdom to state: toward an integrative theory of the evolution of polity. Sociological Perspectives 53:419–442.

Alessa, L., and F. S. Chapin, III. 2008. Anthropogenic biomes: a key contribution to earth-system science. Trends in Ecology and Evolution 23:529–531.

Allendorf, F. W., P. A. Hohenlohe, and G. Luikart. 2010. Genomics and the future of conservation genetics. Nature Reviews Genetics 11:697–709.

Alloway, B. J., and D. C. Ayres. 1997. Chemical principles of environmental pollution. Second edition. Chapman and Hall, New York, New York, USA.

Ambrose, S. H. 2001. Paleolithic technology and human evolution. Science 291:1748–1753.

Ames, K. M. 2007. The archaeology of rank. Pages 487–513 *in* R. A. Bentley, H. D. G. Maschner, and C. Chippindale, editors. Handbook of archaeological theories. AltaMira Press, Lanham, Maryland, USA.

Antón, S. C., R. Potts, and L. C. Aiello. 2014. Evolution of early Homo: an integrated biological perspective. Science 345:1236828.

Antrop, M. 2006. Sustainable landscapes: contradiction, fiction or utopia? Landscape and Urban Planning 75:187–197.

Apicella, C. L., F. W. Marlowe, J. H. Fowler, and N. A. Christakis. 2012. Social networks and cooperation in hunter-gatherers. Nature 481:497–501.

Archibald, S., A. C. Staver, and S. A. Levin. 2012. Evolution of human-driven fire regimes in Africa. Proceedings of the National Academy of Sciences USA 109:847–852.

Ausubel, J. H., and P. E. Waggoner. 2008. Dematerialization: variety, caution, and persistence. Proceedings of the National Academy of Sciences USA 105:12774–12779.

Baccini, P., and P. H. Brunner. 2012. Metabolism of the anthroposphere: analysis, evaluation, design. MIT Press, Cambridge, Massachusetts, USA.

Balaguer, L., A. Escudero, J. F. Martín-Duque, I. Mola, and J. Aronson. 2014. The historical reference in restoration ecology: re-defining a cornerstone concept. Biological Conservation 176:12–20.

Balée, W. 2006. The research program of historical ecology. Annual Review of Anthropology 35:75–98.

Barbier, E. B. 2010. Scarcity and frontiers: how economies have developed through natural resource exploitation. Cambridge University Press, Cambridge, UK.

Barceló, J. A., G. Capuzzo, and I. Bogdanovic. 2014. Modeling expansive phenomena in early complex societies: the transition from Bronze Iron Age in prehistoric Europe. Journal of Archaeological Method and Theory 21:486–510.

Barnosky, A. D. 2008. Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. Proceedings of the National Academy of Sciences USA 105:11543–11548.

Barnosky, A. D. 2014. Palaeontological evidence for defining the Anthropocene. Geological Society, London, Special Publications 395:149–165.

Barnosky, A. D., et al. 2012. Approaching a state shift in Earth's biosphere. Nature 486:52–58.

Bar-Oz, G., and D. Nadel. 2013. Worldwide large-scale trapping and hunting of ungulates in past societies. Quaternary International 297:1–7.

Basalla, G. 1988. The evolution of technology. Cambridge University Press, Cambridge, UK.

Bellwood, P. 2001. Early agriculturalist population diasporas? Farming, languages, and genes. Annual Review of Anthropology 30:181–207.

Bellwood, P. S. 2004. The first farmers: the origins of agricultural societies. Wiley-Blackwell, Oxford, UK.

Bengtsson, J., P. Angelstam, T. Elmqvist, U. Emanuelsson, C. Folke, M. Ihse, F. Moberg, and M. Nyström. 2003. Reserves, resilience and dynamic landscapes. AMBIO: A Journal of the Human Environment 32:389–396.

Bennett, A. F., J. Q. Radford, and A. Haslem. 2006. Properties of land mosaics: implications for nature conservation in agricultural environments. Biological Conservation 133:250–264.

Bergen, S. D., S. M. Bolton, and J. L. Fridley. 2001. Design principles for ecological engineering. Ecological Engineering 18:201–210.

Berkes, F., J. Colding, and C. Folke. 2000. Rediscovery of traditional ecological knowledge as adaptive management. Ecological Applications 10:1251–1262.

Bettencourt, L., and G. West. 2010. A unified theory of urban living. Nature 467:912–913.

Bettencourt, L. M. A. 2013. The origins of scaling in cities. Science 340:1438–1441.

Bettencourt, L. M. A., J. Lobo, D. Helbing, C. Kühnert, and G. B. West. 2007. Growth, innovation, scaling, and the pace of life in cities. Proceedings of the National Academy of Sciences USA 104:7301–7306.

Bettinger, R. 2009. Macroevolutionary theory and archaeology: Is there a big picture? Pages 275–295 *in* A. Prentiss, I. Kuijt, and J. C. Chatters, editors. Macroevolution in human prehistory. Springer, New York, New York, USA.

Bijker, W. E., T. P. Hughes, T. Pinch, and D. G. Douglas. 1987. The social construction of technological systems: new directions in the sociology and history of technology. MIT Press, Cambridge, Massachusetts, USA.

Bird, D. W., R. B. Bird, and C. H. Parker. 2005. Aboriginal burning regimes and hunting strategies in Australia's Western Desert. Human Ecology 33:127–142.

Bird, D. W., and J. F. O'Connell. 2006. Behavioral ecology and archaeology. Journal of Archaeological Research 14:143–188.

Blackmore, S. 1999. The meme machine. Oxford University Press, Oxford, UK.

Bliege Bird, R., D. W. Bird, B. F. Codding, C. H. Parker, and J. H. Jones. 2008. The "fire stick farming" hypothesis: Australian Aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. Proceedings of the National Academy of Sciences USA 105:14796–14801.

Bocquet-Appel, J.-P. 2011. The agricultural demographic transition during and after the agriculture inventions. Current Anthropology 52:S497–S510.

Boden, T. A., G. Marland, and R. J. Andres. 2012. Global, regional, and national fossil-fuel CO_2 emissions. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, USA.

Bohac, J., and R. Fuchs. 1991. The structure of animal communities as bioindicators of landscape deterioration. Pages 165–178 *in* B. Madden and D. W. Jefferey, editors. Bioindicators and environmental management. Academic Press, London, UK.

Bonduriansky, R. 2012. Rethinking heredity, again. Trends in Ecology and Evolution 27:330–336.

Bonduriansky, R., and T. Day. 2009. Nongenetic inheritance and its evolutionary implications. Annual Review of Ecology, Evolution, and Systematics 40:103–125.

Bowles, S. 2006. Group competition, reproductive leveling, and the evolution of human altruism. Science 314:1569–1572.

Bowles, S. 2009. Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? Science 324:1293–1298.

Bowman, D. M. J. S., et al. 2011. The human dimension of fire regimes on Earth. Journal of Biogeography 38:2223–2236.

Bowman, D. M. J. S., and S. G. Haberle. 2010. Paradise burnt: how colonizing humans transform landscapes with fire. Proceedings of the National Academy of Sciences USA 107:21234–21235.

Boyd, R., and P. J. Richerson. 1985. Culture and the evolutionary process. University of Chicago Press, Chicago, Illinois, USA.

Boyd, R., and P. J. Richerson. 2008. Gene–culture coevolution and the evolution of social institutions. Pages 305–323 *in* C. Engel and W. Singer, editors. Better than conscious? Decision making, the human mind, and implications for institutions. MIT Press, Cambridge, Massachusetts, USA.

Boyd, R., and P. J. Richerson. 2009. Culture and the evolution of human cooperation. Philosophical Transactions of the Royal Society B 364:3281–3288.

Boyd, R., P. J. Richerson, and J. Henrich. 2011. The cultural niche: Why social learning is essential for human adaptation.

Proceedings of the National Academy of Sciences USA 108:10918–10925.

Boyden, S. V. 2004. The biology of civilisation: understanding human culture as a force in nature. University of New South Wales Press, Kensington, Australia.

Bradley, B. A., D. M. Blumenthal, D. S. Wilcove, and L. H. Ziska. 2010. Predicting plant invasions in an era of global change. Trends in Ecology and Evolution 25:310–318.

Bradshaw, C. J. A., and B. W. Brook. 2014. Human population reduction is not a quick fix for environmental problems. Proceedings of the National Academy of Sciences USA 111:16610–16615.

Brenner, N., and C. Schmid. 2011. Planetary urbanisation. Pages 11–13 *in* M. Gandy, editor. Urban constellations. Jovis, Berlin, Germany.

Briggs, J. M., K. A. Spielmann, H. Schaafsma, K. W. Kintigh, M. Kruse, K. Morehouse, and K. Schollmeyer. 2006. Why ecology needs archaeologists and archaeology needs ecologists. Frontiers in Ecology and the Environment 4:180–188.

Brown, G. R., T. E. Dickins, R. Sear, and K. N. Laland. 2011*a*. Evolutionary accounts of human behavioural diversity. Philosophical Transactions of the Royal Society B 366:313–324.

Brown, J. H., W. R. Burnside, A. D. Davidson, J. P. DeLong, W. C. Dunn, M. J. Hamilton, J. C. Nekola, J. G. Okie, and N. Mercado-Silva. 2011*b*. Energetic limits to economic growth. BioScience 61:19–26.

Bruckner, M., S. Giljum, C. Lutz, and K. S. Wiebe. 2012. Materials embodied in international trade: global material extraction and consumption between 1995 and 2005. Global Environmental Change 22:568–576.

Brughmans, T. 2013. Thinking through networks: a review of formal network methods in archaeology. Journal of Archaeological Method and Theory 20:623–662.

Brynjolfsson, E., and A. McAfee. 2014. The second machine age: work, progress, and prosperity in a time of brilliant technologies. W. W. Norton, New York, New York, USA.

Buera, F. J., and J. P. Kaboski. 2009. The rise of the service economy. National Bureau of Economic Research, Cambridge, Massachusetts, USA.

Burnside, W. R., J. H. Brown, O. Burger, M. J. Hamilton, M. Moses, and L. M. A. Bettencourt. 2012. Human macroecology: linking pattern and process in big-picture human ecology. Biological Reviews 87:194–208.

Butzer, K. W. 1982. Archaeology as human ecology: method and theory for a contextual approach. Cambridge University Press, Cambridge, UK.

Butzer, K. W. 2012. Collapse, environment, and society. Proceedings of the National Academy of Sciences USA 109:3632–3639.

Butzer, K. W., and G. H. Endfield. 2012. Critical perspectives on historical collapse. Proceedings of the National Academy of Sciences USA 109:3628–3631.

Campbell, D. T. 1983. The two distinct routes beyond kin selection to ultrasociality: Implications for the humanities and social sciences. Pages 11–41 *in* D. L. Bridgeman, editor. The nature of prosocial development: theories and strategies. Academic Press, New York, New York, USA.

Carpenter, S. R., et al. 2009. Science for managing ecosystem services: beyond the Millennium Ecosystem Assessment. Proceedings of the National Academy of Sciences USA 106:1305–1312.

Castro, L., and M. A. Toro. 2010. Cultural transmission and evolution. eLS, John Wiley and Sons, Chichester, UK. http://dx.doi.org/10.1002/9780470015902.a0022858

Cavalli-Sforza, L. L., and M. W. Feldman. 1981. Cultural transmission and evolution: a quantitative approach. Princeton University Press, Princeton, New Jersey, USA.

Chan, K. M., R. M. Pringle, J. Ranganathan, C. L. Boggs, Y. L. Chan, P. R. Ehrlich, P. K. Haff, N. E. Heller, K. Al-Khafaji, and D. P. Macmynowski. 2007. When agendas collide: human welfare and biological conservation. Conservation Biology 21:59–68.

Chapin, F. S., III, et al. 2011. Earth Stewardship: science for action to sustain the human-earth system. Ecosphere 2:art89.

Chase-Dunn, C. 2006. World systems theorizing. Pages 745 *in* J. H. Turner, editor. Handbook of sociological theory. Springer, Dordrecht, The Netherlands.

Chase-Dunn, C. K., and B. Lerro. 2013. Social change: globalization from the Stone Age to the present. Paradigm, Boulder, Colorado, USA.

Chase-Dunn, C., and E. S. Manning. 2002. City systems and world systems: four millennia of city growth and decline. Cross-Cultural Research 36:379–398.

Christaller, W. 1933. Die zentralen Orte in Süddeutschland. Gustav Fischer, Jena, Germany. [Translated by C. W. Baskin. 1966. Central places in southern Germany. Prentice-Hall, Englewood Cliffs, New Jersey, USA.]

Christian, D., and W. H. McNeill. 2004. Maps of time: an introduction to big history. University of California Press, Oakland, California, USA.

Chudek, M., and J. Henrich. 2011. Culture–gene coevolution, norm-psychology and the emergence of human prosociality. Trends in Cognitive Sciences 15:218–226.

Cohen, J. E. 1995. Population growth and Earth's human carrying capacity. Science 269:341–346.

Collins, S. L., et al. 2011. An integrated conceptual framework for long-term social–ecological research. Frontiers in Ecology and the Environment 9:351–357.

Corcoran, P. L., C. J. Moore, and K. Jazvac. 2014. An anthropogenic marker horizon in the future rock record. GSA Today 24:4–8.

Corenblit, D., A. C. W. Baas, G. Bornette, J. Darrozes, S. Delmotte, R. A. Francis, A. M. Gurnell, F. Julien, R. J. Naiman, and J. Steiger. 2011. Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: a review of foundation concepts and current understandings. Earth-Science Reviews 106:307–331.

Costanza, R., et al. 2012. Developing an integrated history and future of people on earth (IHOPE). Current Opinion in Environmental Sustainability 4:106–114.

Costin, C. 2001. Craft production systems. Pages 273–327 *in* G. Feinman and T. D. Price, editors. Archaeology at the millennium. Springer, New York, New York, USA.

Costin, C. L. 1991. Craft specialization: issues in defining, documenting, and explaining the organization of production. Archaeological Method and Theory 3:1–56.

Cowgill, G. L. 2004. Origins and development of urbanism: archaeological perspectives. Annual Review of Anthropology 33:525–549.

Craig, O. E., et al. 2013. Earliest evidence for the use of pottery. Nature 496:351–354.

Crain, R., C. Cooper, and J. L. Dickinson. 2014. Citizen science: a tool for integrating studies of human and natural systems. Annual Review of Environment and Resources 39:641–665.

Cristescu, M. E. 2014. From barcoding single individuals to metabarcoding biological communities: towards an integrative approach to the study of global biodiversity. Trends in Ecology and Evolution 29:566–571.

Cronon, W. 1983. Changes in the land: Indians, colonists, and the ecology of New England. Hill and Wang, New York, New York, USA.

Crowther, R. 2002. Space junk: protecting space for future generations. Science 296:1241–1242.

Crutzen, P. J. 2002. Geology of mankind. Nature 415:23.

Cuddington, K. 2012. Legacy effects: the persistent impact of ecological interactions. Biological Theory 6:203–210.

Daily, G. C., P. R. Ehrlich, and G. A. Sanchez-Azofeifa. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. Ecological Applications 11:1–13.

Dale, P. J., B. Clarke, and E. M. G. Fontes. 2002. Potential for the environmental impact of transgenic crops. Nature Biotechnology 20:567–574.

Danchin, É. 2013. Avatars of information: towards an inclusive evolutionary synthesis. Trends in Ecology and Evolution 28:351–358.

Danchin, É., A. Charmantier, F. A. Champagne, A. Mesoudi, B. Pujol, and S. Blanchet. 2011. Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. Nature Reviews Genetics 12:475–486.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. First edition. Murray, London, UK.

Darwin, C. 1871. The descent of man: and selection in relation to sex. John Murray, London, UK.

Dawkins, R. 1976. The selfish gene. Oxford University Press, Oxford, UK.

Dean, L. G., R. L. Kendal, S. J. Schapiro, B. Thierry, and K. N. Laland. 2012. Identification of the social and cognitive processes underlying human cumulative culture. Science 335:1114–1118.

Dean, L. G., G. L. Vale, K. N. Laland, E. Flynn, and R. L. Kendal. 2014. Human cumulative culture: a comparative perspective. Biological Reviews 89:284–301.

Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14:342–355.

de Chardin, P. T. 1955. The phenomenon of man. HarperCollins, New York, New York, USA.

DeFries, R., et al. 2012. Planetary opportunities: a social contract for global change science to contribute to a sustainable future. BioScience 62:603–606.

DeFries, R. S., J. A. Foley, and G. P. Asner. 2004. Land-use choices: balancing human needs and ecosystem function. Frontiers in Ecology and the Environment 2:249–257.

DeFries, R., and C. Rosenzweig. 2010. Toward a whole-landscape approach for sustainable land use in the tropics. Proceedings of the National Academy of Sciences USA 107:19627–19632.

Del Tredici, P. 2010. Wild urban plants of the northeast: a field guide. Cornell University Press, Ithaca, New York, USA.

Derex, M., M.-P. Beugin, B. Godelle, and M. Raymond. 2013. Experimental evidence for the influence of group size on cultural complexity. Nature 503:389–391.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. Science 345:401–406.

D'Odorico, P., J. A. Carr, F. Laio, L. Ridolfi, and S. Vandoni. 2014. Feeding humanity through global food trade. Earth's Future 2:2014EF000250.

Dornelas, M., et al. 2013. Quantifying temporal change in biodiversity: challenges and opportunities. Proceedings of the Royal Society B 280:20121931.

Doughty, C. E. 2013. Preindustrial human impacts on global and regional environment. Annual Review of Environment and Resources 38:503–527.

Dunbar, R. I. M. 1998. The social brain hypothesis. Evolutionary Anthropology: Issues, News, and Reviews 6:178–190.

Durham, W. H. 1991. Coevolution: genes, culture, and human diversity. 1991 reprint edition. Stanford University Press, Stanford, California, USA.

Dyball, R., and B. Newell. 2014. Understanding human ecology: a systems approach to sustainability. Routledge, London, UK.

Dyson-Hudson, R., and E. A. Smith. 1978. Human territoriality: an ecological reassessment. American Anthropologist 80:21–41.

Earle, T. 2010. Exchange systems in prehistory. Pages 205–217 *in* C. D. Dillian and C. L. White, editors. Trade and exchange. Springer, New York, New York, USA.

Edgeworth, M. 2014. The relationship between archaeological stratigraphy and artificial ground and its significance in the Anthropocene. Geological Society, London, Special Publications 395:91–108.

Eerkens, J., and C. Lipo. 2007. Cultural transmission theory and the archaeological record: providing context to understanding variation and temporal changes in material culture. Journal of Archaeological Research 15:239–274.

Ellis, E. C. 2011. Anthropogenic transformation of the terrestrial biosphere. Proceedings of the Royal Society A: Mathematical, Physical and Engineering Science 369:1010–1035.

Ellis, E. C. 2013. Sustaining biodiversity and people in the world's anthropogenic biomes. Current Opinion in Environmental Sustainability 5:368–372.

Ellis, E. C. 2015. Too big for nature. Pages 24–31 *in* B. A. Minteer and S. J. Pyne, editors. After preservation: saving American nature in the age of humans. University of Chicago Press, Chicago, Illinois, USA.

Ellis, E. C., E. C. Antill, and H. Kreft. 2012. All is not loss: plant biodiversity in the Anthropocene. PLoS ONE 7:e30535.

Ellis, E. C., D. Q. Fuller, J. O. Kaplan, and W. G. Lutters. 2013*a*. Dating the Anthropocene: Towards an empirical global history of human transformation of the terrestrial biosphere. Elementa: Science of the Anthropocene 1:000018.

Ellis, E. C., and P. K. Haff. 2009. Earth science in the Anthropocene: new epoch, new paradigm, new responsibilities. EOS Transactions 90:473.

Ellis, E. C., J. O. Kaplan, D. Q. Fuller, S. Vavrus, K. Klein Goldewijk, and P. H. Verburg. 2013*b*. Used planet: a global history. Proceedings of the National Academy of Sciences USA 110:7978–7985.

Ellis, E. C., K. Klein Goldewijk, S. Siebert, D. Lightman, and N. Ramankutty. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography 19:589–606.

Ellis, E. C., and N. Ramankutty. 2008. Putting people in the map: anthropogenic biomes of the world. Frontiers in Ecology and the Environment 6:439–447.

Ellis, E. C., and S. M. Wang. 1997. Sustainable traditional agriculture in the Tai Lake Region of China. Agriculture, Ecosystems and Environment 61:177–193.

Ellison, A. M. 2004. Niches: looking backwards, looking forwards. Ecology 85:880–882.

Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecology Letters 10:1135–1142.

Enard, W., M. Przeworski, S. E. Fisher, C. S. L. Lai, V. Wiebe, T. Kitano, A. P. Monaco, and S. Paabo. 2002. Molecular evolution of FOXP2, a gene involved in speech and language. Nature 418:869–872.

Erwin, D. H. 2008. Macroevolution of ecosystem engineering, niche construction and diversity. Trends in Ecology and Evolution 23:304–310.

Estes, J. A., et al. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

Fairhead, J., M. Leach, and I. Scoones. 2012. Green grabbing: a new appropriation of nature? Journal of Peasant Studies 39:237–261.

Falkowski, P., et al. 2000. The global carbon cycle: a test of our knowledge of Earth as a system. Science 290:291–296.

Fehr, E., and U. Fischbacher. 2003. The nature of human altruism. Nature 425:785–791.

Feinman, G. M., and C. P. Garraty. 2010. Preindustrial markets and marketing: archaeological perspectives. Annual Review of Anthropology 39:167–191.

Felson, A. J., M. A. Bradford, and T. M. Terway. 2013. Promoting Earth stewardship through urban design experiments. Frontiers in Ecology and the Environment 11:362–367.

Felson, A. J., and S. T. A. Pickett. 2005. Designed experiments: new approaches to studying urban ecosystems. Frontiers in Ecology and the Environment 3:549–556.

Fischer-Kowalski, M., F. Krausmann, and I. Pallua. 2014. A sociometabolic reading of the Anthropocene: modes of subsistence, population size and human impact on Earth. Anthropocene Review 1:8–33.

Fischer-Kowalski, M., and M. Swilling. 2011. Decoupling: natural resource use and environmental impacts from economic growth. United Nations Environment Programme, Nairobi, Kenya.

Fisher, S. E., and M. Ridley. 2013. Culture, genes, and the human revolution. Science 340:929–930.

Flannery, K. V. 1972. The cultural evolution of civilizations. Annual Review of Ecology and Systematics 3:399–426.

Foley, J. A., et al. 2011. Solutions for a cultivated planet. Nature 478:337–342.

Foley, R. A., and M. Mirazón Lahr. 2011. The evolution of the diversity of cultures. Philosophical Transactions of the Royal Society B 366:1080–1089.

Folke, C. 2006. Resilience: The emergence of a perspective for social-ecological systems analyses. Global Environmental Change 16:253–267.

Folke, C., T. Hahn, P. Olsson, and J. Norberg. 2005. Adaptive governance of social-ecological systems. Annual Review of Environment and Resources 30:441–473.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207–231.

Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. Ecosystems 1:96–119.

Fraser, L. H., et al. 2013. Coordinated distributed experiments: an emerging tool for testing global hypotheses in ecology and environmental science. Frontiers in Ecology and the Environment 11:147–155.

Frolking, S., T. Milliman, K. C. Seto, and M. A. Friedl. 2013. A global fingerprint of macro-scale changes in urban structure from 1999 to 2009. Environmental Research Letters 8:024004.

Fuller, D. Q. 2010. An emerging paradigm shift in the origins of agriculture. General Anthropology 17:1–12.

Fuller, D. Q., T. Denham, M. Arroyo-Kalin, L. Lucas, C. J. Stevens, L. Qin, R. G. Allaby, and M. D. Purugganan. 2014. Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record. Proceedings of the National Academy of Sciences USA 111:6147–6152.

Fuller, D. Q., G. Willcox, and R. G. Allaby. 2011. Cultivation and domestication had multiple origins: arguments against the core area hypothesis for the origins of agriculture in the Near East. World Archaeology 43:628–652.

Galloway, J. N., et al. 2004. Nitrogen cycles: past, present, and future. Biogeochemistry 70:153–226.

Geels, F. W. 2002. Technological transitions as evolutionary reconfiguration processes: a multi-level perspective and a case-study. Research Policy 31:1257–1274.

Geels, F. W., and J. Schot. 2007. Typology of sociotechnical transition pathways. Research Policy 36:399–417.

Gelfand, M. J., et al. 2011. Differences between tight and loose cultures: a 33-nation study. Science 332:1100–1104.

Gerstner, K., C. F. Dormann, A. Stein, A. M. Manceur, and R. Seppelt. 2014. Effects of land use on plant diversity: a global meta-analysis. Journal of Applied Ecology 51:1690–1700.

Giddens, A. 2013. The constitution of society: outline of the theory of structuration. Wiley, Hoboken, New Jersey, USA.

Gignoux, C. R., B. M. Henn, and J. L. Mountain. 2011. Rapid, global demographic expansions after the origins of agriculture. Proceedings of the National Academy of Sciences USA 108:6044–6049.

Gill, J. L. 2014. Ecological impacts of the late Quaternary megaherbivore extinctions. New Phytologist 201:1163–1169.

Gillson, L., and R. Marchant. 2014. From myopia to clarity: sharpening the focus of ecosystem management through the lens of palaeoecology. Trends in Ecology and Evolution 29:317–325.

Gintis, H. 2011. Gene–culture coevolution and the nature of human sociality. Philosophical Transactions of the Royal Society B 366:878–888.

Gliessman, S. R. 2015. Agroecology: the ecology of sustainable food systems. Third edition. CRC Press, Boca Raton, Florida, USA.

Godfrey-Smith, P. 2012. Darwinism and cultural change. Philosophical Transactions of the Royal Society B 367:2160–2170.

Gorman, A. C. 2014. The Anthropocene in the solar system. Journal of Contemporary Archaeology 1:87–91.

Gray, R. D., Q. D. Atkinson, and S. J. Greenhill. 2011. Language evolution and human history: what a difference a date makes. Philosophical Transactions of the Royal Society B 366:1090–1100.

Gray, R. D., D. Bryant, and S. J. Greenhill. 2010. On the shape and fabric of human history. Philosophical Transactions of the Royal Society B 365:3923–3933.

Grayson, D. 2001. The archaeological record of human impacts on animal populations. Journal of World Prehistory 15:1–68.

Grigg, D. B. 1974. The agricultural systems of the world: an evolutionary approach. Cambridge University Press, Cambridge, UK.

Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. Wu, X. Bai, and J. M. Briggs. 2008. Global change and the ecology of cities. Science 319:756–760.

Gruber, N., and J. N. Galloway. 2008. An Earth-system perspective of the global nitrogen cycle. Nature 451:293–296.

Guglielmino, C. R., C. Viganotti, B. Hewlett, and L. L. Cavalli-Sforza. 1995. Cultural variation in Africa: role of mechanisms of transmission and adaptation. Proceedings of the National Academy of Sciences USA 92:7585–7589.

Gurney, W. S. C., and J. H. Lawton. 1996. The population dynamics of ecosystem engineers. Oikos 76:273–283.

Haff, P. 2014. Humans and technology in the Anthropocene: six rules. Anthropocene Review 1:126–136.

Hall, T. D., P. Nick Kardulias, and C. Chase-Dunn. 2011. World-systems analysis and archaeology: continuing the dialogue. Journal of Archaeological Research 19:233–279.

Hamilton, M. J., O. Burger, J. P. DeLong, R. S. Walker, M. E. Moses, and J. H. Brown. 2009. Population stability, cooperation, and the invasibility of the human species. Proceedings of the National Academy of Sciences USA 106:12255–12260.

Hamilton, M. J., B. T. Milne, R. S. Walker, and J. H. Brown. 2007. Nonlinear scaling of space use in human hunter-gatherers. Proceedings of the National Academy of Sciences USA 104:4765–4769.

Hancock, G. J., S. G. Tims, L. K. Fifield, and I. T. Webster. 2014. The release and persistence of radioactive anthropogenic nuclides. Geological Society, London, Special Publications 395:265–281.

Harrison, R. M., R. E. Hester, and Royal Society of Chemistry. 2011. Nuclear power and the environment. Royal Society of Chemistry, London, UK.

Harvey, D. 1996. Justice, nature, and the geography of difference. Blackwell, Oxford, UK.

Hawley, A. H. 1944. Ecology and human ecology. Social Forces 22:398–405.

Hedström, P., and P. Ylikoski. 2010. Causal mechanisms in the social sciences. Annual Review of Sociology 36:49–67.

Helmus, M. R., D. L. Mahler, and J. B. Losos. 2014. Island biogeography of the Anthropocene. Nature 513:543–546.

Henrich, J. 2001. Cultural transmission and the diffusion of innovations: adoption dynamics indicate that biased cultural transmission is the predominate force in behavioral change. American Anthropologist 103:992–1013.

Henrich, J. 2004. Cultural group selection, coevolutionary processes and large-scale cooperation. Journal of Economic Behavior and Organization 53:3–35.

Henrich, J. 2015. Culture and social behavior. Current Opinion in Behavioral Sciences 3:84–89.

Henrich, J., R. Boyd, S. Bowles, C. Camerer, E. Fehr, H. Gintis, and R. McElreath. 2001. In search of homo economicus: behavioral experiments in 15 small-scale societies. American Economic Review 91:73–78.

Henrich, J., R. Boyd, and P. Richerson. 2008. Five misunderstandings about cultural evolution. Human Nature 19:119–137.

Henrich, J., and R. McElreath. 2003. The evolution of cultural evolution. Evolutionary Anthropology: Issues, News, and Reviews 12:123–135.

Henshilwood, C. S., and C. W. Marean. 2003. The origin of modern human behavior: critique of the models and their test implications. Current Anthropology 44:627–651.

Higgs, E., D. A. Falk, A. Guerrini, M. Hall, J. Harris, R. J. Hobbs, S. T. Jackson, J. M. Rhemtulla, and W. Throop. 2014. The changing role of history in restoration ecology. Frontiers in Ecology and the Environment 12:499–506.

Hill, K., M. Barton, and A. M. Hurtado. 2009. The emergence of human uniqueness: Characters underlying behavioral modernity. Evolutionary Anthropology: Issues, News, and Reviews 18:187–200.

Hobbs, R. J., et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15:1–7.

Hobbs, R. J., et al. 2014. Managing the whole landscape: historical, hybrid and novel ecosystems. Frontiers in Ecology and the Environment 12:557–564.

Hobbs, R. J., L. M. Hallett, P. R. Ehrlich, and H. A. Mooney. 2011. Intervention ecology: applying ecological science in the twenty-first century. BioScience 61:442–450.

Hodder, I. 2011. Human-thing entanglement: towards an integrated archaeological perspective. Journal of the Royal Anthropological Institute 17:154–177.

Hodgson, G. 2002. The evolution of institutions: an agenda for future theoretical research. Constitutional Political Economy 13:111–127.

Hoffmann, A. A., and C. M. Sgro. 2011. Climate change and evolutionary adaptation. Nature 470:479–485.

Hornborg, A., and C. L. Crumley, editors. 2007. The world system and the earth system: global socioenviromental change and sustainability since the Neolithic. Left Coast Press, Walnut Creek, California, USA.

House, B. R., J. B. Silk, J. Henrich, H. C. Barrett, B. A. Scelza, A. H. Boyette, B. S. Hewlett, R. McElreath, and S. Laurence. 2013. Ontogeny of prosocial behavior across diverse societies. Proceedings of the National Academy of Sciences USA 110:14586–14591.

Huston, M. A. 2005. The three phases of land-use change: implications for biodiversity. Ecological Applications 15:1864–1878.

Inglehart, R. 2000. Globalization and postmodern values. Washington Quarterly 23:215–228.

IPCC. 2013. Climate change 2013: the physical science basis. A report of Working Group I of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Ives, C. D., and D. Kendal. 2014. The role of social values in the management of ecological systems. Journal of Environmental Management 144:67–72.

Jackson, S. T., and R. J. Hobbs. 2009. Ecological restoration in the light of ecological history. Science 325:567–569.

Jantz, P., S. Goetz, and N. Laporte. 2014. Carbon stock corridors to mitigate climate change and promote biodiversity in the tropics. Nature Climate Change 4:138–142.

Janzen, D. H. 1983. No park is an island: increase in interference from outside as park size decreases. Oikos 41:402–410.

Jones, C. G., J. L. Gutiérrez, J. E. Byers, J. A. Crooks, J. G. Lambrinos, and T. S. Talley. 2010. A framework for understanding physical ecosystem engineering by organisms. Oikos 119:1862–1869.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Kaplan, H. S., P. L. Hooper, and M. Gurven. 2009. The evolutionary and ecological roots of human social organization. Philosophical Transactions of the Royal Society B 364:3289–3299.

Kaplan, J. O., K. M. Krumhardt, E. C. Ellis, W. F. Ruddiman, C. Lemmen, and K. Klein Goldewijk. 2011. Holocene carbon emissions as a result of anthropogenic land cover change. Holocene 21:775–791.

Karl, J. W., J. K. Gillan, and J. E. Herrick. 2013. Geographic searching for ecological studies: a new frontier. Trends in Ecology and Evolution 28:383–384.

Keeley, L. H. 1988. Hunter-gatherer economic complexity and "population pressure": a cross-cultural analysis. Journal of Anthropological Archaeology 7:373–411.

Kembel, S. W., E. Jones, J. Kline, D. Northcutt, J. Stenson, A. M. Womack, B. J. M. Bohannan, G. Z. Brown, and J. L. Green. 2012. Architectural design influences the diversity and structure of the built environment microbiome. ISME Journal 6:1469–1479.

Kendal, J., J. J. Tehrani, and J. Odling-Smee. 2011. Human niche construction in interdisciplinary focus. Philosophical Transactions of the Royal Society B 366:785–792.

Kirch, P. V. 2005. Archaeology and global change: the Holocene record. Annual Review of Environment and Resources 30:409.

Kleijn, D., M. Rundlöf, J. Scheper, H. G. Smith, and T. Tscharntke. 2011. Does conservation on farmland contribute to halting the biodiversity decline? Trends in Ecology and Evolution 26:474–481.

Klein, R. G. 2009. The human career: human biological and cultural origins. Third edition. University of Chicago Press, Chicago, Illinois, USA.

Klein, R. G. 2013. Modern human origins. General Anthropology 20:1–4.

Klein Goldewijk, K., A. Beusen, and P. Janssen. 2010. Long-term dynamic modeling of global population and built-up area in a spatially explicit way: HYDE 3.1. Holocene 20:565–573.

Kline, M. A., and R. Boyd. 2010. Population size predicts technological complexity in Oceania. Proceedings of the Royal Society B 277:2559–2564.

Kowarik, I. 2003. Human agency in biological invasions: secondary releases foster naturalisation and population expansion of alien plant species. Biological Invasions 5:293–312.

Kowarik, I. 2011. Novel urban ecosystems, biodiversity, and conservation. Environmental Pollution 159:1974–1983.

Krausmann, F., K.-H. Erb, S. Gingrich, H. Haberl, A. Bondeau, V. Gaube, C. Lauk, C. Plutzar, and T. D. Searchinger. 2013. Global human appropriation of net primary production doubled in the 20th century. Proceedings of the National Academy of Sciences USA 110:10324–10329.

Kueffer, C., and C. N. Kaiser-Bunbury. 2014. Reconciling conflicting perspectives for biodiversity conservation in the Anthropocene. Frontiers in Ecology and the Environment 12:131–137.

Kwan, M.-P. 2012. The uncertain geographic context problem. Annals of the Association of American Geographers 102:958–968.

Laland, K. N., and G. Brown. 2011. Sense and nonsense: evolutionary perspectives on human behaviour. Oxford University Press, Oxford, UK.

Laland, K., J. Kendal, and G. Brown. 2007. The niche construction perspective: implications for evolution and human behaviour. Journal of Evolutionary Psychology 5:51–66.

Laland, K. N., and M. J. O'Brien. 2012. Cultural niche construction: an introduction. Biological Theory 6:191–202.

Laland, K. N., F. J. Odling-Smee, and M. W. Feldman. 1999. Evolutionary consequences of niche construction and their implications for ecology. Proceedings of the National Academy of Sciences USA 96:10242–10247.

Laland, K. N., J. Odling-Smee, and M. W. Feldman. 2000. Niche construction, biological evolution, and cultural change. Behavioral and Brain Sciences 23:131–146.

Laland, K. N., J. Odling-Smee, and M. W. Feldman. 2001. Cultural niche construction and human evolution. Journal of Evolutionary Biology 14:22–33.

Laland, K. N., J. Odling-Smee, and S. Myles. 2010. How culture shaped the human genome: bringing genetics and the human sciences together. Nature Reviews Genetics 11:137–148.

Lambin, E. F., et al. 2001. The causes of land-use and land-cover change: moving beyond the myths. Global Environmental Change 11:261–269.

Lambin, E. F., and P. Meyfroidt. 2011. Global land use change, economic globalization, and the looming land scarcity. Proceedings of the National Academy of Sciences USA 108:3465–3472.

Larson, G., and D. Q. Fuller. 2014. The evolution of animal domestication. Annual Review of Ecology, Evolution, and Systematics 66:115–136.

Larson, G., et al. 2014. Current perspectives and the future of domestication studies. Proceedings of the National Academy of Sciences USA 111:6139–6146.

Lenski, G. E. 1966. Power and privilege: a theory of social stratification. University of North Carolina Press, Chapel Hill, North Carolina, USA.

Leopold, A. 1949. The land ethic. Page 240 *in* Sand County almanac, and sketches here and there. Oxford University Press, Oxford, UK.

Levin, S., et al. 2013. Social-ecological systems as complex adaptive systems: modeling and policy implications. Environment and Development Economics 18:111–132.

Lewis, H. M., and K. N. Laland. 2012. Transmission fidelity is the key to the build-up of cumulative culture. Philosophical Transactions of the Royal Society B 367:2171–2180.

Lewontin, R. C. 1983. Gene, organism, and environment. Pages 273–285 *in* D. S. Bendall, editor. Evolution from molecules to men. Cambridge University Press, Cambridge, UK.

Li, J., Y. Zhao, Q. Xu, Z. Zheng, H. Lu, Y. Luo, Y. Li, C. Li, and H. Seppä. 2014. Human influence as a potential source of bias in pollen-based quantitative climate reconstructions. Quaternary Science Reviews 99:112–121.

Lightfoot, K., R. Cuthrell, C. Striplen, and M. Hylkema. 2013. Rethinking the study of landscape management practices among hunter-gatherers in North America. American Antiquity 78:285–301.

Liu, J., et al. 2007. Complexity of coupled human and natural systems. Science 317:1513–1516.

Liu, J., et al. 2013. Framing sustainability in a telecoupled world. Ecology and Society 18:26.

Lockwood, J. L., M. F. Hoopes, and M. P. Marchetti. 2013. Invasion ecology. Wiley, Hoboken, New Jersey, USA.

Longcore, T., and C. Rich. 2004. Ecological light pollution. Frontiers in Ecology and the Environment 2:191–198.

Loos, J., D. J. Abson, M. J. Chappell, J. Hanspach, F. Mikulcak, M. Tichit, and J. Fischer. 2014. Putting meaning back into "sustainable intensification." Frontiers in Ecology and the Environment 12:356–361.

Lucht, W. 2010. Commentary: Earth system analysis and taking a crude look at the whole. Pages 19–31 *in* H. J. Schellnhuber, M. Molina, N. Stern, V. Huber, and S. Kadner, editors. Global sustainability: a nobel cause. Cambridge University Press, Cambridge, UK.

Mace, G. M. 2014. Whose conservation? Science 345:1558–1560.

Mace, R., and C. J. Holden. 2005. A phylogenetic approach to cultural evolution. Trends in Ecology and Evolution 20:116–121.

Mace, R., and F. M. Jordan. 2011. Macro-evolutionary studies of cultural diversity: a review of empirical studies of cultural transmission and cultural adaptation. Philosophical Transactions of the Royal Society B 366:402–411.

Macy, M. W., and R. Willer. 2002. From factors to actors: computational sociology and agent-based modeling. Annual Review of Sociology 28:143–166.

Magliocca, N. R., D. G. Brown, and E. C. Ellis. 2013. Exploring agricultural livelihood transitions with an agent-based virtual laboratory: global forces to local decision-making. PLoS ONE 8:e73241.

Magliocca, N. R., D. G. Brown, and E. C. Ellis. 2014. Cross-site comparison of land-use decision-making and its consequences across land systems with a generalized agent-based model. PLoS ONE 9:e86179.

Magliocca, N. R., T. K. Rudel, P. H. Verburg, W. J. McConnell, O. Mertz, K. Gerstner, A. Heinimann, and E. C. Ellis. 2015. Synthesis in land change science: methodological patterns, challenges, and guidelines. Regional Environmental Change 15:211–226.

Malhi, Y. 2014. The metabolism of a human-dominated planet. Pages 142–163 *in* I. Goldin, editor. Is the planet full? Oxford University Press, Oxford, UK.

Marlowe, F. W. 2005. Hunter-gatherers and human evolution. Evolutionary Anthropology: Issues, News, and Reviews 14:54–67.

Marris, E. 2011. Rambunctious garden: saving nature in a post-wild world. Bloomsbury, New York, New York, USA.

Marris, E. 2014. 'New conservation' is an expansion of approaches, not an ethical orientation. Animal Conservation 17:516–517.

Marsh, G. P. 1865. Man and nature: or, physical geography as modified by human action. Scribner, New York, New York, USA.

Martin, L. J., B. Blossey, and E. Ellis. 2012. Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. Frontiers in Ecology and the Environment 10:195–201.

Martin, L. J., et al. 2014. Biodiversity conservation opportunities across the world's anthromes. Diversity and Distributions 20:745–755.

Marvier, M. 2014. A call for ecumenical conservation. Animal Conservation 17:518–519.

Matthews, B., L. De Meester, C. G. Jones, B. W. Ibelings, T. J. Bouma, V. Nuutinen, J. van de Koppel, and J. Odling-Smee. 2014. Under niche construction: an operational bridge between ecology, evolution, and ecosystem science. Ecological Monographs 84:245–263.

Matthews, R. B., N. G. Gilbert, A. Roach, J. G. Polhill, and N. K. Gotts. 2007. Agent-based land-use models: a review of applications. Landscape Ecology 22:1447–1459.

McGill, B. J., M. Dornelas, N. J. Gotelli, and A. E. Magurran. 2015. Fifteen forms of biodiversity trend in the Anthropocene. Trends in Ecology and Evolution 30:104–113.

McIntyre, N. E., K. Knowles-Yánez, and D. Hope. 2000. Urban ecology as an interdisciplinary field: differences in the use of "urban" between the social and natural sciences. Urban Ecosystems 4:5–24.

Medin, D. L., and M. Bang. 2014. The cultural side of science communication. Proceedings of the National Academy of Sciences USA 111:13621–13626.

Mellars, P. 2005. The impossible coincidence. A single-species model for the origins of modern human behavior in Europe. Evolutionary Anthropology: Issues, News, and Reviews 14:12–27.

Mellars, P. 2006. Why did modern human populations disperse from Africa ca. 60,000 years ago? A new model. Proceedings of the National Academy of Sciences USA 103:9381–9386.

Mendenhall, C. D., D. S. Karp, C. F. J. Meyer, E. A. Hadly, and G. C. Daily. 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. Nature 509:213–217.

Mesoudi, A. 2011. Cultural evolution: how Darwinian theory can explain human culture and synthesize the social sciences. University of Chicago Press, Chicago, Illinois, USA.

Mesoudi, A., et al. 2013. Is non-genetic inheritance just a proximate mechanism? A corroboration of the extended evolutionary synthesis. Biological Theory 7:189–195.

Mesoudi, A., and M. O'Brien. 2008*a*. The learning and transmission of hierarchical cultural recipes. Biological Theory 3:63–72.

Mesoudi, A., and M. J. O'Brien. 2008*b*. The cultural transmission of Great Basin projectile-point technology I: an experimental simulation. American Antiquity 73:3–28.

Mesoudi, A., A. Whiten, and K. N. Laland. 2004. Perspective: is human cultural evolution Darwinian? Evidence reviewed from the perspective of The Origin of Species. Evolution 58:1–11.

Mesoudi, A., A. Whiten, and K. N. Laland. 2006. Towards a unified science of cultural evolution. Behavioral and Brain Sciences 29:329–347.

Meyfroidt, P., and E. F. Lambin. 2011. Global forest transition: prospects for an end to deforestation. Annual Review of Environment and Resources 36:343–371.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: health synthesis. World Health Organization, Geneva, Switzerland.

Mooney, H. A., and E. E. Cleland. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences USA 98:5446–5451.

Mooney, H. A., A. Duraiappah, and A. Larigauderie. 2013. Evolution of natural and social science interactions in global change research programs. Proceedings of the National Academy of Sciences USA 110:3665–3672.

Moore, J. W. 2011. Transcending the metabolic rift: a theory of crises in the capitalist world-ecology. Journal of Peasant Studies 38:1–46.

Morgan, T. J. H., et al. 2015. Experimental evidence for the co-evolution of hominin tool-making teaching and language. Nature Communications 6:6029.

Mulder, M. B., et al. 2009. Intergenerational wealth transmission and the dynamics of inequality in small-scale societies. Science 326:682–688.

Murdock, G. P., and D. R. White. 1969. Standard cross-cultural sample. Ethnology 8:329–369.

Murdock, G. P., and D. R. White. 2006. Standard cross-cultural sample: on-line edition. Social dynamics and complexity. Working Papers Series: Paper sStandard cross-cultural sample. University of California, Irvine, California, USA. https://escholarship.org/uc/item/62c5c02n#page-1

Murphy, G. E. P., and T. N. Romanuk. 2014. A meta-analysis of declines in local species richness from human disturbances. Ecology and Evolution 4:91–103.

Muthukrishna, M., B. W. Shulman, V. Vasilescu, and J. Henrich. 2014. Sociality influences cultural complexity. Proceedings of the Royal Society B 281:20132511.

Naidoo, R., A. Balmford, R. Costanza, B. Fisher, R. E. Green, B. Lehner, T. R. Malcolm, and T. H. Ricketts. 2008. Global mapping of ecosystem services and conservation priorities. Proceedings of the National Academy of Sciences USA 105:9495–9500.

Nelson, R. R. 1994. The co-evolution of technology, industrial structure, and supporting institutions. Industrial and Corporate Change 3:47–63.

Nepstad, D., et al. 2014. Slowing Amazon deforestation through public policy and interventions in beef and soy supply chains. Science 344:1118–1123.

Neumann, K., P. H. Verburg, E. Stehfest, and C. Müller. 2010. The yield gap of global grain production: a spatial analysis. Agricultural Systems 103:316–326.

Nolan, P., and G. E. Lenski. 2010. Human societies: an introduction to macrosociology. Eleventh edition. Paradigm, Boulder, Colorado, USA.

Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology 4:355–364.

Nowell, A. 2010. Defining behavioral modernity in the context of neandertal and anatomically modern human populations. Annual Review of Anthropology 39:437–452.

O'Brien, M. J., and K. N. Laland. 2012. Genes, culture, and agriculture: an example of human niche construction. Current Anthropology 53:434–470.

O'Brien, M. J., R. L. Lyman, A. Mesoudi, and T. L. VanPool. 2010. Cultural traits as units of analysis. Philosophical Transactions of the Royal Society B 365:3797–3806.

Odling-Smee, F. J. 1988. Niche-constructing phenotypes. Pages 73–132 *in* H. C. Plotkin, editor. The role of behavior in evolution. MIT Press, Cambridge, Massachusetts, USA.

Odling-Smee, F. J., K. N. Laland, and M. W. Feldman. 1996. Niche construction. American Naturalist 147:641–648.

Odling-Smee, F. J., K. N. Laland, and M. W. Feldman. 2003*a*. Human niche construction, learning, and cultural processes. Page 472 *in* Niche construction: the neglected process in evolution. Princeton University Press, Princeton, New Jersey, USA.

Odling-Smee, F. J., K. N. Laland, and M. W. Feldman. 2003*b*. Niche construction and ecology. Pages 194–238 *in* Niche construction: the neglected process in evolution. Princeton University Press, Princeton, New Jersey, USA.

Odling-Smee, F. J., K. N. Laland, and M. W. Feldman. 2003*c*. Niche construction: the neglected process in evolution. Princeton University Press, Princeton, New Jersey, USA.

Odling-Smee, J., D. H. Erwin, E. P. Palkovacs, M. W. Feldman, and K. N. Laland. 2013. Niche construction theory: a practical guide for ecologists. Quarterly Review of Biology 88:3–28.

Odling-Smee, J., and K. N. Laland. 2012. Ecological inheritance and cultural inheritance: What are they and how do they differ? Biological Theory 6:220–230.

O'Doherty, K. C., J. D. Neufeld, F. S. L. Brinkman, H. Gardner, D. S. Guttman, and R. G. Beiko. 2014. Opinion: conservation and stewardship of the human microbiome. Proceedings of the National Academy of Sciences USA 111:14312–14313.

Odum, E. P. 1953. Fundamentals of ecology. First edition. W. B. Saunders, Philadelphia, Pennsylvania, USA.

Oka, R., and C. Kusimba. 2008. The archaeology of trading systems, part 1: towards a new trade synthesis. Journal of Archaeological Research 16:339–395.

Olson, D. M., et al. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. BioScience 51:933–938.

Olsson, P., C. Folke, and F. Berkes. 2004. Adaptive comanagement for building resilience in social–ecological systems. Environmental Management 34:75–90.

Ortman, S. G., A. H. F. Cabaniss, J. O. Sturm, and L. M. A. Bettencourt. 2014. The pre-history of urban scaling. PLoS ONE 9:e87902.

Ortman, S. G., A. H. F. Cabaniss, J. O. Sturm, and L. M. A. Bettencourt. 2015. Settlement scaling and increasing returns in an ancient society. Science Advances 1:e1400066.

Pääbo, S. 2014. The human condition: a molecular approach. Cell 157:216–226.

Palkovacs, E. P., M. T. Kinnison, C. Correa, C. M. Dalton, and A. P. Hendry. 2012. Fates beyond traits: ecological consequences of human-induced trait change. Evolutionary Applications 5:183–191.

Palomo, I., C. Montes, B. Martín-López, J. A. González, M. García-Llorente, P. Alcorlo, and M. R. G. Mora. 2014. Incorporating the social–ecological approach in protected areas in the Anthropocene. BioScience 64:181–191.

Pfaffenberger, B. 1992. Social anthropology of technology. Annual Review of Anthropology 21:491–516.

Pickett, S. A. 2013. The flux of nature: changing worldviews and inclusive concepts. Pages 265–279 *in* R. Rozzi, S. T. A. Pickett, C. Palmer, J. J. Armesto, and J. B. Callicott, editors. Linking ecology and ethics for a changing world. Springer Netherlands, Dordrecht, The Netherlands.

Pickett, S. T. A., M. L. Cadenasso, J. M. Grove, C. H. Nilon, R. V. Pouyat, W. C. Zipperer, and R. Costanza. 2001. Urban ecological systems: linking terrestrial ecological, physical, and socio-economic components of metropolitan areas. Annual Review of Ecology and Systematics 32:127–157.

Pickett, S. T. A., and M. J. McDonnell. 1993. Humans as components of ecosystems: a synthesis. Pages 310–316 *in* M. J. McDonnell and S. T. A. Pickett, editors. Humans as components of ecosystems: the ecology of subtle human effects and populated areas. Springer, New York, New York, USA.

Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, and J. O. Sexton. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344:6187.

Pinker, S. 2010. The cognitive niche: Coevolution of intelligence, sociality, and language. Proceedings of the National Academy of Sciences USA 107:8993–8999.

Poe, M. R., K. C. Norman, and P. S. Levin. 2014. Cultural dimensions of socioecological systems: key connections and guiding principles for conservation in coastal environments. Conservation Letters 7:166–175.

Potts, R. 2012. Evolution and environmental change in early human prehistory. Annual Review of Anthropology 41:151–167.

Powell, A., S. Shennan, and M. G. Thomas. 2009. Late Pleistocene demography and the appearance of modern human behavior. Science 324:1298–1301.

Price, T. D., and O. Bar-Yosef. 2011. The origins of agriculture: new data, new ideas: an introduction to supplement 4. Current Anthropology 52:S163–S174.

Queiroz, C., R. Beilin, C. Folke, and R. Lindborg. 2014. Farmland abandonment: threat or opportunity for biodiversity conservation? A global review. Frontiers in Ecology and the Environment 12:288–296.

Quinn, J., R. Johnson, and J. Brandle. 2014. Identifying opportunities for conservation embedded in cropland anthromes. Landscape Ecology 29:1811–1819.

Rackham, O. 1980. Ancient woodland, its history, vegetation and uses in England. Edward Arnold, London, UK.

Rand, D. G., and M. A. Nowak. 2014. Human cooperation. Trends in Cognitive Sciences 17:413–425.

Redford, K. H., W. Adams, and G. M. Mace. 2013. Synthetic biology and conservation of nature: wicked problems and wicked solutions. PLoS Biology 11:e1001530.

Redman, C. L. 1999. Human impact on ancient environments. University of Arizona Press, Tucson, Arizona, USA.

Redman, C. L., J. M. Grove, and L. H. Kuby. 2004. Integrating social science into the Long-Term Ecological Research (LTER) network: social dimensions of ecological change and ecological dimensions of social change. Ecosystems 7:161–171.

Redpath, S. M., et al. 2013. Understanding and managing conservation conflicts. Trends in Ecology and Evolution 28:100–109.

Reed, M. S. 2008. Stakeholder participation for environmental management: a literature review. Biological Conservation 141:2417–2431.

Rendell, L., L. Fogarty, and K. N. Laland. 2011. Runaway cultural niche construction. Philosophical Transactions of the Royal Society B 366:823–835.

Ricciardi, A. 2007. Are modern biological invasions an unprecedented form of global change? Conservation Biology 21:329–336.

Richerson, P. J., and R. Boyd. 1998. The evolution of human ultra-sociality. Pages 71–95 *in* I. Eibl-Eibisfeldt and F. Salter, editors. Indoctrinability, ideology, and warfare: evolutionary perspectives. Berghahn Books, New York, New York, USA.

Richerson, P. J., and R. Boyd. 1999. Complex societies. Human Nature 10:253–289.

Richerson, P. J., and R. Boyd. 2005. Not by genes alone: how culture transformed human evolution. University of Chicago Press, Chicago, Illinois, USA.

Richerson, P. J., R. Boyd, and J. Henrich. 2010. Gene-culture coevolution in the age of genomics. Proceedings of the National Academy of Sciences USA 107:8985–8992.

Richter, D. D., et al. 2011. Human–soil relations are changing rapidly: proposals from SSSA's Cross-Divisional Soil Change Working Group. Soil Science Society of America Journal 75:2079–2084.

Rivers, R., C. Knappett, and T. Evans. 2013. What makes a site important? Centrality, gateways and gravity. Pages 125–150 *in* C. Knappett, editor. Network analysis in archaeology: new approaches to regional interaction. Oxford University Press, Oxford, UK.

Robbins, P., and S. A. Moore. 2013. Ecological anxiety disorder: diagnosing the politics of the Anthropocene. Cultural Geographies 20:3–19.

Rockstrom, J., et al. 2009. A safe operating space for humanity. Nature 461:472–475.

Rosenzweig, M. L. 2003. Win-win ecology: how the Earth's species can survive in the midst of human enterprise. Oxford University Press, New York, New York, USA.

Roth, G., and U. Dicke. 2005. Evolution of the brain and intelligence. Trends in Cognitive Sciences 9:250–257.

Rowley-Conwy, P., and R. Layton. 2011. Foraging and farming as niche construction: stable and unstable adaptations. Philosophical Transactions of the Royal Society B 366:849–862.

Ruddiman, W. F. 2013. The Anthropocene. Annual Review of Earth and Planetary Sciences 41:45–68.

Ruddiman, W. F., and E. C. Ellis. 2009. Effect of per-capita land use changes on holocene forest clearance and CO_2 emissions. Quaternary Science Reviews 28:3011–3015.

Rudel, T. K., et al.. 2009. Agricultural intensification and changes in cultivated areas, 1970–2005. Proceedings of the National Academy of Sciences USA 106:20675–20680.

Sahlins, M. D., T. G. Harding, and E. R. Service. 1960. Evolution and culture. University of Michigan Press, Ann Arbor, Michigan, USA.

Sanderson, S. K. 2006. Evolutionary theorizing. Pages 435–455 *in* J. H. Turner, editor. Handbook of sociological theory. Springer, New York, New York, USA.

Sandler, R. 2014. The ethics of reviving long extinct species. Conservation Biology 28:354–360.

Sandom, C., S. Faurby, B. Sandel, and J.-C. Svenning. 2014. Global late Quaternary megafauna extinctions linked to humans, not climate change. Proceedings of the Royal Society B 281:20141574.

Sayre, N. F. 2008. The genesis, history, and limits of carrying capacity. Annals of the Association of American Geographers 98:120–134.

Scales, I. R. 2014. Green consumption, ecolabelling and capitalism's environmental limits. Geography Compass 8:477–489.

Schich, M., C. Song, Y.-Y. Ahn, A. Mirsky, M. Martino, A.-L. Barabási, and D. Helbing. 2014. A network framework of cultural history. Science 345:558–562.

Schmill, M. D., L. M. Gordon, N. R. Magliocca, E. C. Ellis, and T. Oates. 2014. GLOBE: analytics for assessing global representativeness. Pages 25–32 *in* Computing for Geospatial Research and Application (COM.Geo), 2014 Fifth International Conference, Washington, D.C., USA. IEEE, Piscataway, New Jersey, USA.

Scott, J. C. 2014. The art of not being governed: an anarchist history of upland Southeast Asia. Yale University Press, New Haven, Connecticut, USA.

Scott-Phillips, T. C., K. N. Laland, D. M. Shuker, T. E. Dickins, and S. A. West. 2014. The niche construction perspective: a critical appraisal. Evolution 68:1231–1243.

Seto, K. C., A. Reenberg, C. G. Boone, M. Fragkias, D. Haase, T. Langanke, P. Marcotullio, D. K. Munroe, B. Olah, and D. Simon. 2012. Urban land teleconnections and sustainability.

Proceedings of the National Academy of Sciences USA 109:7687–7692.

Shea, J. J. 2006. The origins of lithic projectile point technology: evidence from Africa, the Levant, and Europe. Journal of Archaeological Science 33:823–846.

Shennan, S. 2001. Demography and cultural innovation: a model and its implications for the emergence of modern human culture. Cambridge Archaeological Journal 11:5–16.

Shennan, S. 2011*a*. Descent with modification and the archaeological record. Philosophical Transactions of the Royal Society B 366:1070–1079.

Shennan, S. 2011*b*. Property and wealth inequality as cultural niche construction. Philosophical Transactions of the Royal Society B 366:918–926.

Sherratt, T. N., and D. M. Wilkinson. 2009. When did we start to change things? Pages 312 *in* T. N. Sherratt and D. M. Wilkinson, editors. Big questions in ecology and evolution. Oxford University Press, Oxford, UK.

Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications 4:367–387.

Silbernagel, J., S. R. Martin, M. R. Gale, and J. Chen. 1997. Prehistoric, historic, and present settlement patterns related to ecological hierarchy in the Eastern Upper Peninsula of Michigan, U.S.A. Landscape Ecology 12:223–240.

Simberloff, D. 2014. The "balance of nature"—evolution of a panchreston. PLoS Biology 12:e1001963.

Skoglund, P., H. Malmström, M. Raghavan, J. Storå, P. Hall, E. Willerslev, M. T. P. Gilbert, A. Götherström, and M. Jakobsson. 2012. Origins and genetic legacy of neolithic farmers and hunter-gatherers in Europe. Science 336:466–469.

Smil, V. 1991. Population growth and nitrogen: an exploration of a critical existential link. Population and Development Review 17:569–601.

Smil, V. 2008. Energy in nature and society: general energetics of complex systems. MIT Press, Cambridge, Massachusetts, USA.

Smillie, C. S., M. B. Smith, J. Friedman, O. X. Cordero, L. A. David, and E. J. Alm. 2011. Ecology drives a global network of gene exchange connecting the human microbiome. Nature 480:241–244.

Smith, B. D. 2007*a*. Niche construction and the behavioral context of plant and animal domestication. Evolutionary Anthropology: Issues, News, and Reviews 16:188–199.

Smith, B. D. 2007*b*. The ultimate ecosystem engineers. Science 315:1797–1798.

Smith, B. D. 2011. General patterns of niche construction and the management of 'wild' plant and animal resources by small-scale pre-industrial societies. Philosophical Transactions of the Royal Society B 366:836–848.

Smith, B. D. 2012. A cultural niche construction theory of initial domestication. Biological Theory 6:260–271.

Smith, B. D. 2013*a*. Modifying landscapes and mass kills: human niche construction and communal ungulate harvests. Quaternary International 297:8–12.

Smith, B. D., and M. A. Zeder. 2013. The onset of the Anthropocene. Anthropocene 4:8–13.

Smith, E. A. 2013*b*. Agency and adaptation: new directions in evolutionary anthropology. Annual Review of Anthropology 42:103–120.

Smith, E. A., K. Hill, F. W. Marlowe, D. Nolin, P. Wiessner, M. Gurven, S. Bowles, M. B. Mulder, T. Hertz, and A. Bell. 2010*a*. Wealth transmission and inequality among hunter-gatherers. Current Anthropology 51:19–34.

Smith, E. A., M. B. Mulder, S. Bowles, M. Gurven, T. Hertz, and M. K. Shenk. 2010*b*. Production systems, inheritance, and inequality in premodern societies: conclusions. Current Anthropology 51:85–94.

Smith, E. A., and M. Wishnie. 2000. Conservation and subsistence in small-scale societies. Annual Review of Anthropology 29:493–524.

Smith, M. E. 2004. The archaeology of ancient state economies. Annual Review of Anthropology 33:73–102.

Smith, M. L. 2014. The archaeology of urban landscapes. Annual Review of Anthropology 43:307–323.

Smith, M. R., and L. Marx. 1994. Does technology drive history? The dilemma of technological determinism. MIT Press, Cambridge, Massachusetts, USA.

Smith, N. 2008. Uneven development: nature, capital, and the production of space. University of Georgia Press, Athens, Georgia, USA.

Smith, O., G. Momber, R. Bates, P. Garwood, S. Fitch, M. Pallen, V. Gaffney, and R. G. Allaby. 2015. Sedimentary DNA from a submerged site reveals wheat in the British Isles 8000 years ago. Science 347:998–1001.

Smith, T. B., M. T. Kinnison, S. Y. Strauss, T. L. Fuller, and S. P. Carroll. 2014. Prescriptive evolution to conserve and manage biodiversity. Annual Review of Ecology, Evolution, and Systematics 45:1–22.

Speight, M. D., and E. Castella. 2001. An approach to interpretation of lists of insects using digitised biological information about the species. Journal of Insect Conservation 5:131–139.

Steffen, W., P. J. Crutzen, and J. R. McNeill. 2007. The Anthropocene: are humans now overwhelming the great forces of nature? AMBIO: A Journal of the Human Environment 36:614–621.

Steffen, W., J. Grinevald, P. Crutzen, and J. McNeill. 2011. The Anthropocene: conceptual and historical perspectives. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 369:842–867.

Steinberger, J. K., F. Krausmann, and N. Eisenmenger. 2010. Global patterns of materials use: a socioeconomic and geophysical analysis. Ecological Economics 69:1148–1158.

Sterelny, K. 2011. From hominins to humans: how sapiens became behaviourally modern. Philosophical Transactions of the Royal Society B 366:809–822.

Sterelny, K. 2014. A Paleolithic reciprocation crisis: symbols, signals, and norms. Biological Theory 9:65–77.

Stewart, J. Q. 1947. Empirical mathematical rules concerning the distribution and equilibrium of population. Geographical Review 37:461–485.

Stiner, M., and S. Kuhn. 2006. Changes in the 'connectedness' and resilience of Paleolithic societies in Mediterranean ecosystems. Human Ecology 34:693–712.

Stiner, M. C. 2001. Thirty years on the "Broad Spectrum Revolution" and paleolithic demography. Proceedings of the National Academy of Sciences USA 98:6993–6996.

Stork, N. 2010. Re-assessing current extinction rates. Biodiversity and Conservation 19:357–371.

Sutherland, W. J., et al. 2013. Identification of 100 fundamental ecological questions. Journal of Ecology 101:58–67.

Syvitski, J. P. M., and A. Kettner. 2011. Sediment flux and the Anthropocene. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 369:957–975.

Tainter, J. A. 2006*a*. Archaeology of overshoot and collapse. Annual Review of Anthropology 35:59–74.

Tainter, J. A. 2006*b*. Social complexity and sustainability. Ecological Complexity 3:91–103.

Tainter, J. A. 2011. Energy, complexity, and sustainability: a historical perspective. Environmental Innovation and Societal Transitions 1:89–95.

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16:284–307.

Therborn, G. 2011. Why and how place matters. *In* R. E. Goodin, editor. Oxford handbook of political science. Oxford University Press, Oxford, UK. http://www.oxfordhandbooks.com/view/10.1093/oxfordhb/9780199604456.001.0001/oxfordhb-9780199604456-e-025

Thomas, C. D. 2011. Translocation of species, climate change, and the end of trying to recreate past ecological communities. Trends in Ecology and Evolution 26:216–221.

Thomas, C. D. 2013. The Anthropocene could raise biological diversity. Nature 502:7–7.

Tilman, D., C. Balzer, J. Hill, and B. L. Befort. 2011. Global food demand and the sustainable intensification of agriculture. Proceedings of the National Academy of Sciences USA 108:20260–20264.

Tomasello, M. 1999. The human adaptation for culture. Annual Review of Anthropology 28:509–529.

Tomasello, M. 2014. The ultra-social animal. European Journal of Social Psychology 44:187–194.

Tomasello, M., M. Carpenter, J. Call, T. Behne, and H. Moll. 2005. Understanding and sharing intentions: the origins of cultural cognition. Behavioral and Brain Sciences 28:675–691.

Tomasello, M., A. C. Kruger, and H. H. Ratner. 1993. Cultural learning. Behavioral and Brain Sciences 16:495–511.

Tomich, T. P., et al. 2011. Agroecology: a review from a global-change perspective. Annual Review of Environment and Resources 36:193–222.

Turchin, P., T. E. Currie, E. A. L. Turner, and S. Gavrilets. 2013. War, space, and the evolution of Old World complex societies. Proceedings of the National Academy of Sciences USA 110:16384–16389.

Turner, W. 2014. Sensing biodiversity. Science 346:301–302.

van Noordwijk, M., B. Leimona, R. Jindal, G. B. Villamor, M. Vardhan, S. Namirembe, D. Catacutan, J. Kerr, P. A. Minang, and T. P. Tomich. 2012. Payments for environmental services: evolution toward efficient and fair incentives for multifunctional landscapes. Annual Review of Environment and Resources 37:389–420.

Vegvari, C., and R. A. Foley. 2014. High selection pressure promotes increase in cumulative adaptive culture. PLoS ONE 9:e86406.

Verburg, P. H., E. C. Ellis, and A. Letourneau. 2011. A global assessment of market accessibility and market influence for global environmental change studies. Environmental Research Letters 6:034019.

Vernadsky, V. I. 1998. Biosphere: complete annotated edition. Copernicus: Springer, New York, New York, USA.

Vitousek, P. M., C. M. Dantonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997*a*. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21:1–16.

Vitousek, P. M., P. R. Ehrlich, A. H. Ehrlich, and P. A. Matson. 1986. Human appropriation of the products of photosynthesis. BioScience 36:368–373.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997*b*. Human domination of Earth's ecosystems. Science 277:494–499.

von Thünen, J. H., and H. Schumacher-Zarchlin. 1875. Der isolirte Staat in Beziehung auf Landwirthschaft und Nationalökonomie. Wiegant, Hempel and Parey, Berlin, Germany.

Vörösmarty, C. J., and D. Sahagian. 2000. Anthropogenic disturbance of the terrestrial water cycle. BioScience 50:753–765.

Waltner-Toews, D., J. J. Kay, C. Neudoerffer, and T. Gitau. 2003. Perspective changes everything: managing ecosystems from the inside out. Frontiers in Ecology and the Environment 1:23–30.

Western, D. 2001. Human-modified ecosystems and future evolution. Proceedings of the National Academy of Sciences USA 98:5458–5465.

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

Whiten, A., R. A. Hinde, K. N. Laland, and C. B. Stringer. 2011. Culture evolves. Philosophical Transactions of the Royal Society B 366:938–948.

Wilkinson, B. H. 2005. Humans as geologic agents: a deep-time perspective. Geology 33:161–164.

Willemen, L., A. Veldkamp, P. H. Verburg, L. Hein, and R. Leemans. 2012. A multi-scale modelling approach for analysing landscape service dynamics. Journal of Environmental Management 100:86–95.

Williams, M. 2008. A new look at global forest histories of land clearing. Annual Review of Environment and Resources 33:345.

Wilson, D. S., S. C. Hayes, A. Biglan, and D. D. Embry. 2014. Evolving the future: toward a science of intentional change. Behavioral and Brain Sciences 37:395–416.

Wilson, E. O. 1975. Sociobiology: the new synthesis. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.

Wilson, E. O. 2012. The social conquest of Earth. Liveright, New York, New York, USA.

Wolf, M., and J. Krause. 2014. Why personality differences matter for social functioning and social structure. Trends in Ecology and Evolution 29:306–308.

Wollstonecroft, M. 2011. Investigating the role of food processing in human evolution: a niche construction approach. Archaeological and Anthropological Sciences 3:141–150.

Wrangham, R., and N. Conklin-Brittain. 2003. Cooking as a biological trait. Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology 136:35–46.

Wright, J. P., and C. G. Jones. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. BioScience 56:203–209.

Zalasiewicz, J., P. J. Crutzen, and W. Steffen. 2012. The Anthropocene. Pages 1033–1040 *in* F. M. Gradstein, J. G. Ogg, M. Schmitz, and G. Ogg, editors. The geologic time scale 2012. Elsevier Science, Oxford, UK.

Zalasiewicz, J., et al. 2015. When did the Anthropocene begin? A mid-twentieth century boundary level is stratigraphically optimal. Quaternary International. http://dx.doi.org/10.1016/j.quaint.2014.11.045

Zalasiewicz, J., C. N. Waters, and M. Williams. 2014. Human bioturbation, and the subterranean landscape of the Anthropocene. Anthropocene 6:3–9.

Zeder, M. A. 2012. The Broad Spectrum Revolution at 40: resource diversity, intensification, and an alternative to optimal foraging explanations. Journal of Anthropological Archaeology 31:241–264.

Zimov, S. A., V. I. Chuprynin, A. P. Oreshko, F. S. Chapin, III, J. F. Reynolds, and M. C. Chapin. 1995. Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. American Naturalist 146:765–794.